Agenda Item 9 Cooperation with other Bodies

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Secretariat’s Note

The Rules of Procedure adopted at the ASCOBANS 8th Meeting of Parties remain in force until and unless an amendment is called for and adopted.

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North Sea Cetacean Special

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Lutra is a scientific journal published by the Dutch Mammal Society (Zoogdiervereniging). The society is dedicated to the study and protection of native mammals in Europe. Lutra publishes peer-reviewed scientific papers on mammals across all disciplines, but tends to focus on ecology, biogeography, behaviour and morphology. Although exceptions are made in some cases, Lutra generally publishes articles on mammal species native to Europe, including marine mammals. Lutra publishes full articles as well as short notes which may include novel research methods or remarkable observations of mammals. In addition Lutra publishes book reviews. Lutra publishes in British English and in Dutch. Lutra is an open access journal and Lutra has no page charges. Lutra publishes two issues per year and Lutra is indexed in 'Biological Abstracts' and 'Zoological Record' and 'Artik'.

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Chris Smeenk, 1942 – 2017

Previous page: Chris Smeenk studying a coloured plate of rough-toothed dolphin (*Steno bredanensis*) at Teylers Museum in Haarlem, 11 July 2014, to prepare his chapter on this species in the Atlas of the Mammals of the Netherlands (2016). *Photo: H. Voogd, Teylers Museum*.

In the course of 2017, Peter Evans, long-running and well-known marine ecologist with over 40 years experience working on seabirds and marine mammals, approached the Lutra Editorial Board with the suggestion of a special issue as a commemorative volume in memory of the life work of Chris Smeenk, who had passed away in March of that year. The idea was to present a broad overview of cetacean research undertaken around the North Sea, a subject on which Chris had been one of the leading experts for many years. The Board immediately responded with enthusiasm, and asked Peter to implement his ideas. Together with marine mammalogist colleagues, Graham Pierce and Carl Kinze, they formed a guest Editorial Board. They invited contributions from a number of active researchers from the region, and received an excellent response.

It is with great pride that the Lutra Editorial Board presents here the intended North Sea Special. The editorial staff greatly appreciates the extensive work, both qualitatively and quantitatively, of the three guest editors, and especially of Peter Evans, and warmly welcomes the result obtained. The Board also thanks the guest editors for their own contributions to the result presented here. Finally, the Board thanks the management of Naturalis Biodiversity Center in Leiden, who made the release of this special issue financially possible by making a generous subsidy available.

The Lutra Editorial Board

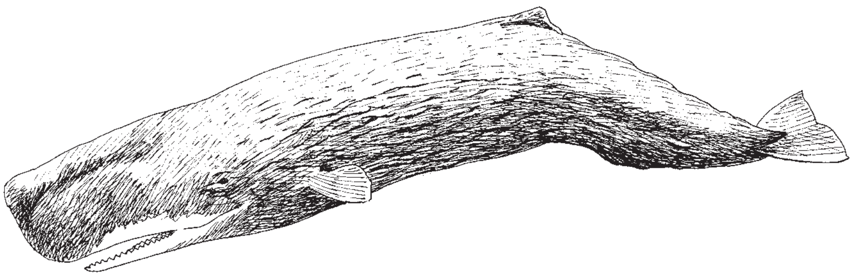
Preface

This Special Issue of *Lutra* on Cetaceans of the North Sea has been produced in memory of Chris Smeenk (1942-2017) who sadly passed away in March 2017. For thirty years, he ran the Dutch marine mammal strandings scheme and also served as Curator of Mammals at Rijksmuseum van Natuurlijke Historie (RMNH) in Leiden, now known as the Naturalis Biodiversity Center. Chris was Managing Editor of Lutra, for eighteen years (1981-1998), where he applied his linguistic skills (he was better at the English language than most native English speakers), his attention to detail, and his scholarly approach to everything he researched, wrote or reviewed. He was a member of the small group who founded the European Cetacean Society and was its first treasurer, as well as editing (with Jan Willem Broekema) its first conference proceedings. Chris was one of the first to draw attention to apparent status declines of the harbour porpoise in the North Sea, and then documented its later recovery. He drew attention to concerns about bycatch in Dutch waters long before others recognised this as a potential national issue. Throughout his career at RMNH, he welcomed researchers from all over the world and was always ready to assist them in their studies, mentoring many students, always supported by his loving wife, Nellie.

Chris long had an interest in sperm whale strandings and before his death, he had a manuscript nearing completion cataloguing records from the North Sea from the thirteenth century to the present. Another example of his scholarly efforts was the investigation of the history of nomenclature of the rough-toothed dolphin. Both topics of study are brought to fruition in this special issue.

Our knowledge of cetaceans in the North Sea has burgeoned over the last half century, and the present volume reflects this with a variety of contributions on a number of species occurring in the region. We thank all authors for their contributions and the following who, in addition to ourselves, kindly served as reviewers: Louise Allcock, Kees Camphuysen, Ewan Fordyce, Anita Gilles, Jan Haelters, Phil Hammond, Tom Jefferson, Mardik Leopold, Ron Macdonald, Hanna Nuuttila, Vincent Ridoux, Patricia Rosel, and Ursula Siebert.

Peter G.H. Evans
Carl Chr. Kinze
Graham J. Pierce



North Sea cetacean research since the 1960s: advances and gaps

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In the 1960s, our knowledge of cetaceans in the North Sea depended largely upon strandings schemes that existed in the countries that surround the southern North Sea, particularly the UK (Fraser 1974, Sheldrick 1976, 1989, Sheldrick et al. 1992, 1994), Belgium (De Smet 1974, 1979, 1981, Van Gompel 1991, 1996), and the Netherlands (van Bree 1977, Smeenk 1987, Addink & Smeenk 1999). Scarcely any sightings programmes existed until the 1970s (Verwey 1975, Evans 1976, 1980, Evans et al. 1986). In those years between the 1960s and 1980s, increasing concern was expressed for the status of the harbour porpoise (*Phocoena phocoena*) which appeared to be declining in the North Sea and beyond (Evans 1980, Kayes 1985, Kroger 1986, Kremer 1987, Smeenk 1987). The result was that a small group of scientists, including the late Chris Smeenk to whom this special issue is dedicated, came together to form the European Cetacean Society in 1987, and then issued a statement of concern on behalf of the society (Evans et al. 1987) to the 2nd North Sea Ministerial Conference held in London in 1987. A number of non-governmental organisations (notably WWF-Germany, WWF-Sweden, and Greenpeace) lobbied for conservation action.

With the status of the harbour porpoise in the North Sea and environs very much at the forefront of environmental concern, one of the first regional agreements under Article IV of the Convention on the Conservation of Migratory Species of Wild Animals (UNEP/CMS or Bonn Convention), which had come into force in 1983, was ASCOBANS, the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas. The Final Act was signed in September 1991, and then opened for signature by Range States, at the UN Headquarters in New York in March 1992.

Two human pressures were highlighted at the time that could be having a negative impact upon porpoises in and around the North Sea. These were prey depletion caused by a combination of overfishing and environmental change (Evans 1990, Reijnders 1992) and fisheries bycatch (Northridge 1988), although the potential impact of bycatch was not fully appreciated until the 1990s (Bjørge et al. 1994, Lowry & Teilmann 1994, Donovan & Bjørge 1995, Kock & Benke 1996, Vinther 1999, Northridge & Hammond 1999). During the 1990s, the potential harmful effects of chemical pollution (Reijnders et al. 1999) and underwater noise (Richardson et al. 1995) on marine mammals also started to get noticed.

The evidence for earlier declines in the harbour porpoise had been based largely upon stranding trends and changes in sightings rates from fairly limited sightings surveys (often shore-based). The first large-scale survey of the North Sea using line transect Distance methodology to derive abundance estimates, was the SCANS survey undertaken in July 1994 (Hammond et al. 2002). These yielded an abundance estimate of ca. 170,000 porpoises in the central and southern North Sea whilst independent observers aboard a sample of fishing vessels estimated annual mortality from bycatch alone to be ca. 4,450, or 2.6% of the population size (Vinther 1999, Northridge & Hammond 1999, Hammond et al. 2002, Vinther & Larsen 2004). Based upon knowledge of their life history parameters, the regional conservation agreement, ASCOBANS, concluded that annual total mortality exceeding 1.7% of porpoise population size would not be sustainable, and that therefore action was needed urgently by Parties. Out of this concern came a new regulation within the EU Common Fisheries Policy – Reg. 812/2004. This required member states to deploy Acoustic Deterrent Devices (ADDs) known as pingers to be used on fishing vessels of 12 metres length or more using bottom set gillnets or entangling nets. The Regulation also issued a requirement for at sea observer schemes on vessels of 15 metres length or more, and for smaller vessels, to take the necessary steps to collect scientific data on incidental catches by means of appropriate scientific studies or pilot projects. Earlier studies in both US and Danish waters had shown that pingers could be very effective at alerting porpoises to the presence of nets (although there have been concerns about habituation, and, conversely, habitat exclusion when applied over wide areas). The Regulation was generally welcome but, unfortunately, has not been totally successful although pressure from bycatch may not be as great as it was due to an overall reduction in fishing effort.

Following the 1994 SCANS survey, further large-scale surveys were undertaken in July 2005 (SCANS II - Hammond et al. 2013) and July 2016 (SCANS III - Hammond et al. 2017). They showed no significant change in numbers of harbour porpoise in the North Sea, although between 1994 and 2005, there appeared to be a major re-distribution of animals from the concentrations observed in the north-western North Sea in 1994 to the highest abundance in the southernmost North Sea in 2005, which has persisted through to at least 2016. Since the early 1990s, concerns for declines in the Northern Isles of Scotland possibly due to local reductions in sand eel numbers, had been expressed (Evans et al. 1993, Evans & Borges 1995) whilst increases in the southernmost North Sea and eastern part of the Channel had been reported by a number of authors (Camphuysen & Leopold 1993, Camphuysen 1994, Witte et al. 1998, Camphuysen 2004, Haelters & Camphuysen 2009).

Besides the snapshot large-scale SCANS surveys, most cetacean survey effort in the 1980s and 1990s relied upon measures of relative abundance and did not necessarily follow a systematic line transect design (Northridge et al. 1995, Reid et al. 2003, van der Meij & Camphuysen 2006). From the 2000s onwards, there was increasing use of aerial surveys to determine both seasonal and annual trends in abundance (Scheidat et al. 2004, 2012, Siebert et al. 2006, Gilles et al. 2009, 2016). These could make use of brief windows of good weather and cover large areas in a short time. Those surveys were initiated to identify and monitor areas of persistent high density that could then be proposed as Special Areas of Conservation for harbour porpoise as part of the EU Habitats Directive's Natura 2000 network, and to establish the potential impacts of offshore renewable development in the form of wind farms. For the latter, aerial surveys were combined with click detectors (first T-PODs and later, C-PODs) to monitor changes in porpoise presence in the vicinity of pile driving activities during the construction phase of wind turbines (Gilles et al. 2009, Tougaard et al. 2009, Brandt et al. 2011, Scheidat et al. 2011, Dähne et al. 2013, Peschko et al. 2016). Studies in the North Sea and Baltic found different levels of impact at different sites, thought to reflect the context in which the site was used by the species. At Horn Rev, for example, effects were found up to ca. 20 km from the pile driving activity (Brandt et al. 2011) and in the test area of "*alpha ventus*" more than 25 km (Dähne et al. 2013). However, a review of the effects of the construction of eight offshore wind farms in the German North Sea between 2009 and 2013, could find no long-term population effects (Brandt et al. 2016).

In examining for population level effects of human activities like fisheries and noise, it is important to have a good understanding of population structure. A combination of genetics, morphometrics, life history parameters, stable isotope and contaminant loads, and telemetry studies has been used to establish management units (demographically distinct populations) for various small cetacean species (Evans & Teilmann 2009, ICES WGMME 2014). Within the North Sea, these remain tentative, and there is still debate as to whether North Sea porpoises should be considered a single, two, or even three management units (ASCOBANS 2014).

Research on cetaceans in the North Sea has tended to focus upon the harbour porpoise, probably because it is the commonest and most widespread cetacean species with between 300,000 and 350,000 estimated across the region (Hammond et al. 2017). However, several other cetacean species inhabit the North Sea either year-round (e.g. bottlenose dolphin *Tursiops truncatus*, white-beaked dolphin *Lagenorhynchus albirostris*) or seasonally (e.g. minke whale *Balaenoptera acutorostrata*, fin whale *Balaenoptera physalus*), and some species (e.g. Atlantic white-sided dolphin *Lagenorhynchus acutus*, killer whale *Orcinus orca*, long-finned pilot whale *Globicephala melas*) which normally live further offshore in deeper waters do annually come into the northern North Sea (Evans et al. 2003, Reid et al. 2003, Camphuysen & Peet 2006).

Although bottlenose dolphins were once a regular feature off the Dutch coast (Verwey 1975, Kompanje 2001), nowadays the species occurs mainly in eastern Scotland, particularly the Moray Firth where it has been studied intensively (see, for example, Wilson et al. 1997, 1999, 2004), with a population size of around 200 (Cheney et al. 2012, 2014). Since the 1990s, the species has extended its range southwards from the Moray Firth as far south as Yorkshire, with occasional sightings off Norfolk. Bottlenose dolphins in the North Sea are recorded only occasionally away from the coastal zone (Reid et al. 2003, Cheney et al. 2012).

White-beaked dolphins are widely distributed in the North Sea, with a population size of between 20,000 and 30,000, although numbers appear to be greatest in the central and northern sectors (Northridge et al. 1995, Evans et al. 2003, Reid et al. 2003, Hammond et al. 2002, 2013, 2017). Surprisingly, we have relatively poor information on the biology of the species, although in recent years, there have been new studies on its habitat preferences, life history, diet, and genetics (Kinze et al. 1997, Canning et al. 2008, Banguera-Hinestroza et al. 2010, Jansen et al. 2010, Galatius & Kinze 2016). Camphuysen & Peet (2006) have suggested that the southern North Sea cetacean community changed markedly during the 20th century, from a *Tursiops/Delphinus* (bluefin tuna/great shearwater) constellation midcentury towards a white-beaked dolphin 'constellation' by the end of the 20th century.

The minke whale is the most common and widely distributed baleen whale in the North Sea (Northridge et al. 1995, Evans et al. 2003, Reid et al. 2003), with a population size somewhere between 5,000 and 15,000 (Hammond et al. 2002, 2013, 2017). In the north-western North Sea, it suffers incidental entanglement in creel lines and other ropes as well as ghost netting (Northridge et al. 2010). The much rarer humpback whale, which is experiencing something of a resurgence in the region (Evans et al. 2003, Smeenk et al. 2003, Camphuysen 2007, Leopold et al., this volume), is also a victim of entanglement in similar gear, causing additional concern (Ryan et al. 2016).

One cetacean species, not a native of the region, above all others attracts much media attention when it wanders into the North Sea. That is the sperm whale (*Physeter macrorhynchus*). Strandings of several sperm whales have occurred on a number of occasions in the southernmost North Sea, the most recent notable examples being in March 1996, December 1997, and January-February 2016. Many theories are discussed as possible factors resulting in these strandings, including increasing sperm whale stocks, side effects of migrating animals, solar storms, diseases, chemical pollution, temperature anomalies and anthropogenic noise (Sonntag & Lütkebohle 1998, Wright 2005, Vanselow & Ricklefs 2005, Pierce et al. 2007, Vanselow et al. 2009, 2017), although some believe there is no need to seek elaborate explanations for these "accidents" (Evans 1997, Smeenk 1997). Chris Smeenk took a special interest in documenting the sperm whale strandings that have occurred across the centuries, and studiously corrected a number of records that were misleading or wrong. In this special issue, a catalogue of strandings of this species in the North Sea since the thirteenth century is presented.

In the last two decades, strandings schemes have consolidated in all the countries bordering the North Sea, with increased emphasis upon investigations to determine causes of death (Clausen & Andersen 1988, Baker & Martin 1992, Siebert et al. 2001, Wünschmann et al. 2001, Jepson et al. 2000, 2009, Jauniaux et al. 2002, Jepson 2005, Camphuysen et al. 2008, Haelters & Camphuysen 2009, Kinze et al. 2010, Deaville & Jepson 2011). Post mortem studies have also been extremely valuable for stomach contents analysis for dietary studies (see, for example, Pierce et al. 2004, Canning et al. 2008, Jansen et al. 2010), analyses of contaminants and their effects (Bruhn et al. 1999, Siebert et al. 1999, Das et al. 2004, 2006, Beineke et al. 2006, Law et al. 2010, Jepson et al. 2005, 2016; Murphy et al. 2015), reproductive (Addink & Smeenk 1999, Lockyer 2003, Learmonth et al. 2014), morphometric (Kinze 1985) and genetic studies (Tolley et al. 1999, Andersen et al. 2001, Banguera-Hinestroza et al. 2010).

The North Sea, particularly its southernmost sector, has been experiencing profound changes to its climate (Rayner et al. 2003, Hughes et al. 2017) which in turn has affected plankton (Edwards et al. 2001, 2002, 2013, Beare et al. 2002), cephalopod (van der Kooij et al. 2016), and fish (Perry et al. 2005) communities. The marked expansion of cephalopod numbers in the North Sea may account for a recent increase in occurrence of Risso's dolphin (*Grampus griseus*) in the central and north-western North Sea, and, similarly, the spread of sardine and anchovy may be why common dolphins (*Delphinus delphis*) are now being seen regularly in this same region (Evans & Bjørge 2013). In coming years, we may expect increased frequency of occurrence of species that have their main range in warmer waters to the south, such as striped dolphin (*Stenella coeruleoalba*) and Cuvier's beaked whale (*Ziphius cavirostris*), but a northward shift increasingly out of the area of the more northern species, white-beaked dolphin and Atlantic white-sided dolphin.

In the last half century, our knowledge of the cetacean fauna of the North Sea has increased tremendously. Nevertheless, there are still many gaps. We little understand movements within the North Sea for most species and there remains great uncertainty over their population structure and demographies. Much of the focus for study has been upon the harbour porpoise (and, in Scotland, the bottlenose dolphin); there is scope for increased research effort on white-beaked dolphin and minke whale, not to mention some of the other species that may become a regular component of the North Sea cetacean fauna. This special issue of Lutra commemorates the life of Chris Smeenk who over the period under review here has made so many significant contributions to cetacean research in the North Sea.

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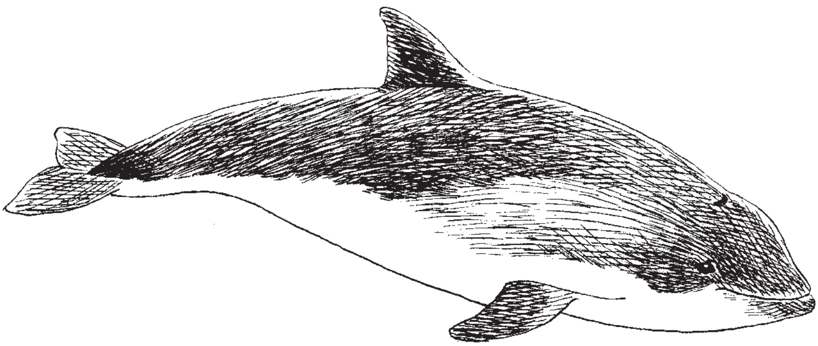

Chris Smeenk
1942-2017

On 23 March 2017, Chris (Christiaan) Smeenk, aged 74 years, passed away in Leiden. He was born on 6 July 1942, in 'Oost- en West-Souburg', a small community near Vlissingen at Walcheren (Zeeland, in the Dutch delta area). After he graduated from gymnasium-α, in 1961, Chris commenced with his biology studies, first at Utrecht University and later at the University of Leiden where he met Nellie Enserink whom he married in 1971.

During his studies Chris investigated differences in the prey choice and clutch size of tawny owls (*Strix aluco*) and long-eared owl (*Asio otus*; Smeenk 1969b), supervised by Professor K.H. Voous. The results of these investigations (Smeenk 1972) were such that Voous nominated Chris for a comparative study of the ecological relationships of five species of raptors in the Tsavo National Park in Kenya (1970-1973). These studies formed the basis of his PhD, which he successfully defended in 1974 at the Free University in Amsterdam (Smeenk 1974).

From 1974 to 1976, Chris was employed as a wildlife manager at the Pandam Wildlife Park in Nigeria and, when he returned to the Netherlands, he became conservator of the mammal collections of the National Museum of Natural History (Rijksmuseum van Natuurlijke Historie, RMNH) in Leiden, succeeding A.M. Husson. While in this post he and Nellie continued to publish articles based on their research on African raptors (Smeenk & Smeenk-Enserink 1977, 1983).

Chris' work with mammals at the RMNH, led him to become increasingly engaged with the Society for the Study and Conservation of Mammals, the VZZ (*Vereniging voor Zoogdierkunde en Zoogdierbescherming*, now the *Zoogdiervereniging* or Dutch Mammal Society). In 1981 he became editor-in-chief of its journal '*Lutra*' and remained editor-in-chief until 1998, when he was succeeded by Sim Broekhuizen. Chris did much to improve *Lutra* and turned it from the newsletter-like periodical that it was when he became editor into a genuine scientific journal. In 1992 he was rewarded the 'Dr. A. Scheygrond Prize' partly for his important contributions to the VZZ, but more for his work with *Lutra*.

With his exceptional editorial skills, Chris was the most suitable editor-in-chief of the first Atlas of mammals in the Netherlands (Broekhuizen et al. 1992), the more so because at RMNH, where he worked, he had immediate access to an extensive library and therefore to virtually all scientific publications dealing with mammals in the Netherlands, including a wealth of 'grey literature' (a variety of reports and publications from small clubs and organisations) of which he was very proud.

Chris had a considerable historical interest. As an example, he co-wrote a thorough overview of the history of the knowledge of the geographical distribution of mammals in the Netherlands with Bauke Hoekstra (Hoekstra & Smeenk 1992). He enjoyed unearthing historical documents and original accounts in archives, in order 'to remove the dust of the centuries', as he liked to call it (see list of publications on history). As a conservator at the RMNH, he developed an exceptional knowledge of a large variety of mammalian species. Animal systematics and taxonomy became his prime interests (see list of publications – taxonomy). He updated and improved the field guide *Säugetiere Afrikas und Madagaskars* (Haltenorth & Diller 1977), which was published as the '*Elseviers gids van de Afrikaanse zoogdieren*' in 1979 (Elsevier's guide of African mammals).

Chris' predecessor A.M. Husson and two colleagues from Amsterdam, P.J.H. (Peter) van Bree and W.L. (Wim) van Utrecht, compiled and published lists of cetaceans that had been found stranded in the Netherlands between 1968 and 1976 and rebuilt the valuable 'strandings alert network', continuing the important work that had started in the mid-1930s by A.B. van Deinse. When Husson retired in 1976, Chris stepped in and continued with this task. The first strandings report with which he was involved in covered 1976 and 1977 (van Bree & Smeenk 1978), and this was the first in a long series of papers published in Lutra (van Bree & Smeenk 1982, Smeenk 1986a, 1989, 1992a, 1995a, 2003, Camphuysen et al. 2008). Nowadays, strandings data are freely accessible via a website (www.walvisstrandingen.nl), but these publications are still essential to guarantee that identifications are checked and, where possible, confirmed. Few people were as strict in that respect as Chris Smeenk. His efforts to ensure that the overview of stranding events (historical cases included) was error-free culminated in 2016, just a year before he died, when he co-authored and meticulously checked the factual data for 27 chapters on cetaceans in the new Atlas of Dutch Mammals in the Netherlands (Broekhuizen et al. 2016). Together with Kees Camphuysen he worked on the chapters in which all available strandings and sightings of cetaceans in Dutch waters were accurately summarised. During that work - which wasn't always easy, given the large number of editors involved and which led to a multitude of viewpoints - he often remarked to his co-author that this would be his last (major) work on Dutch marine mammals. And even only for that reason, it had to be good.

When he became involved in the strandings reports, Chris developed a keen interest in cetaceans, which were still surrounded by much mystery. Not much was known about cetaceans in the wild at the time, and strandings formed an important source of information. Accurate identification is the first step in the process and Chris had endless stories about animals reported to him with completely the wrong name, or animals that were reported alive but were in fact dead, the observed movements being the advanced work of multitudes of maggots. He used these stories to stress the importance of keen observation in collecting accurate data. Personally he preferred to have a look himself, whenever possible and barely trusted the opinion of others. Stranded harbour porpoises, (*Phocoena phocoena*), still very rare in the 1970s and early 1980s (a dozen or two per year), were usually picked up from the beaches by Chris himself, at any time, in any weather, at first often assisted by his wife Nellie, and in later years often by his

Chris Smeenk at the primate collection at Naturalis Biodiversity Center, May 2008. Photo: Dolph Cantrijn.

student Marjan Addink. What followed were pioneering necropsies, and a number of published reports and papers (see lists of publications on strandings and necropsy studies). It was during these necropsies that he started to see a pattern: at least some of these animals had drowned, most likely in fishing gear. He rang a first alarm bell on this in a paper presented at a conference in Sweden (Smeenk et al. 2004), which was never properly published, given the political sensitivity of the issues and outstanding uncertainties with his diagnosis. As always, if he wasn't sure, he wouldn't let it go out. Factual evidence stood above all else.

As a result, Chris soon developed into an internationally respected and well known specialist on cetaceans. He became one of the founding fathers of the European Cetacean Society, initially a small network of interested scientists and amateurs, but an organisation that gradually developed into one of the more important cetacean organisations within Europe, which now exchanges the rapidly accumulating knowledge about cetaceans with others on a regular basis. Chris developed a particular interest in both the historical and more recent strandings of sperm whales (*Physeter macrocephalus*) within the North Sea ("the North Sea is a sperm whale trap"; Smeenk & Addink 1992, Smeenk 1997a, 1997b, 1999, Pierce et al. 2007), he analysed the trends in strandings of bottlenose dolphins (*Tursiops truncatus*), common dolphins (*Delphinus delphis*) and white-beaked dolphins (*Lagenorhynchus albirostris*) (see list of publications on trend analyses). He was also interested in rare cases, such as the find of apparently recent bones of northern right whales (*Eubalaena glacialis*) within the North Sea (Kompanje & Smeenk 1996), a tropical form of the common dolphin, the 'Arabian dolphin' (*Delphinus* cf. *tropicalis*; Smeenk et al. 1996), the Cuvier's beaked whale (*Ziphius cavirostris*) (Van Waerebeek et al. 1997) and the rough-toothed dolphin (*Steno bredanensis*) (Addink & Smeenk 2001).

His research and interest in stranded whales and dolphins gave great opportunities for others to collect data on, for example, reproductive status (breeding condition), their stomach's contents (diet) (Smeenk & Gaemers 1987, Santos et al. 2001, 2002, Jansen et al. 2010), the occurrence and frequency of pathogens and ecto- or endoparasites (Fransen & Smeenk 1991, Jauniaux et al. 1998) and even in historical material (Holthuis et al. 1998) and the burden of chlorinated hydrocarbons (PCB's etc.; e.g. Addink et al. 1993, van Scheppingen et al. 1996, Pierce et al. 2007, 2008; see list of publications on necropsy studies). On many occasions and with many studies, he was a great, and critical, and therefore much appreciated help, even if he just ended up in the acknowledgements section of papers of which he wasn't awarded a co-authorship.

His knowledge, in combination with his linguistic skills, meant that Chris was often invited to contribute to major handbooks: The Handbook of Marine Mammals (Reeves et al. 1999a, 1999b), Swift as a Shadow: Extinct and Endangered Animals (van den Hoek Ostende et al. 1999), Mammals of the British Isles, 4th edition (Harris & Yalden (eds) 2008), The Second Edition of the Encyclopedia of Marine Mammals (Rudolph & Smeenk 2009) and, last but not least, both Atlasses of Dutch Mammals (Broekhuizen et al. (eds) 1992, Broekhuizen et al. (eds) 2016 ; and see the chapters by Camphuysen & Smeenk (2016) and Smeenk & Camphuysen (2016)). Even though Chris often remarked that the work on that last atlas was to be his last contribution to 'cetology', we all desperately hoped, that this was untrue even after we knew that he had become ill. For years he had been working on the cetaceans of the Red Sea, an area he had visited years ago. Again, it was mainly his efforts, combined with his meticulous precision, that formed the basis of a fine book that finally saw the light of day, but, sadly, was published posthumously (Notarbartolo di Sciara et al. (eds) 2017).

Official lists aside, Chris found sufficient time to publish more popular accounts on cetaceans, often with Marjan Addink, in Dutch journals such as Waddenbulletin, Zoogdier and Duin (most of which are included in the list below). Alongside his interest in whales and dolphins he had a fascination with bats. He felt that providing accurate adequate information was a first important step into the conservation of these creatures (see list of publications on bats). His work and ideas were instrumental in the development of a robust and unique set of conservation measures and also led to a special volume on bats '*Vleermuizen*' (Voûte & Smeenk 1991), to which he contributed a chapter on the origin and development of bats.

With Chris passing away, his wife, Nellie, has lost a caring husband, we have lost a dear friend and colleague, and science has lost a highly capable zoologist and taxonomist.

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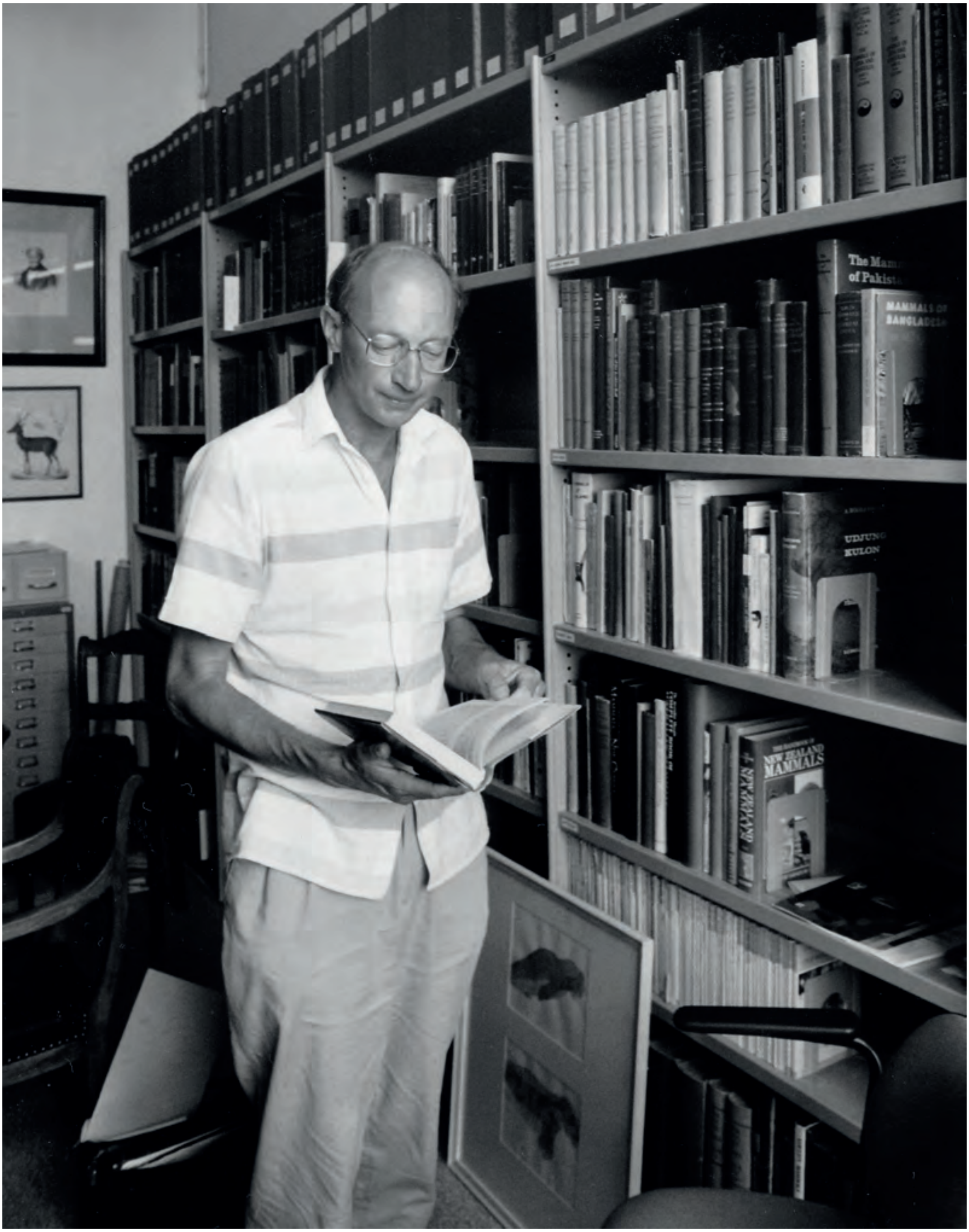

Chris Smeenk in his office at the National Museum of Natural History, Leiden (year unknown). *Photo archive B. Hoekstra.*

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Review of sperm whale (*Physeter macrocephalus*) strandings around the North Sea

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Abstract: Young adult male sperm whales (*Physeter macrocephalus*) undergo extensive nomadic movements to high latitudes. Although an oceanic species favouring deep waters, on occasions they enter the North Sea from the eastern North Atlantic. In the central and southern sectors they invariably strand on the shores of northern Europe. Although recorded in the region in all months of the year, most strandings occur between November and March. Records of sperm whale strandings along North Sea coasts from the thirteenth century to the present are documented with details of date, location, numbers of individuals and their lengths where known, and a list of published sources. Although historical estimates of lengths are likely to have been inaccurate, there is some evidence that the larger (16 m or greater), more mature, individuals recorded in earlier times have become scarce in the region since the mid 1980s.

Keywords: sperm whale, *Physeter macrocephalus*, strandings, North Sea, historical time series, ecology, migration, cetaceans.

Introduction: the occurrence of sperm whales in the North Sea

The sperm whale (*Physeter macrocephalus* L., 1758) is an oceanic species with a worldwide distribution. Many animals undertake large-scale seasonal migrations. Groups of females and young stay in warm or warm-temperate waters, in the Northeast Atlantic generally below 45° N. Young-adult males of about 14-21 years old form “bachelor” groups which migrate to higher latitudes. In summer the animals reach cold-temperate regions, as far north as Iceland and the northern Norwegian Sea. Old males, in particular, roam over great distances and may even penetrate into the Arctic Ocean (Øien 1990, Christensen et al. 1992). The seasonal movements of males are not well understood and appear rather nomadic (Mesnick 2014). Many animals seem to return to warmer areas in autumn or the beginning of winter, whereas others may stay in colder waters for long periods of time (Whitehead 2003). An important migration route appears to be the Faroe-Shetland Channel and Rockall Trough (Evans 1997, Hastie et al. 2003). Sperm whales normally live beyond the 200-m depth line, but often stray onto the continental shelf, thereby approaching Shetland, Orkney, mainland Scotland and Ireland (Evans 1997, Reid et al. 2003, Pierce et al. 2007, Gordon & Evans 2008).

Sperm whales feed mainly on deep-sea squid. In the Northeast Atlantic, their princi-

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pal diet consists of *Gonatus fabricii*, the most abundant species in the area which, however, does not normally occur in the North Sea. The stomachs of most sperm whales stranded on the coasts of the North Sea have been found empty, but if not, they contained mainly (generally >90% in numbers and reconstructed weight) beaks of *Gonatus*, often in very large quantities, showing that shortly before stranding, the animals had been feeding in oceanic waters further north (Lick et al. 1996, Clarke 1997, Santos Vázquez 1998, Santos et al. 1999, 2002, Simon et al. 2003, Pierce et al., this volume). The sizes of the squid beaks have corresponded with those of mature specimens. The main spawning period of *Gonatus* in the Norwegian Sea is from December to April. During that time, the females, laden with eggs, form huge concentrations of very nutritious prey, easy to catch as they have lost the ability to swim actively, thus attracting many predators including sperm whales (Arkhipkin & Bjørke 1999, Bjørke 2001, Simon et al. 2003, Pierce et al. 2007). This may explain the prolonged presence of sperm whales in northern waters far into the winter or early spring, although this needs further investigation.

On their way south, sperm whales that have been feeding in Norwegian waters must migrate in a southwesterly or even westerly direction, in order to pass the continental shelf edge west of Shetland and mainland Scotland. Animals that would keep too far east are in danger of straying into the North Sea. It is not known whether this happens frequently, as there are very few sightings of sperm whales in the North Sea (Evans et al. 2003, Reid et al. 2003, Camphuysen & Peet 2006, van der Meij & Camphuysen 2006). However, if animals do enter the North Sea and continue swimming south, they will find themselves in progressively shallow waters, characterised by complicated systems of sandbanks, mudflats and tidal currents. The oceanic sperm whale appears to have great difficulty navigating in such areas. This can be deduced from the behaviour of (groups of) sperm whales approaching the coast, which swim very hesitantly, milling around and showing every sign of being disoriented. With outgoing tide, such whales become easily trapped or beached in shallow water. Due to social cohesion in a group, animals that still could escape, may stay near others already in distress, and eventually become stranded as well (Smeenk & Addink 1993, Smeenk 1997, Jensen 1998, Jensen & Tougaard 1998; and several unpublished witness accounts). Finally, sperm whales that have been roaming through the North Sea for some time without food will eventually become weakened and stressed and, if they do not find a way out in time, will be fatally lost. Carcasses of animals that have died at sea often become washed up onto the shore. In view of its oceanographic character and its position at the edge of a traditional feeding area and migration route, the North Sea has been characterized as a natural “sperm whale trap” (Smeenk 1997, Jauniaux et al. 1998). This explains why most mass strandings of sperm whales occur in the southern part of the North Sea, on the sandy coasts of the German Bight and of the Netherlands, Belgium and Southeast England. Judging from the rarity of sperm whales in The Channel, only very few animals seem to escape that way. An analysis of the Sea Watch Foundation sightings database for the North Sea and environs (UK EEZ extending north to include Shetland and Orkney) compared with strandings, gave strandings to sightings ratios of 0.12 between 57°N and 63°N, 0.19 between 54°N and 57°N, and 4.50 between 51°N and 54°N, emphasising the fact that in waters averaging less than 50 metres depth south of 54°N, the probability of animals stranding is very high (Evans 2016).

Sperm whale strandings in the North Sea have always aroused excitement, of public and scientists alike, and have been documented since the 16th century. Looking at the historic data, it appears that strandings are not evenly distributed in time, even if one takes into account that in previous centuries many cases must have gone unnoticed due to a far lower human population, inaccessibility of remote beaches, and the absence of modern means of communication and media. There are periods in which hardly any sperm whales were reported, against years with great numbers of strandings. The most recent period showing peak numbers started in the 1990s, and has led to an increased interest in the phenomenon of sperm whale strandings, and to some wild speculations about the causes of such events; see, e.g., Sonntag & Lütkebohle (1998) and Wright (2005).

Analyses of sperm whale strandings and sightings in and off the British Isles during the 20th century are given by Berrow et al. (1993) and Evans (1997); for the Northeast Atlantic, a review was attempted by Camphuysen (1996) which, however, is very incomplete. These authors found an increase in strandings during the 20th century, particularly since the 1980s. Smeenk (1997, 1999) gave an overview of documented strandings in the North Sea since the 16th century and showed that periods with great numbers of strandings had occurred before, with the peak in the early 1760s being particularly obvious. Based upon those data, Vanselow & Ricklefs (2005), Vanselow et al. (2009) and Pierce et al. (2007) have tried to explain trends (see also Vanselow et al. (2017) in relation to the most recent mass stranding in January / February 2016). Vanselow and his colleagues have reported positive correlations between sperm whale strandings and solar activity. They noticed an increase in winter strandings during periods of shorter sunspot cycles, and suggested that changes in the earth's magnetic field caused by increased solar activity might disturb navigation in sperm whales. Pierce et al. rather sought an explanation in climatic factors, as they found an association between high numbers of strandings and periods of higher temperatures, which they supposed could have influenced the distribution and abundance of spawning squid in the Northeast Atlantic.

Since publication of these reviews and analyses of sperm whale strandings in the North Sea, several additional cases have been discovered and many incomplete or erroneous data could be completed or corrected. In view of the continuing interest in the subject, it is important that the underlying data are as complete and exact as possible. Therefore, a revised documentation of strandings appears useful; this is presented here. For every record, the earliest published sources have been retrieved, although it has not been feasible to try and trace the countless local archives, annals, chronicles and newspapers in the various contries; that would have taken a lifetime or more. Hence, many published records are necessarily second-hand, but all publications, scientific and popular alike, have been consulted and scrutinised for possible errors. All sources are given in the references.

Preliminary remarks

Area covered

An attempt has been made to bring together all documented strandings of sperm whales which have stranded around the North Sea. The area covered includes the east coast of the Scottish mainland south of Duncansby Head and the east coast of England north of Dover, the coast of France north of Cap Gris Nez, the shores of Belgium, the Netherlands, Germany, Denmark, Sweden, and of Norway south of Boknafjorden; as well as the Baltic Sea. Of course, these boundaries are somewhat artificial, but one has to draw the line somewhere. The sperm whale forms part of the regular fauna of the Atlantic Ocean west of Shetland and Orkney. Strandings (and sightings) in and around those islands are quite common and are not considered here.

Strandings

Defining a sperm whale stranding seems simple enough, but is not always easy. There are records of sperm whales which seemed very close to a stranding and appeared trapped between sandbanks or islands at low tide, sometimes for days, but escaped at the last moment ("near-strandings"); see, e.g., the five sperm whales off the Dutch island of Ameland in April 1993, reported by Camphuysen & Reijnders (1993) and Smeenk & Addink (1993). Other animals that seemed to have stranded, got free again with the rising tide without human aid as, e.g., the sperm whale off the Belgian coast in December 1991, reported by Vandewalle (1992). Such events are regarded as sightings and have not been counted here, although this is, of course, somewhat arbitrary.

In old records, the number of sperm whales stranded on one occasion is not always documented exactly and sometimes there are discrepancies between sources, so one has to judge which report seems most reliable. Apart from this, it may be difficult or impossible to decide whether an event concerns the stranding of a single animal, a multiple or group-stranding, or forms part of a series of strandings which are in some way connected.

Associations between males may be loose, with the animals swimming far apart but likely staying in acoustic contact. On other occasions, they may form tight groups; and if one or more members of such a group are in distress, social cohesion or panic may prevent the others from turning back in time, resulting in a true multiple stranding. The earliest account of such an event where some animals became stranded and others escaped, is from November 1577 on the Dutch coast. The most recent and spectacular mass strandings were those on the Danish island of Rømø in 1996 and 1997. Also, groups that are connected in some way may gradually fall apart and become widely scattered, with some animals stranded whereas others seem to escape, maybe to become stranded later, in different places and on different days; see the confusing situation in the southern North Sea in January/February 1762 and, recently, in January/February 2016.

Finally, sperm whales may die at sea, and the body may float about for some time before it is washed up onto the shore. Sometimes a beached carcass may come afloat again with the tide to be washed up somewhere else, the most baffling example being the sperm whale that was found in The Wash at the end of January 2004, drifted away around 15 February, and was found again on 26 February on the Belgian coast. The animal was recognisable beyond doubt, as in England its lower jaw had been sawn off. Other carcasses may disintegrate and sink; skeletal parts washed up or fished up in nets have not been considered here. A few cases are included where a carcass was found floating close to the shore and towed inland by a ship such as, e.g., the sperm whale found off Seaton Snook in the Tees Estuary in November 1766, over which there has been considerable confusion, due to a falsified document.

Many reports describe the fate of sperm whales that were stranded alive and died after a considerable time or, in the past, were slaughtered by people who saw a ready profit. But in many cases, it cannot be concluded with certainty whether an animal became live-stranded or was already dead when coming ashore. Animals stranded during the night may be found the following morning; in remote places, then may even be discovered one or more days after the event. A carcass moving in the surf is sometimes reported as still being alive. Therefore, no distinction has been made between strandings of live and dead animals here until the most recent cases.

For our knowledge of the occurrence of sperm whales in the North Sea, sightings of live animals are an additional source (Evans 1997). Such observations are fairly rare in this area, although they have increased during the last few decades, with the increasing observer effort at sea and from coastal sites. In some cases, sightings have been associated with strandings in the same period, but generally, the fate of the animals seen remains unknown (Smeenk 1997, Camphuysen & Peet 2006, van der Meij & Camphuysen 2006). No sightings

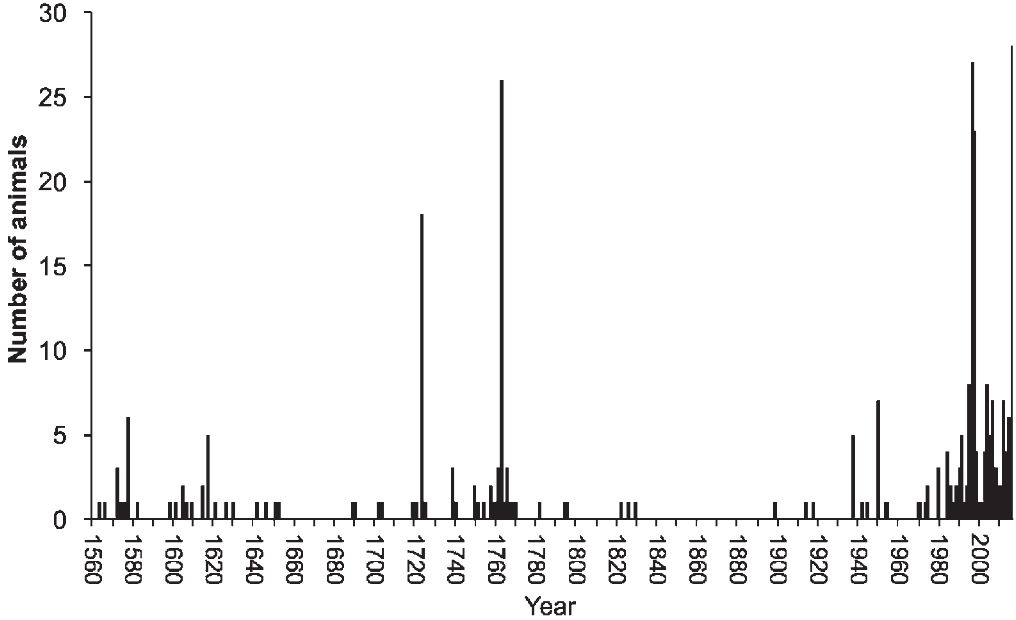


Figure 1. Occurrence of sperm whale stranding events reported in the North Sea from the 1500s to 2016.

records are included here; escaping sperm whales which were seen in the company of others that became stranded are mentioned, but it cannot always be established how many there were.

In the following, events that could be regarded as multiple or group-strandings, with or without escapes, are given in bold type. Events that may have been related (serial strandings) are indicated as such in the text, also in bold. The most obvious years in which such events occurred are the winters of 1761/62, 1994/95 and 2016 (see also figure 1).

Identification

In the past, many whales and larger dolphins have been recorded as "sperm whale" or its equivalent in other languages, or were regarded as such by later authors as, e.g., van Deinse (1918, 1931), Sliggers & Wertheim (1992) and Camphuysen (1996). However, many of such cases are insufficiently documented, and identification is often based on very inadequate descriptions to say the least. All those records, as well as other incomplete reports from past centuries, have been carefully re-considered. Many identifications turned out to be doubtful assumptions only, or proved obviously wrong: a striking example being the "sperm whale" stranded on the English coast in 1532, which was clearly described by Gesner (1558) as a large baleen whale (see below).

The name "sperm whale" often was (and sometimes still is) misapplied to other species, particularly bottlenose whales *Hyperoodon rostratus* (Forster 1770) and pilot whales *Globicephala melas* (Traill 1809). A clear example of this is the account by T. Browne (quoted by Southwell 1881) of sperm whale strandings in Norfolk in 1626 and 1646, in which it says: "and not far off, eight or nine came ashore, and two had young ones after they were forsaken by the water"; these can only have been pilot whales. Sibbald (1692: cited from the 1773 edition) too, when describing a mass stranding of pilot whales in Orkney which had been communicated to him by others, mixed up the characters of sperm and pilot whales. [This was not recognised by Linnæus (1758) who

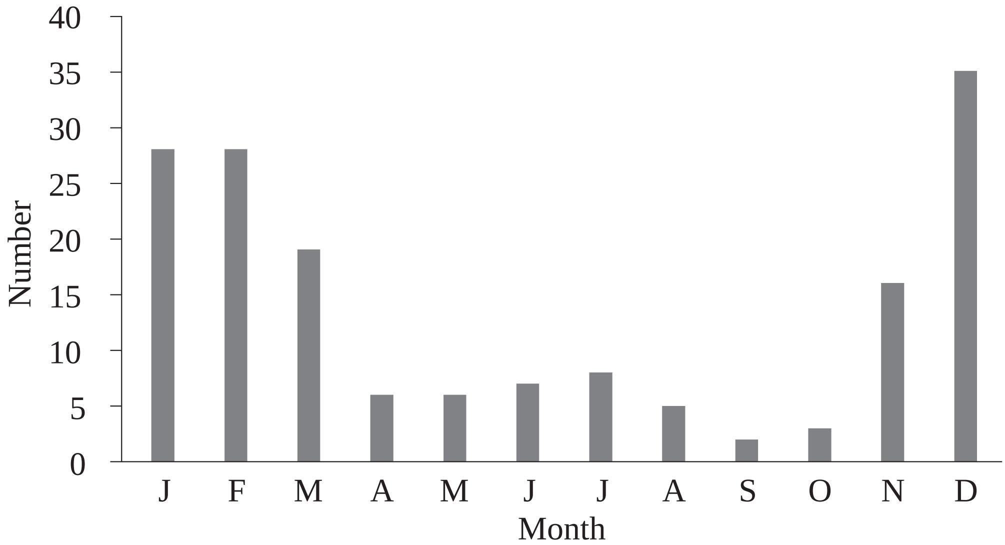


Figure 2. Seasonal distribution of sperm whale strandings in the North Sea.

had no first-hand knowledge of these species, when he described *Physeter Catodon* based on Sibbald's composite description. This has been demonstrated and extensively discussed by Husson & Holthuis (1974), but despite their sound nomenclatural reasoning and conclusions, some authors still stubbornly use the name *Physeter catodon* L., 1758 for the sperm whale.

In the following, identification as a sperm whale is accepted only where there is an unmistakable description or drawing, or where the presence of teeth (in combination with length) or of spermaceti (with its equivalent terms in other languages) is recorded. Some doubtful or insufficiently documented cases have provisionally been included nonetheless; these are given in italics.

Date

The exact date of a stranding cannot always be traced; for many cases only the month is known, or not even that. Many old records are incomplete, inaccurate or even contradictory. Sometimes a carcass had already been reported floating off the coast before being washed ashore (or was towed ashore, see above). Strandings often occur during the night and are discovered the following day; animals stranded in remote places are often found one or more days after the stranding. In general, the earliest date mentioned is given here. In a few cases a discrepancy in dates affects the recorded month of stranding, in one instance even the year (Germany, 1720/1721). Inaccuracies in reporting have sometimes led to double-counts in the literature; where possible, these have been corrected. Years with a notoriously "chaotic" documentation were 1617 and particularly 1762, with strandings later misdated 1788 or double-counted for both years.

A particular problem in dating historical strandings is the change from the Julian to the Gregorian calendar which is used today. The Gregorian calendar was not adopted simultaneously throughout Europe, but various countries, or even regions within a country, changed dates in different years, varying from 1582 to 1753. Generally, the correction meant a loss of 11 days, which means that 1 January on the Julian calendar became 12 January in the Gregorian reckoning, and 25 December Julian became 5 January in the following year.

[Note that corrections have been made here for the Netherlands, but not for other countries.]

Although strandings in the North Sea have occurred in every month of the year, there is a strong peak between November and March (figure 2). Sperm whale males in the Norrth Atlantic are known to spend the summer at high latitudes, particularly around Iceland and northern Norway, but also north and west of the British Isles (Evans 1997). Some clearly remain in the North Atlantic into the winter months, when stranding is most likely to occur.

Place

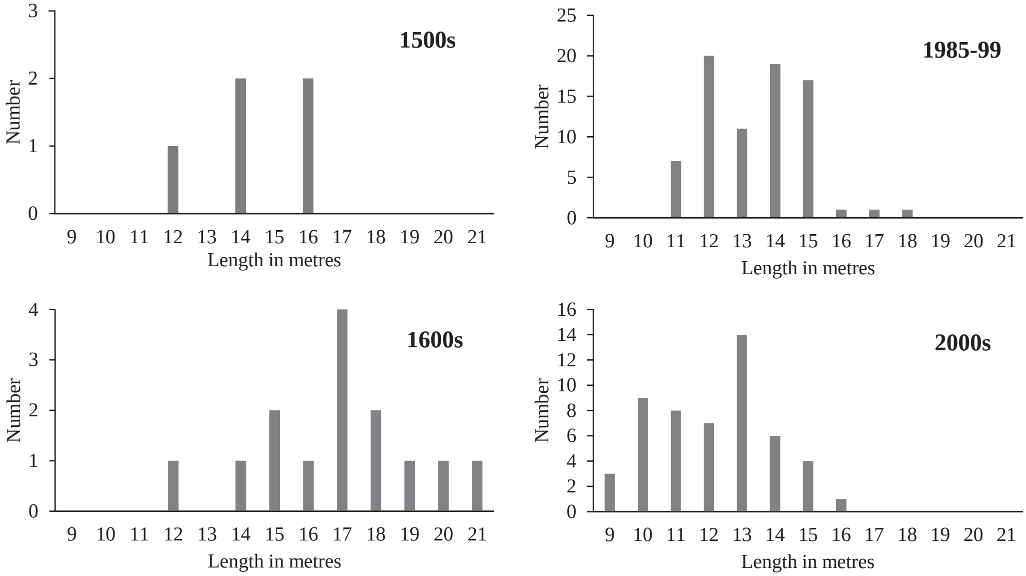
Most places of stranding are well-documented, but for some old records only the general area is known, and the exact site cannot be established. In one case, a sandbank could not be located: "Blyth Sand" mentioned for 30 January 1762 has been assumed by some to be near Blyth in Northumberland, whereas the context makes it obvious that the animal, which was towed to London, was stranded somewhere in the Thames Estuary, and another record of the same animal gives Hope Point as the locality. Sperm whales stranded in between two villages are sometimes recorded for either, and occasionally not the site itself, but a larger town further inland is given. Such facts are easy to reconstruct. Later authors have sometimes mixed up places (and dates), but such problems could be solved by going back to the oldest records. In the following, the most accurate site of stranding that could be traced, is given. Restrandings are recorded for the original site.

In a few cases, later authors confounded places. The alleged sperm whale (baleen whale) of 1532 mentioned above was described by Gesner from Tynemouth in North England, but in later publications this was misinterpreted as Teignmouth in Devon. The sperm whale stranded in 1575 has been reported for Tondern in Germany as well as for Tønder in Denmark, so has previously been counted separately for both countries. At the time of stranding, that town (which is no longer on the sea) belonged to Schleswig-Holstein, so was mentioned by its German name. The most hilarious confusion again concerns some strandings in January / February 1762: two of the sperm whales stranded in The Wash were found in the district of Holland in Lincolnshire. Needless to say, some later authors interpreted this as the Netherlands, so these animals became double-counted for both sides of the North Sea.

Apart from the above cases, assigning the country of stranding poses no problem. In all cases, the present political borders are observed, ignoring the many changes that have occurred during past centuries, as there are the border shifts between Denmark and Schleswig-Holstein mentioned above, and the separation of Belgium from the Netherlands in 1830. In view of the length of the British coastline, Scotland and England are specified separately.

Gender

Sperm whales exhibit the greatest sexual dimorphism of all cetaceans; females rarely exceed 12 m in length, adult males may reach over 18 m. All sperm whales in the North Sea described or figured with any accuracy have been males, which agrees with their known migration pattern. There are some early records of males and females stranded together, but these either turned out to concern pilot whales (see above), or lacked a comparative description, such as the absence as opposed to the presence of a penis, which is unmistakable in stranded sperm whales, or the relatively smaller head of females. Animals estimated to be of smaller size which were seen to escape from a mass stranding, were sometimes assumed to be females. Strangely, the sperm whale stranded on 2 December 1993 near Heacham is reported as a female by the Natural History Museum, London (unpublished data) without comment, although its length is given as 14.5 m, which is far too large for a female. A note on the



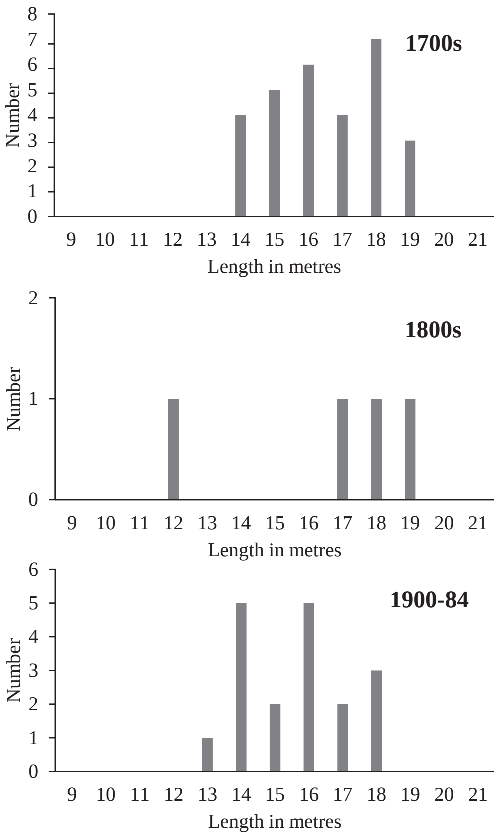


Figure 3. Distribution of sperm whale lengths from strandings in the North Sea from the 1500s to the present.

same stranding (Anonymous 1993) records the length of the animal as 12 m, which could correspond to a large female, but gives no further details; the published photograph looks like a male. Up to now, the presence of female sperm whales in the North Sea could not be substantiated.

Length

Most historic measurements are probably very inexact: at least in some cases, measuring was done in a sloppy way as, e.g., by a man walking over the body, dragging a measuring tape behind him, as can be seen in some old pictures. Such procedures inevitably will result in too high values. Moreover, there was – and still is – a general trend to over-estimate or exaggerate the size of stranded whales in reports and drawings. Many past length records are no more than rough estimates, neatly rounded off, and records of one and the same animal often vary considerably between sources, with some carcasses seeming to grow with time. Finally, in the past there was no standard unit of length, every area or city used its own ells, feet, inches and equivalents in other languages, and in some places different units were in use simultaneously. No attempt has been made to convert the published values into metres, as this might suggest an accuracy that is unrealistic.

In the following, for every animal that has been estimated or measured in some way, the length is given as it appears in the original record; unlikely figures are given in "quotation marks". However, if lengths have been expressed in more than one set of units, both have been given. This applies to some of the most recent records and it is assumed that the metric system will have been more accurate than feet as often expressed in UK press reports. Even records in recent (press) reports may show a great variation in length (see above).

Bearing in mind the above provisos, nevertheless, plots of the distribution of measurements where given to the nearest metre / foot, show similar average values from the 1500s through to the late 1980s: 15.47m (1500s), 17.43m (1600s), 17.07m (1700s), 17.22m (1800s), and 16.05m (1900-84) (see figure 3). Since the moratorium on whaling came into force in 1985, sperm whale lengths of strandings in the North Sea have been much lower, averaging 13.88m between 1985-99 and 12.58m between 2000-16 (figure 3). This may reflect a change in the age structure on the breeding grounds with more young animals moving away to higher latitudes. The most intense period of whaling for sperm whales in the North Atlantic (Azores, Madeira, Iceland) was from the late 1940s to the end of the 1970s (Martin 1980, Brito 2008). Over this period, male sperm whale lengths from catches also declined, with a marked reduction in the occurrence of large individuals (Martin 1980, 1981, Avilo de Melo & Martin 1985). Thus, despite the difficulty in interpreting early measurements from North Sea strandings, it would appear that, in recent years, there have been few large males in the North Sea compared with earlier times (and possibly more, younger, animals although in earlier centuries, these may have escaped attention).

Acknowledgements: The bulk of the research for this catalogue was undertaken by Chris Smeenk, with input from Carl Kinze (historical Danish records) and Peter Evans (historical UK records). Sadly, Chris Smeenk died before he was able to complete the work, which has been finished by Peter Evans, who would like to thank Nellie Smeenk-Enserink for all her help in this regard, and both Graham Pierce and Carl Kinze for their input.

Catalogue of documented strandings in the North Sea

Early records

1254/57 – Stavoren, the Netherlands; Enkhuizen(?), the Netherlands (2 animals).
Gesner 1558, De Haaze [1723] 1724, G. Cuvier 1825, Mulder 1836, Gervais 1855, Van Beneden & Gervais 1880, Killermann 1919, van Deinse 1933, 1946, IJsseling & Scheygrond 1943, van Laar 1963b, Taekema & Wijnandts 1991, Sliggers & Wertheim 1992, Peet 1993, Camphuysen 1996, Smeenk & Camphuysen 2016.
Note – Strandings badly documented, possibly related.

1291 *– Weichselmünde (near Gdańsk), Baltic Sea, Poland.*
Length: 29 ells or 58 ft.
Hensche 1861, Japha 1909, Kinze et al. 2011.
(Insufficiently documented, but a toothed whale of 58 ft is indicative of a sperm whale).

1402/04, 9 July (20 July) or 12 November (23 November) – Oostende, Belgium (8 animals).
Length of 1 animal: "nearly 70 ft".
Dewhurst 1832, van Deinse 1931, De Smet, 1974, 1981, 1997.
(Insufficiently documented, dates contradictory, but a multiple stranding of large whales is indicative of sperm whales).

1455, 15 April (21 April) *– Frische Nehrung (Mierzeja Wiślana), Baltic Sea, Poland/Russia.*
Length: "66 ft".
Hensche 1861, Japha 1907, 1909, Schultz 1970a, b.
(Insufficiently documented, but a toothed whale of large size is indicative of a sperm whale.)

16th Century

Note – *There is a considerable confusion regarding an alleged sperm whale stranding in 1532 near Tynemouth in England. Gesner (1558), citing an anonymous letter, describes a large whale which he called "Cetus britanicus", stranded near Tynemouth in August 1532. On pp. 251-252 he writes: "Apographum ex literis ad Polydorũ Vergilium, ex urbe Tynemutho in partibus Angliæ Borealibus. Proiecit in arenas apud Tynemuthũ mare hoc nostrum mense Augusto (anno Domini 1532.) mortuam beluam, molis & magnitudinis ingentissimæ… Aiunt qui primùm beluã uiderunt, & uti poterant diligenter perscripserunt, longitudinam illam fuisse triginta ulnarum, hoc est pedum nonaginta… certum non habetur. nam uicesimoseptimo die Augusti ipse ibi affui, fœtente iam belua, ut uix ferri posset odor... Tres uentres ueluti uastos specus: & triginta guttura, quorum quinque prægrandia sunt. Palato adhærebant quaso laminæ corneæ, una ex parte pilosæ: qualem iam unã uides, supra mille, (non est fabula Polydore, sed res uerissima,) quamuis non omnes unius magnitudinis… Aiunt genitale ei fuisse prodigiosæ magnitudini, membrum inquam masculum… In capite duo magna foramina erant: per quæ putatur beluam, plurimam aquam ueluti per fistulas eiectasse. Nulli illi fuêre dentes…" Gesner very clearly describes here a huge baleen whale, a male said to be 90 ft long, heavily decomposed, washed onto the sands of Tynemouth in North England around 27 August 1532 (7 September according to the Gregorian calander). It had 30 throat grooves, five of which very large. It had no teeth, the palate having over a thousand horny and hairy plates of different length. There were two large blowholes through which one supposed that the animal had ejected great quantities of water. However, the woodcut on p. 256 bears no resemblance to any existing marine mammal; the picture on p. 851, to which the caption also refers, is a very poor representation of a killer whale. It seems incomprehensible how G. Cuvier (1825), followed by Gray (1850, 1866) came to regard this animal as a sperm whale. Moreover, and as inexplicably, these authors transferred the stranding site from Tynemouth in Yorkshire to Teignmouth in Devon. In a Dutch manuscript from 1584/85 by Adriaan Coenenszoon van Schilperoort ("Coenen"), Gesner's description is partly quoted but, though the locality is correctly given here, the text has been grossly misread, the horny plates having been translated as "teeth like horns". To make matters worse, the author illustrated the story with a drawing of a sperm whale stranded at Ter Heijde in the Netherlands in November 1577, which he had seen himself; see Egmond & Mason (2003) who, however, did not notice these errors.*

1563, December – Grimsby, Lincolnshire, England.
Smeenk 1997, Howes 2010.

1566, 11 March (22 March) – Zandvoort, the Netherlands.
Length: 42 ft.
Mulder 1836, van Bemmelen 1864, Van Beneden 1888, Maitland 1898, van Deinse 1918, 1931, Boschma 1938a, van Laar 1963b, Schultz 1970b, Sliggers & Wertheim 1992, Egmond & Mason 1992, 2003, Camphuysen 1996, Smeenk 1997, Barthelmess 1998a, Camphuysen & Peet 2006, Smeenk & Camphuysen 2016.

1572, 1/2 November (12/13 November) – Skallingerkraag, Denmark (3 animals).
Rørdam 1896, Smeenk 1997.

1574 [1575?], 9 July (20 July) – Isle of Thanet, Kent, England.
Length: "20 ells".
Thorburn 1921, Smeenk 1997, Redman 2004.

1575 –Tønder (Tondern), Denmark.
Mohr 1931, 1935, 1967, Schultz 1970a, b, Kinze 1995, Camphuysen 1996, Lick et al. 1996, Smeenk 1997.

1577, 2-5 July (13-16 July) – Westerschelde, the Netherlands/Belgium (≥3 animals, scattered).
Length of 1 animal: 58 ft.
Clusius 1605, De Haaze [1723] 1724, Houttuyn 1762, Pasteur 1800, G. Cuvier 1825, F. Cuvier 1836, Mulder 1836, de Selys-Longchamps 1842, Deby 1848, Gervais 1855, Blasius 1857, van Bemmelen 1864, Mulder Bosgoed 1873, Van Beneden & Gervais 1880, Van Beneden 1888, Maitland 1898, D'Arcy W. Thompson 1918, 1928, van Deinse 1918, 1931, 1949, Slijper 1938, Boschma 1938a, 1951, Frechkop 1958, Jux & Rosenbauer 1959, Timm 1961, Dudok van Heel 1962, Mol 1969, Schultz 1970b, Husson & Holthuis 1974, De Smet 1974, 1976, 1977, 1978, 1981, 1997, Rappé 1977, van Berge Henegouwen 1988, Smeenk & Addink 1990b, 1993, Barthelmeß & Münzing 1991, Sliggers & Wertheim 1992, Egmond & Mason 1992, 2003, van Rossum 1995, Weisscher 1995, Camphuysen 1996, Barthelmess 1997, 1998a, Smeenk 1997, Faust 2002, Egmond 2005, Bekker 2010, Smeenk & Camphuysen 2016.
(Situation confused, see De Smet (1974); only 1 animal: near Doel, Belgium, is well documented; total number perhaps 3-6 animals).

1577, 22/23 November (3/4 December) – Ter Heijde, the Netherlands (3 stranded, 10-11 escaped).
Lengths: 48, 49, 55 ft.
Houttuyn 1762, Pasteur 1800, Mulder 1836, de Selys-Lonchamps 1842, van Bemmelen 1864, Van Beneden 1888, Maitland 1898, van Deinse 1918, 1931, Mohr 1935, 1967, Boschma 1938a, 1944, Dudok van Heel 1962, van Laar 1963b, Schultz 1970b, Husson & Holthuis 1974, Schama 1988, Smeenk & Addink 1990b, 1993, Barthelmeß & Münzing 1991, Sliggers & Wertheim 1992, Egmond & Mason 1992, 2003, van Rossum 1995, Camphuysen 1996, Barthelmess 1997, 1998a, Egmond 1997, 2005, Smeenk 1997, Faust 2002, Camphuysen & Peet 2006, Smeenk 2016a, Smeenk & Camphuysen 2016.

c. 1582 – Caister, Great Yarmouth, Norfolk, England.
Southwell 1881, 1904, Millais 1906, Patterson 1912, van Deinse 1918, Harmer 1918, Redman 2004 (Editor's Note: it is possible that the skull of this whale formed the "Devil's Seat" of the church of St Nicholas, Great Yarmouth, recorded as being painted in churchwardens' accounts in 1606, although Southwell (1881) suggests it may be of some antiquity).

1598, 3 February – Berckhey (near Wassenaar), the Netherlands.
Length: 52-53 ft.
Anonymous 1599, Clusius 1605, Houttuyn 1762, Pasteur 1800, G. Cuvier 1825, F. Cuvier 1836, Mulder 1836, Anonymous 1839, Blasius 1857, van Bemmelen 1864, Mulder Bosgoed 1873, Van Beneden & Gervais 1880, Van Beneden 1888, Maitland 1898, van Deinse 1918, 1931, Boschma 1938a, 1951, IJsseling & Scheygrond 1943, Brewington & Brewington 1969, Schultz 1970b, Husson & Holthuis 1974, Kraaijenga 1984, Puyn 1984, Frank 1986, van Berge Henegouwen 1988, Schama 1988, Nols 1989, Smeenk & Addink 1990b, Barthelmess 1989, 1997, Barthelmeß & Münzing 1991, Egmond & Mason 1992, Sliggers & Wertheim 1992, Weisscher 1995, Camphuysen 1996, Smeenk 1997, 2002, Faust 2002, Redman 2010a, Smeenk & Camphuysen 2016.

17th Century

1601, 19 December – Wijk aan Zee, the Netherlands.

Length: 60 ft.
Clusius 1605, Houttuyn 1762, Pasteur 1800, G. Cuvier 1825, F. Cuvier 1836, Mulder 1836, Gervais 1855, Blasius 1857, van Bemmelen 1864, Mulder Bosgoed 1873, Van Beneden & Gervais 1880, Van Beneden 1888, Maitland 1898, van Deinse 1918, 1931, Killermann 1919, Boschma 1938a, 1951, Timm 1961, Brewington & Brewington 1969, Schultz 1970b, Husson & Holthuis 1974, Kraaijenga 1984, Frank 1986, Schama 1988, Barthelmess 1989, 1997, Barthelmeß & Münzing 1991, Sliggers & Wertheim 1992, Camphuysen 1996, Barthelmess 1997, Smeenk 1997, Faust 2002, Smeenk & Camphuysen 2016.

***1603, 17 December** – Westerschelde, Belgium.*
Length: 42 ft.
Houttuyn 1762, Pasteur 1800, Mulder 1836, Van Bemmelen 1864, Maitland 1898, van Deinse 1918, 1931, 1949, Boschma 1938, 1951, Frechkop 1958, Jux & Rosenbauer 1959, Schultz 1970b, Husson & Holthuis 1974, De Smet 1974, 1976, 1978, 1981, 1997, Barthelmeß & Münzing 1991, Sliggers & Wertheim 1992 Camphuysen 1996, Barthelmess 1997, Smeenk 1997, Bekker 2010, Smeenk & Camphuysen 2016.
(Insufficiently documented: identity unclear).

1604, November – Pellworm, Germany (2 animals).
De Haaze [1723] 1724, Mohr 1935, 1967, Schultz 1970a, b, Smeenk & Addink 1993, Camphuysen 1996, Lick et al. 1996, Smeenk 1997.

1606, 14 January – Springersplaat (Grevelingen), the Netherlands.
Length: 72 ft.
Van Bemmelen 1864, Van Beneden 1888, Maitland 1898, van Deinse 1918, 1919, 1931, Boschma 1938a, Anonymous 1970a, Schultz 1970b, Frank 1986, Nols 1989, Barthelmess 1989, Barthelmeß & Münzing 1991, Sliggers & Wertheim 1992, Camphuysen 1996, Smeenk 1997, Smeenk & Camphuysen 2016.

1609, 26 March – Rammekens, the Netherlands.
Length: 60 ft.
Barthelmeß & Münzing 1991, Barthelmess 1997, Smeenk 1997, Bekker 2010, Smeenk & Camphuysen 2016.

1614, 2 January – Walden, France.
Length: 49 ft.
De Smet 1981, Duguy 1983, Smeenk 1997, Robineau 2005.

1614, 28 December – Noordwijk, the Netherlands.
Length: 58 ft (or 52 ft).
Mulder 1836, van Bemmelen 1864, Mulder Bosgoed 1873, Van Beneden 1888, Maitland 1898, Van Deinse 1918, 1931, Killermann 1919, Timm 1961, Brewington & Brewington 1969, Schultz 1970b, Frank 1986, Barthelmeß & Münzing 1991, Sliggers & Wertheim 1992, Camphuysen 1996, Barthelmess 1997, Smeenk 1997, Faust 2002, Baalbergen & Baalbergen 2003, Smeenk & Camphuysen 2016.

***1617, January** – Friesland, the Netherlands.*
Pasteur 1800, van Bemmelen 1864, Maitland 1898, Schultz 1970b, Camphuysen 1996, Smeenk & Camphuysen 2016.
(Insufficiently documented).

1617, 21 January – Berckhey (near Wassenaar), the Netherlands.
Length: 52 ft 3 in.
Houttuyn 1762, Pasteur 1800, Camper 1820, F. Cuvier 1836, Mulder 1836, Gray 1850, 1866, van Bemmelen 1864, Van Beneden 1888, Maitland 1898, van Deinse 1918, 1931, 1954b, Killermann 1919, Boschma 1944, Dudok van Heel 1962, Schultz 1970b, Frank 1986, Schama 1988, Barthelmeß & Münzing 1991, Sliggers & Wertheim 1992, Smeenk & Addink 1993, Camphuysen 1996, Barthelmess 1997, Smeenk 1997, Faust 2002, Smeenk 2002, Camphuysen & Peet 2006, Redman 2010a, Smeenk & Camphuysen 2016.

1617, January/February – Voorne/Goeree, the Netherlands (2 animals).
Houttuyn 1762, Pasteur 1800, van Bemmelen 1864, Maitland 1898, van Deinse 1918, 1931, Sliggers & Wertheim 1992, Smeenk & Addink 1993, Camphuysen 1996, Barthelmess 1997, Smeenk 1997, Faust 2002, Smeenk & Camphuysen 2016.

1617, 1 February – Harwich, Essex, England.
Length: 56 ft.
Barthelmess 1998a, Faust 2002.

1617, 6 February – Noordwijk, the Netherlands (1 stranded, several escaped).
Length: 54½ ft.
Houttuyn 1762, Pasteur 1800, van Bemmelen 1864, Maitland 1898, van Deinse 1918, 1931, Boschma 1944, Timm 1961, Sliggers & Wertheim 1992, Barthelmess 1997, Smeenk 1997, Smeenk & Camphuysen 2016.

Note – Documentation of 1617 strandings confused, possibly more strandings and sightings; all probably related.

1620, March – Rozenbug/Zwartewaal, the Netherlands.
Length: 56 ft.
Van Deinse 1931, Schultz 1970b, Sliggers & Wertheim 1992, Camphuysen 1996, Smeenk 1997, Smeenk & Camphuysen 2016, Archive RMNH.

1626, December *– Terneuzen, the Netherlands.*
Archive RMNH, Smeenk & Camphuysen 2016.
(Insufficiently documented).

1626, 6 December – Holme-next-the-Sea, Norfolk, England.
Length: 57 ft.
Booth 1781, Southwell 1881, 1904, Lydekker 1895, Millais 1906, Patterson 1912, D'Arcy W. Thompson 1918, Thorburn 1921, Schultz 1970b, Husson & Holthuis 1974, Smeenk 1997, Redman 2004.

Note – Initially, this stranding was wrongly dated June 1626 by Southwell (1881) who also noted another record twenty years late in the month of December, quoting Booth's History of Norfolk (1781, vol. ix, page 33). The confusion has been perpetuated by later authors. It was correctly documented by Southwell (1902), but, apparently, that paper was overlooked, so the mistake has persisted in the literature. The original reference is in a book of manuscripts held at Hunstanton Hall, notes relating to their estate, kept by Sir Hamon le Strange and Sir Nicholas le Strange between the years 1612 and 1723. There is a mention of 8-9 coming ashore nearby, two with young ones but it is not clear whether these were indeed sperm whales; it depends how one interprets "young ones".)

1629, January *– Zoutelande, the Netherlands.*
Archive RMNH, Smeenk & Camphuysen 2016.
(Insufficiently documented).

1629, 4 January – Noordwijk, the Netherlands.
Length: 63 ft.
Mulder 1836, van Bemmelen 1864, Mulder Bosgoed 1873, Van Beneden 1888, Maitland 1898, van Deinse 1918, 1931, IJsseling & Scheygrond 1943, Timm 1961, van Laar 1963b, Brewington & Brewington 1969, Schultz 1970b, Barthelmeß & Münzing 1991, Sliggers & Wertheim 1992, Camphuysen 1996, Smeenk 1997, Faust 2002. Baalbergen & Baalbergen 2003, Smeenk & Camphuysen 2016.

1635 *– Scheveningen, the Netherlands.*
Zorgdrager 1720, Houttuyn 1762, Pasteur 1800, Mulder 1836, van Bemmelen 1864, Van Beneden 1888, Maitland 1898, van Deinse 1918, 1931, Schultz 1970b, Sliggers & Wertheim 1992, Camphuysen 1996, Smeenk 2016b, Smeenk & Camphuysen 2016.
(Insufficiently documented).

1641, 5 October – Callantsoog, the Netherlands.
Length: 68 ft.
Houttuyn 1762, Pasteur 1800, Mulder 1836, van Bemmelen 1864, Van Beneden 1888, Maitland 1898, van Deinse 1918, 1931, Schultz 1970b, Barthelmeß & Münzing 1991, Sliggers & Wertheim 1992, Camphuysen 1996, Smeenk 1997, Faust 2002, Smeenk & Camphuysen 2016.

c. 1646 – Wells-next-the-Sea, Norfolk, England.
Length: 62 ft.
Brown 1658, Southwell 1881, 1904, Lydekker 1895, Millais 1906, Patterson 1912, D'Arcy W. Thompson 1918, Schultz 1970b, Husson & Holthuis 1974, Smeenk & Addink 1993, Camphuysen 1996, Smeenk 1997.

c. 1650/51 – Scheveningen, the Netherlands.
Sliggers & Wertheim 1992, Smeenk 2016b.

c. 1652 – Great Yarmouth, Norfolk, England.
Southwell 1881, 1904, Lydekker 1895, Millais 1906, Patterson 1912, Schultz 1970b, Camphuysen 1996, Smeenk 1997.

***1656** – Scheveningen, the Netherlands.*
Van Deinse 1918, 1931, Timm 1961, Schultz 1970b, Sliggers & Wertheim 1992, Camphuysen 1996, Camphuysen & Peet 2006.
(Insufficiently documented; probably confusion with 1635).

***1689** – Norfolk, England*
Millais 1906, Schultz 1970b, Smeenk 1997.
(Insufficiently documented).

1689, February – Limekilns, Fife, Scotland.
Length: 52 ft.
Sibbaldus [1692] 1773, Houttuyn 1762, G. Cuvier 1825, F. Cuvier 1836, Gray 1850, 1866, Blasius 1857, Turner 1871, 1872, Walker 1871/72, Van Beneden & Gervais 1880, Van Beneden 1888, Millais 1906, Thorburn 1921, D'Arcy W. Thompson 1918, 1928, Boschma 1938, Schultz 1970b, Smeenk 1997.

1690 – The Nore, Thames Estuary, Kent, England.
Length: 57 ft.
Millais 1906, Smeenk 1997, Faust 2002.

***1692/93, March** – Lincolnshire, England.*
Lyddekker 1895, P.G.H. Evans, unpublished, Smeenk 1997.
(Insufficiently documented).

18th Century

1701, 12 July – Cramond Island, Firth of Forth, Scotland.
Length: 52 ft.
Turner 1871, 1872, Walker 1871/72, Van Beneden & Gervais 1880, Millais 1906, D'Arcy W. Thompson 1918, 1928, Smeenk 1997, Faust 2002.

1703, 23 February – Monifieth, Angus, Scotland.
Length: 57 ft.
Turner 1871, 1872, Walker 1871/72, Van Beneden & Gervais 1880, Millais 1906, Boschma 1938a, Schultz 1970b, Smeenk 1997.

1718? (early 1700s) – Læsø, Denmark.
Kinze, unpublished, Smeenk 1997.

1718, November – Stora Överön, Sweden.
Length: "22 ells".
Bernström 1949, Lepiksaar 1966, Schultz 1970b, Mathiasson 1989, Smeenk 1997, Barthelmess & Svanberg 2009, Kinze et al. 2011.

1720, 31 December – Wischhafen, Germany.
Length: 60-70 ft.
Anderson 1746, Anonymous 1784, Pasteur 1800, G. Cuvier 1825, F. Cuvier 1836, Eschricht 1844, Blasius 1857, Van Beneden 1888, Mohr 1935, 1967, Dudok van Heel 1962, Schultz 1970a, b, Camphuysen 1996, Lick et al. 1996, Smeenk 1997, Kölmel & Wurche

1998, Faust 2002.

1723, 2/3 December – Neuwerk/Scharhörn, Germany (c. 18 stranded, 3 escaped).
Length: 70-80 ft.
Anderson 1746, Houttuyn 1762, Anonymous 1784, Pasteur 1800, G. Cuvier 1825, F. Cuvier 1836, Gervais 1855, Blasius 1857, Van Beneden 1888, Southwell 1902, D'Arcy W. Thompson 1918, 1928, Mohr 1931, 1935, 1967, Boschma 1938, 1951, Dudok van Heel 1962, Schultz 1970a b, Barthelmeß & Münzing 1991, Smeenk & Addink 1993, Camphuysen 1996, Lick et al. 1996, Smeenk 1997, Barthelmeß 1998b, Kölmel 1998, Kölmel & Wurche 1998, Faust 2002, Ellis 2011.

c. 1725 – Cresswell, Northumberland, England
Wallis 1769, Mennell & Perkins 1864, Redman 2004.

1738, 2/24 January – Süderhöft, Germany (3 animals).
Length of 1 animal: 48 ft.
Anderson 1746, Houttuyn 1762, Anonymous 1784, G. Cuvier 1825, F. Cuvier 1836, Blasius 1857, Mohr 1935, 1967, Boschma 1938a, 1951, Schultz 1970a, b, Barfod 1981, Barthelmeß 1995, Camphuysen 1996, Lick et al. 1996, Smeenk 1997, Faust 2002, C.C. Kinze, personal communication.
Note – Documentation confused.

1740, December – Near Cramond, Firth of Forth, Scotland (1 stranded at the start of December + another animal said to strand at Culross in the same year, possibly at the same time but date not given)
Length: 50-60 ft (male)
Derby Mercury, 8 Dec 1740; Caledonian Mercury, 9 March 1741; C.C. Kinze, personal communication.

c. 1749 – Hauxley, Northumberland, England.
Length: 54 ft.
Wallis 1769, Mennell & Perkins 1864.

1749, November – Hunnebostrand, Sweden.
Length: c. 70 ft.
Barthelmess & Svanberg 2009.
1751, February/March – Horumersiel; Jadebusen.
14 March – Minser Oldenoog, Germany (total number 3 animals, scattered).
Length of 1 animal: 54 ft 3 in.
Goethe 1983, Smeenk & Addink 1993, Camphuysen 1996, Lick et al. 1996, Smeenk 1997, Schmidt 2001.

1753, February – Findhorn, Moray, Scotland (3 animals).
Millais 1906, Taylor 1914, Schultz 1970b, Smeenk & Addink 1993, Smeenk 1997.

1757, January *– Aberdeen, Scotland.*
Houttuyn 1762.
(Insufficiently documented).

1757, January – Westervig, Denmark.
Lengths: 28 ells, 52 ft.
Bondesen 1977, Kinze 1993, 1995, 2002, Camphuysen 1996, Smeenk 1997, Jensen & Tougaard 1998.

1757, 10 February – Sønderho (**Fanø), Denmark (3 animals).**
Lengths: 60-62 ft (2 animals), 64 ft.
Københavnske Danske Posttidender 25 February C.C.Kinze, personal communication, Smeenk 1997.

Note – Danish 1757 strandings possibly related.

1758 – Earlsferry, Fife, Scotland.
Length: 52 ft.
Walker 1872, Smeenk 1997.

1759/60, December/January – Eiderstedt, Germany (2 animals).
Length: 58 ft.
Barfod 1981.

1761 – Bovbjerg, Denmark.
Kinze, unpublished, Smeenk 1997.

1761, 5 March – Banc des Laines, Wissant, France (1 stranded, 1 escaped).
Length: 48 ft.
Fischer 1872, Van Beneden & Gervais 1880, Van Beneden 1888, D'Arcy W. Thompson 1918, 1928, Faust 2002.
Note – Fischer (1872) reports that the second animal became stranded on the English coast; this is not further documented.

1761, early December – Eierland (Texel), the Netherlands.
Length: 53½ ft.
Houttuyn 1762, Pasteur 1800, Mulder 1836, van Bemmelen 1864, Van Beneden 1888, Maitland 1898, van Deinse 1918, 1931, Schultz 1970b, Sliggers & Wertheim 1992, Smeenk & Addink 1993, Camphuysen 1996, Smeenk 1997, Faust 2002, Camphuysen & Peet 2006.

1762, January – Terschelling (2 animals), Griend (2-3 animals).
17/18 January – Vlieland, the Netherlands (3 animals).
Length of 1 animal: "75 ft".
Houttuyn 1762, Pasteur 1800, Mulder 1836, Van Bemmelen 1864, Van Beneden 1888, Maitland 1898, van Deinse 1918, 1931, 1946, 1954b, IJsseling & Scheygrond 1943, Dudok van Heel 1962, Schultz 1970b, van Dieren 1980, Smeenk & Addink 1990b, 1993, Sliggers & Wertheim 1992, Peet 1993, Camphuysen 1996, Smeenk 1997, Faust 2002, Camphuysen & Peet 2006, Schmidt 2010.

1762, 18/21 January – Bredene.
Late January – Blankenberge, Belgium.
Length: 62 ft, 64 ft.
Houttuyn 1762, Pasteur 1800, Dewhurst 1832, van Bemmelen 1864, Maitland 1898, Mol 1962, Schultz 1970b, De Smet 1974, 1976, 1978, 1981, 1997, Duyndam 1989, Smeenk & Addink 1990b, 1993, Barthelmeß & Münzing 1991, Sliggers & Wertheim 1992, Camphuysen 1996, Smeenk 1997, Faust 2002.

1762, January – Kachelotplate (near Memmert), Germany.
22 January – Hoge Hörn (Borkum), Germany.
Length of 1 animal: "c. 15 m".
Goethe 1983, Lick et al. 1996, Smeenk 1997, Faust 2002, Schmidt 2010.
Note –Documentation confused; probably 2 animals.

1762, January/February – King's Lynn (2 animals); Essex (2 animals); Holland, Lincolnshire (2 animals).
30 January – Hope Point, Thames Estuary, Kent.
2/4 February – Birchington (2 animals); Broadstairs (2 animals); Deal; (≥ 3 escaped).
Lengths of 4 animals: 54 ft, 58 ft, 60 ft, 62 ft.
Anonymous 1762, Houttuyn 1762, Pennant 1769 [not seen], Pasteur 1800, G. Cuvier 1825, F. Cuvier 1836, Anonymous 1839, Gray 1850, 1866, Flower 1869, Anonymous 1883, Van Beneden 1888, Lydekker 1895, Southwell 1902, Murie 1903, Millais 1906, D'Arcy W. Thompson 1918, 1928, Anonymous 1922, Schultz 1970b, Smeenk & Addink 1993, Barthelmeß 1995, Camphuysen 1996, Smeenk 1997, Faust 2002, Redman 2004.
Note – The documentation of these strandings is extremely confused; the total number was at least 12 animals stranded and 3 or more escaped, some of the latter perhaps re-stranded. Several authors have erroneously dated them for 1763 or even 1763/64, still others for 1788, with varying localities. The source of this confusion is an undated letter on these strandings published in a newspaper of 7 March 1788, which is mentioned by Gray (1866, thereby correcting his error from 1850), and extensively quoted by Southwell (1902); in that letter, the events are erroneously dated February 1763. This has led to numerous misquotations and misdatings in later years, with Millais (1906), Schultz (1970a, b) and Barthelmeß (1995) even double-counting some of these strandings for

1763/64 and 1788. Pennant (1769), followed by various other authors including Faust (2002), located one of them, a live-stranding of 30 January, at "Blyth Sand" (erroneously supposed to be in Northumberland by Anonymous 1839), from where the whale had been towed to Greenland Dock in London. According to the 1788 letter, that animal had become stranded at Hope Point in the Thames Estuary, where at the time there may have been a sandbank of that name. Finally, the district Holland in Lincolnshire has been confounded with Holland, the Netherlands, by Schultz (1970b) and Barthelmeß (1995), though already Van Deinse (1931) had pointed at a likely confusion regarding this locality.

1762, January/February – Scharhörn/Neuwerk, Germany (≥2 animals).
Mohr 1967, Smeenk & Addink 1993, Camphuysen 1996, Lick et al. 1996, Smeenk 1997, Kölmel & Wurche 1998, Faust 2002, Schmidt 2010.

1762, 20 February – Zandvoort/Wijk aan Zee, the Netherlands.
Length: 55½ ft.
Houttuyn 1762, Pasteur 1800, Van Bemmelen 1864, Mulder Bosgoed 1873, Van Beneden 1888, Maitland 1898, van Deinse 1918, 1931, Timm 1961, van Laar 1963b, Brewington & Brewington 1969, Schultz 1970b, Honig & Mol 1971, van Dieren 1980, Barthelmeß & Münzing 1991, Sliggers & Wertheim 1992, Smeenk & Addink 1993, Barthelmeß 1995, Camphuysen 1996, Smeenk 1997, Faust 2002.

Note – All strandings of December 1761 - February 1762 possibly related; date of Bovbjerg, 1761 stranding unknown. The largest historical "invasion" documented.

1763, 30 June – De Hors (Texel), the Netherlands.
Length: 57½ ft.
Houttuyn 1765, Pasteur 1800, van Deinse 1918, 1931, van Laar 1963a, Schultz 1970b, Sliggers & Wertheim 1992, Peet 1993, Camphuysen 1996, Smeenk 1997, Faust 2002.

1764, 15 February – Egmond, the Netherlands.
Length: 60 ft.
Mulder 1836, Mulder Bosgoed 1873, Van Beneden 1888, Maitland 1898, van Deinse 1918, 1931, IJsseling & Scheygrond 1943, Boschma 1944, Timm 1961, Brewington & Brewington 1969, Schultz 1970b, Sliggers & Wertheim 1992, Camphuysen 1996, Smeenk 1997, Faust 2002, Camphuysen & Peet 2006.

1765, January – Bunken Strand, Denmark (2 animals).
Lengths: 48 ft, 60 ft.
Adressenavisen 6 February 1765, Kinze, personal communication, Smeenk 1997, Kinze et al. 2011.

1765, May – Skallingen, Denmark.
Kristensen 1979, Smeenk 1997.

1766, 29 November – Seaton Snook, Hartlepool, Durham, England.
Length: 48 ft.
Anonymous 1839, 1840, Mennell & Perkins 1864, Flower 1869, Drury 1980, Redman 2004.
Note – The incomplete skeleton of this animal was preserved in a crypt at Durham Castle in 1767, where it was re-discovered in 1839. In a letter by "Jo. Duresme" published by J. Raine (Anonymous, 1839), it was alleged to date from 1661. Drury (1980) has shown that this letter was a hoax and has given an extensive account of the event.

1767, February/March? – Thisted District, Denmark.
Kinze, unpublished, Bondesen 1951, 1977, Schultz 1970b, Mathiasson 1989, Kinze 1993, 1995, Camphuysen 1996, Smeenk 1997.

1769 – Kent, England.
Van Beneden & Gervais 1880, Van Beneden 1888, Millais 1906, Schultz 1970b, Smeenk 1997.

(Insufficiently documented; perhaps a confusion with the strandings in 1762).

1769, 22 December – Cramond Island, Firth of Forth, Scotland
Length: 54 ft.
Robertson 1770, Pennant 1776, G. Cuvier 1825, Woods 1829, F. Cuvier 1836, Anonymous 1839, Gray 1850, Turner 1871, 1872, Walker 1871/72, Van Beneden & Gervais 1880, Van Beneden 1888, Lydekker 1895, Millais 1906, D'Arcy W. Thompson 1918, 1928, Boschma 1938a, 1951, Camphuysen 1996, Smeenk 1997.

1770, 1 December – Hjarnø, Denmark (1 stranded, 1 escaped).
Length: 52 ft.
Japha 1907, 1908, Bondesen 1951, 1977, Schultz 1970b, Kinze 1993, 1995, Camphuysen 1996, Smeenk 1997, Kinze et al. 2011.

1781, 17 May – Zandvoort, the Netherlands.
Length: 64 ft.
Camper 1820, Mulder 1836, Eschricht 1844, van Bemmelen 1864, Maitland 1898, van Deinse 1918, 1931, Strijbos 1948, Schultz 1970b, Sliggers & Wertheim 1992, Camphuysen 1996, Smeenk 1997, Camphuysen & Peet 2006.

1794 – Whitstable Bay, Kent, England.
Gray 1850, 1866, Smeenk 1997.

1795, July – Redcar, Yorkshire, England.
Length: 50 ft.
Howes 2010.

19th Century

1822, 8 August – Lynemouth, Northumberland, England.
Length: 63 ft.
Anonymous, s.a. 1839, Drury 1980, Smeenk 1997, Redman 2004.

1825, 28 April – Tunstall beach, Holderness, Yorkshire, England.
Length: 58 ft 6 in.
Alderson 1827, T. Thompson 1829, Beale 1839, Eschricht 1849, Gray 1850, 1866, Flower 1869, Walker 1871/72, Bell et al. 1874, Van Beneden & Gervais 1880, Van Beneden 1888, Lydekker 1895, Millais 1906, D'Arcy W. Thompson 1928, Schultz 1970b, Frost 1994, Camphuysen 1996, Smeenk 1997, Redman 2004, 2010b, Howes 2010.

1829, 16 February – Whitstable, Kent, England.
Length: 62 ft.
Woods 1829, Gray 1866, Bell et al. 1874, Van Beneden & Gervais 1880, Van Beneden 1888, Lydekker 1895, Murie 1903, Millais 1906, D'Arcy W. Thompson 1918, 1928, Schultz 1970b, Smeenk 1997, Redman 2004.

1898, August – Birchington-on-Sea, Kent, England.
Length: 42.5 ft.
Murie 1903.

20th Century

1913, 18 December – Fort George, Inverness, Scotland.
Length: 48 ft.
Taylor 1914, Harmer 1914, 1927, D'Arcy W. Thompson 1918, 1928, Schultz 1970a, b, Camphuysen 1996, Smeenk 1997.

1917, 23 May – Moray Firth near Latheron, Caithness, Sotland.
Length: 59 ft 4 in.
Anonymous 1917, Harmer 1918, 1927, D'Arcy W. Thompson 1918, 1928, Schultz 1970a, b, Camphuysen 1996, Smeenk 1997.

1937, 25 January – Bridlington, Yorkshire, England.
Length: 59 ft.
Clarke 1937, Pycraft 1937, Fraser 1937, 1946,

IJsseling & Scheygrond 1943, Strijbos 1948, van Deinse 1951, Schultz 1970a, b, De Smet 1974, Camphuysen 1996, Smeenk 1997, Redman 2004a, Howes 2010.

1937, 24 February – Middelplaat (Westerschelde), the Netherlands (2 animals).
Length: 16 m, 18.5 m.
Boschma 1938a, b, 1951, Slijper 1939, Kellogg 1940, IJsseling & Scheygrond 1943, Fraser 1937, 1946, Strijbos 1948, van Deinse 1937, 1946, 1951, 1954b, Slijper 1958, Dudok van Heel 1962, Anonymous 1970a, b, van Aken 1970, Schultz 1970a, b, Stock 1973a, b, Husson & Holthuis 1974, De Smet 1974, 1976, 1981, 1997, Rappé 1977, Desmet 1989, Smeenk & Addink 1990b, Fransen & Smeenk 1991, Sliggers 1992, Sliggers & Wertheim 1992, Smeenk & Addink 1993, Kompanje & van Duijn 1994, Beeftink 1995, Camphuysen 1996, Smeenk 1997, Santos et al. 2002, Camphuysen & Peet 2006, Snell & Parry 2009, Bekker 2010, Redman 2010a, Smeenk & Camphuysen 2016.

(January/February 1937 strandings possibly related).

1937, July – Dunkerque, France (2 animals).
Length: 18 m, [22 m?].
Boschma 1938a, Lacroix 1938, IJsseling & Scheygrond 1943, van Deinse 1946, 1951, Schultz 1970a, b, De Smet 1974, 1978, 1997, Smeenk & Addink 1993, Camphuysen 1996, Smeenk 1997, van Gompel et al. 2003.

1941, 10 March – Hirtshals, Denmark.
Length: 16.65 m.
IJsseling & Scheygrond 1943, Bondesen 1951, 1977, Schultz 1970a, b, Kinze 1995, Camphuysen 1996, Smeenk 1997.

1944, 27 February – Skagen, Denmark.
Length: c. 16 m.
Kinze 1995, Camphuysen 1996, Smeenk 1997.

1949, 25-29 December – Fanø; Mandø (2 animals); Knudedyb; Darum, Denmark (5 animals, scattered).
Lengths of 3 animals: c. 12 m (1 animal), c. 16 m (2 animals).
Van Deinse 1951, Bondesen 1951, 1977, Schultz 1970a, b, Smeenk & Addink 1993, Kinze 1995, Camphuysen 1996, Smeenk 1997.

1953, 7 July – De Hors (Texel), the Netherlands.
Length: 15.5 m.
Van Deinse 1953, 1954a, b, Slijper 1958, IJsseling & Scheygrond 1962, van Laar 1963b, Anonymous 1970a, b, Schultz 1970b, Smeenk & Addink 1990b, Sliggers & Wertheim 1992, Peet 1993, Kompanje & van Duijn 1994, Camphuysen 1996, Smeenk 1997, Camphuysen & Peet 2006, Redman 2010a, Smeenk & Camphuysen 2016.

1954, 19 December – Dunkerque, France (restranded at De Panne, Belgium).
Length: 16.5 m.
Van Deinse 1955, Frechkop 1958, Slijper 1958, Jux & Rosenbauer 1959, Anonymous 1970, Schultz 1970a, b, De Smet 1974, 1976, 1978, 1997, Smeenk & Addink 1990b, Sliggers & Wertheim 1992, Camphuysen 1996, Smeenk 1997, van Gompel et al. 2003, Camphuysen & Peet 2006.

1969, 3 April – Westerhever, Germany.
Length: 16.1 m.
Schultz 1970a, b, De Smet 1976, Smeenk 1997.

1970, 3 January – Spijkerplaat (Westerschelde), the Netherlands.
Length: 16.65 m.
Anonymous 1970a, b, van Aken 1970, Schultz 1970b, Husson & van Bree 1972, De Smet & Bultinck 1972, De Smet 1973, 1976, 1978, 1981, 1997, Rappé 1977, Anonymous 1983, Brouwer de Koning 1990, Smeenk & Addink 1990b, Sliggers & Wertheim 1992, Kompanje & van Duijn 1994, Camphuysen 1996, Smeenk 1997, Camphuysen & Peet 2006, Bekker 2010, Smeenk & Camphuysen 2016.

1973, 6 October – Seaton Point, Northumberland, England.
Length: c. 41 ft.
Sheldrick 1989, Smeenk 1997.

1974, 19 January – Saltfleet, Lincolnshire, England.
Length: 49 ft.
Sheldrick 1989, Smeenk 1997.

1974, 12 September – Skagen, Denmark.
Length: c. 20 m.
Bondesen 1977, Kinze 1995, Camphuysen 1996, Smeenk 1997.

1979, 20 February – Tversted, Denmark.
Length: 14.7 m.
Kinze et al. 1987, Kinze 1995, Camphuysen 1996, Smeenk 1997.

1979, 22 August – Cullen Bay, Moray, Scotland.
Length: 46 ft 4 in.
Sheldrick 1989, Smeenk 1997.

1979, 15 December – Egmond/Castricum, the Netherlands.
Length: 15.2 m.
Van Bree & Smeenk 1982, Camphuysen 1982, van Berge Henegouwen 1988, Brouwer de Koning 1990, Smeenk & Addink 1990b, Sliggers & Wertheim 1992, Kompanje & Van Duijn 1994, Camphuysen 1996, Smeenk 1997, Camphuysen & Peet 2006, Redman 2010a, Smeenk & Camphuysen 2016.

1980, 22 February – Trischen, Germany.
Borkenhagen 1993, Smeenk 1997.

1984, 23 January – Henne Strand, Denmark (2 animals).
Length: 13.8 m, 14 m.
Kinze et al. 1987, Tougaard 1991, Smeenk & Addink 1993, Kinze 1995, Camphuysen 1996, Smeenk 1997.

1984, 16 September – Brunbjerg, Denmark.
Kinze et al. 1987, Kinze 1989, 1995, Camphuysen 1996, Smeenk 1997.

1984, 20 November – Tegeler Plate, Germany.
Length: 17.5 m.
Meyer 1994, Stede 1994, Camphuysen 1996, Lick et al. 1996, Smeenk 1997, Schmidt 2001, Redman 2009.

1985, 23 January – Crovie, Aberdeenshire, Scotland.
Sheldrick 1989, Smeenk 1997.

1985, 1 March – Skegness, Lincolnshire, England.
Length: 40-50 ft.
Sheldrick 1989, Smeenk 1997.

1986, 30 November – Holkham Beach, Wells, Norfolk, England.
Length: 50 ft 3 in.
Sheldrick 1989, Smeenk 1997.

1988, 30 November – Sæby, Denmark.
Length: 14.63 m.
Kinze 1989, 1995, Mathiasson 1989, Camphuysen 1996, Smeenk 1997, Kinze et al. 2011.

1988, 11 December – Träslövsläge, Sweden.
Length: 15 m.
Mathiasson 1989, Camphuysen 1996, Smeenk 1997, Kinze et al. 2011.

Note – November/December 1988 strandings possibly related.

1989, 12 February – Koksijde, Belgium.
Length: 17 m.
Asselberg 1989, Desmet 1989, Brouwer de Koning 1990, Smeenk & Addink 1990b, van Gompel 1991, Sliggers & Wertheim 1992, Camphuysen 1996, Smeenk 1997, De Smet 1997, van Gompel et al. 2003, Camphuysen & Peet 2006.

1990, 1 February – Findhorn, Moray, Scotland.

Length: 14.94 m.
Sheldrick et al. 1994, Camphuysen 1996, Smeenk 1997.

1990, 2 April – Noordvaarder (Terschelling), the Netherlands.
Length: 15.2 m.
Brouwer de Koning 1990, Smeenk & Addink 1990a, b, Barthelmeß & Münzing 1991, Taekema & Wijnandts 1991, Sliggers & Wertheim 1992, Peet 1993, Kompanje & van Duijn 1994, Smeenk 1995b, 1997, Camphuysen 1996, Smeenk & Camphuysen 2016.

1990, 17 November – Nymindegab, Denmark.
Length: 11.85 m.
Jensen 1991, Tougaard 1991, Kinze 1995, Camphuysen 1996, Smeenk 1997, Santos Vázquez 1998, Santos et al. 1999.

1991, 12 November – Brancaster, Norfolk, England.
Length: 15.1 m.
Sheldrick et al. 1994, Camphuysen 1996, Smeenk 1997.

1991, 1 December – Fanø, Denmark (3 animals).
Lengths: 11.70 m, 11.73 m, 12.3 m.
Jensen 1991, Kinze 1995, Camphuysen 1996, Smeenk 1997, Santos Vázquez 1998, Santos et al. 1999.

1991, 8 December – De Panne/Koksijde, Belgium (live stranding, animal escaped).
Length: 16 m
Vandewalle 1992, Camphuysen 1996, Smeenk 1997, Camphuysen & Peet 2006, van Gompel et al. 2010.

1992, 14 May – Husby Klit, Denmark.
Length: 11.25 m.
Smeenk 1997, Kinze et al. 1998.

1993, 2 December – Heacham, Norfolk, England.
Length: 14.5 m; [reported as female: probably incorrect]
Natural History Museum, unpublished, Anonymous 1993.

1993, 15 December – Atwick, Yorkshire, England.
Length: 15.85 m.
Natural History Museum, unpublished, Anonymous 1993, Frost 1994, Camphuysen 1996, Smeenk 1997, Howes 2010.

1994, 3 November – Terschelling/Ameland, the Netherlands.
Length: 14.4 m.
Addink 1994, Smeenk & van Gompel 1994, Kompanje & van Duijn 1994, Barthelmeß 1995, Kompanje & Reumer 1995, Barthelmeß 1995, Fokkema 1995, Camphuysen 1996, Clarke 1997, Smeenk 1997, 2003, Smeenk & Camphuysen 2016.

1994, 4 November – Baltrum, Germany.
Length: 13.8 m.
Siebert 1994, Barthelmeß 1995, van Rossum 1995, Camphuysen 1996, Law et al. 1996, Lick et al. 1996, Stede et al. 1996, Smeenk 1997, Schmidt 2001.

1994, 10 November – Hawsker Bottoms, Yorkshire, England.
Length: c. 15.8 m.
Natural History Museum, unpublished, Evans 1994, Barthelmeß 1995, Kompanje & Reumer 1995, van Rossum 1995, Camphuysen 1996, Smeenk 1997, Howes 2010.

1994, 15 November – Gibraltar Point, Lincolnshire, England.
Length: 52 ft.
Howes 2010.

1994, 18 November – Koksijde, (3 animals); Nieuwpoort, Belgium (1 animal).
Lengths: 14.4 m, 14.9 m, 15.4 m (Koksijde), 18.2 m (Nieuwpoort).
Joiris 1994, Kompanje & van Duijn 1994,

Figure 4. Sperm whale stranded on the Rømø Beach, Denmark, April 1996. *Photo: Svend Tougaard.*

Smeenk & van Gompel 1994, Asselberg 1995, Barthelmeß 1995, Holsbeek et al. 1995, Kompanje & Reumer 1995, van Rossum 1995, Camphuysen 1996, Bouquegneau et al. 1997, Jauniaux et al. 1997, 1998, Joiris et al. 1997, Law et al. 1997, Noël 1997, Smeenk 1997, De Smet 1997, Wells et al. 1997, Santos Vázquez 1998, Santos et al. 1999, van Gompel et al. 2003, Camphuysen & Peet 2006.

1995, 12 January – Scheveningen, the Netherlands (3 animals).
Lengths: 15.2 m, 15.35 m, 15.4 m.
Barthelmeß 1995, Kompanje & Reumer 1995, Moeliker 1995, van Rossum 1995, Smeenk 1995a, 2002, Weisscher 1995, Anonymous 1996a, b, Camphuysen 1996, Kompanje & Moeliker 1996, Boon et al. 1996, Law et al. 1996, Jauniaux et al. 1997, 1998, Law et al. 1997, Wells et al. 1997, Smeenk 1997, 2003, Camphuysen & Peet 2006, Redman 2010a, Smeenk & Camphuysen 2016.

Note – All November 1994 - January 1995 strandings possibly related.

1995, 23 March – Carse of Ardersier, Inverness, Scotland.
Length: 13.7 m.
Camphuysen 1996, Smeenk 1997, Wells et al. 1997, Santos Vázquez 1998, Santos et al. 1999.

1996, 25 January – Hulsig, Denmark.
Length: 13.1 m.
Kinze et al. 1998, Santos Vázquez 1998, Santos et al. 1999, Kinze et al. 2011.

1996, 28 January – Cruden Bay, Aberdeenshire, Scotland (6 animals live stranded, died).
Lengths of 5 animals: 12.1 m, 12.6 m, 12.85 m, 13.65 m (2 animals), 13.75 m.
Natural History Museum, unpublished, Santos Vázquez 1998, Santos et al. 1999, Smeenk 1999, Camphuysen & Peet 2006.

1996, 31 January – Norderney, Germany.
Length: 15 m.
Stede et al. 1996, Smeenk 1999, Schmidt 2001.

1996, 21 February – Gjerrild Strand, Denmark (1 animal stranded dead; first stranded at Skagen on 10 February, then at Laesø on 14 February, before finally stranding at Gjerrild Strand)
Length: 12.8 m.
Kinze et al. 1998, Kinze et al. 2011.

1996, 27 March – Rømø, Denmark (16 animals, live stranded, died).
Lengths: 11.75 m, 11.9 m, 12.15 m, 12.2. m, 12.5 m, 12.6 m, 12.7 m (2 animals), 12.8 m (3 animals), 12.9 m, 12.95 m (2 animals), 13.15 m, 13.2 m.
Kinze et al. 1998, Santos Vázquez 1998, Santos et al. 1999, Tougaard & Kinze 1999, Redman 2009, Camphuysen & Peet 2006 (see figure 4)

1996, July – Klitmøller Denmark.
Kinze et al. 1998.

1996, 17 July – Kærgård Strand, Denmark.
Kinze et al. 1998.

Note – July 1996 strandings probably related: both decomposed.

1997, 31 March – Airth, Falkirk, Scotland (live stranded, died).
Length: 15.2 m.
Natural History Museum, unpublished, Santos Vázquez 1998, Santos et al. 1999, Redman 2004.

1997, 27 November – Wassenaarseslag, the Netherlands (live stranded, died)
Length: 11.75 m.
Smeenk 1999, 2002, 2003, Santos et al. 2002, Camphuysen & Peet 2006, Redman 2010a, Smeenk & Camphuysen 2016.

1997, 28 November – Ameland, the Netherlands (4 animals, live stranded, died).
Lengths: 12.9 m, 13.2 m, 13.6 m, 14.21 m.
Smeenk 1999, 2003, Santos et al. 2002, Camphuysen & Peet 2006, Smeenk & Camphuysen 2016.

1997, 2 December – Skegness, Lincolnshire, England (1 animal, dead).
Length: 15 m.
P.G.H. Evans, unpublished, Natural History Museum, unpublished, Smeenk 1999.

1997, 3 December – Trinity Sands, Humber Estuary, England (1 animal, live stranded, died).
Length: “c. 12.19 m” (2x).
Natural History Museum, unpublishes, Smeenk 1999, Howes 2010.

1997, 4 December – Bremerhaven, Sahlenburg, Germany (2 animals, scattered).
Length of 1 animal: 13 m.
Kölmel 1998, Kölmel & Wurche 1998, Smeenk 1999, Schmidt 2001.

1997, 4 December – Rømø, Denmark (13 animals, live stranded, died).
Lengths: 13.6 m, 14.0 m (2 animals), 14.1 m (2 animals), 14.3 m, 14.45 m, 14.5 m (2 animals), 14.7 m (2 animals), 15.1 m, 15.8 m.
Jensen 1998, Jensen & Tougaard 1998, Kinze et al. 1998, Camphuysen & Peet 2006, Redman 2009.

1998, 23 January – Eiderstedt, Germany (3 live stranded, died; 3 escaped).
Smeenk 1999, Camphuysen & Peet 2006.

Note – All November 1997 - January 1998 strandings possibly related.

1998, 26 August – Rosehearty, Aberdeenshire, Scotland (1 animal, dead stranded).
Length: c. 10 m.
Natural History Museum, unpublished.

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2000, 3 June – Rømø, Denmark.
Length: 14.3 m.
Kinze et al. 2010.

2001, 2 April – Kolnes, Norway.
Length: 13 m.
Jørgensen, unpublished.

2002, 15 January [1 February?] – Friedrichskoog, Meldorfer Bucht, Germany (3 animals, dead stranded).
K. Barthelmess, personal communication; Press reports.

2002, 28 June –Hopetoun, South Queensferry, Scotland (1 animal, live stranded, died)
Length: 10.05 m.
Sabin et al. 2003.

2003, 23 January – Breast Sand, near Kings Lynn, The Wash, England (1 animal, dead stranded)
Length: 14.27 m.
Sabin et al. 2004, Deaville & Jepson 2007, Howes 2010.

2003, February – Oslofjorden, Norway.
Jørgensen, unpublished.

2003, 15/16 March – Canty Bay, North Berwick, Scotland (1 stranded, 1 floating off the coast).
Length: 13.7 m.
Sabin et al. 2004.

2003, 27 March – Oye Plage, France.
Length: 14.8 m.
T. Jauniaux, unpublished.

2003, 3 April – West Sand, Stiffkey Marshes, Norfolk, England (dead stranded).
Length: 13.72 m.
Sabin et al. 2004.

2003, 4 May – Cruden Bay, Aberdeenshire, Scotland (dead stranded).
Sabin et al. 2004.

2003, end November / 2 December – Norderney, Germany (2 animals, dead stranded).
Redman 2009.

2004 – Baltiyskaya Kosa, Baltic Sea, Russia (decomposed).
Kinze et al. 2011.

2004, before 28 January – Thornham, near Hunstanton, Norfolk, England; seen floating some days before off Holme-next-the-Sea.
Length: 13 m.
Sabin et al. 2005;
(Lower jaw cut off; carcass washed away c. 15 February; re-stranded **26 February** at Koksijde, Belgium: Haelters et al., this volume).

2004, 21 March – Inner Westmark Knock, Breast Sand, The Wash, England (1 animal live stranded, died).
Length: 12.8 m.
Sabin et al. 2005, Camphuysen & Peet 2006.

2004, 5 June – Noordpolderzijl, the Netherlands (1 animal, dead stranded).
Camphuysen et al. 2008, Smeenk & Camphuysen 2016.

2004, 24 / 26 June –Vlieland, the Netherlands.
Length: 15 m.
Camphuysen et al. 2008, Smeenk & Camphuysen 2016.

Note – June 2004 strandings probably related: both decomposed.

2004, 2 November – Richel (Waddensea), the Netherlands
(2 animals, live stranded, escaped).
Camphuysen & Peet 2006, Camphuysen et al. 2008, Smeenk & Camphuysen 2016.

Figure 5. Sperm whale stranded at Forvie on the coast of Aberdeenshire, Scotland in March 2006. *Photo: G.J. Pierce*.

2006, 4 February – Kilnsea mud, Humber Estuary, England (live stranded, died).
Length: 30 ft.
Howes 2010.

2006, 6 February – Gat Sands (2 animals, 1 re-stranded near Brancaster), England.
Howes 2010.

2006, 15 February – Skegness, England (1 animal, dead stranded).
Length: 13.9 m.
Deaville & Jepson 2007, 2011, Howes 2010.

Note – February 2006 strandings probably related.

2006, 24 March –Hackley Bay, Forvie, Newburgh, Scotland (1 animal, dead stranded)
G.J. Pierce, unpublished (see figure 5)

2006, 8 December – Wrangle Flats, Boston, The Wash, England (1 animal, dead stranded)
P.G.H. Evans, unpublished.

2006, 10 December – Roseisle, Burghead, Scotland.
Length: 13.2 m.
Deaville & Jepson 2007, 2011.

2007, 18 February – RAF Wainfleet, The Wash, England (1 animal, dead stranded)
P.G.H. Evans, unpublished, Deaville & Jepson 2008.

2008, 25 January – Burntisland, Fife, Scotland (1 animal, dead stranded)
Length: c. 12 m.
Press reports.

2008, 5 August – Alturlie Point, Inner Moray Firth, Scotland (1 animal live stranded, died)
Length: 13.93 m.
Press reports, Deaville & Jepson 2009, 2011.

2009, 30 October – Balmedie beach, Aberdeenshire, Scotland (1 animal, dead stranded)
P.G.H. Evans, unpublishes (see figure 6), Deaville & Jepson 2010.

Figure 6. Sperm whale stranded at Balmedie beach on the coast of Aberdeenshire, Scotland in October 2009. *Photo: Sea Watch Foundation.*

2010, 25 January – Collith Hole, Beadnell, England (1 animal live stranded, died).
Length: 12.8 m.
Deaville 2011.

2010, 16 June – Off the coast of Hartlepool, England (1 animal, dead floating).
P.G.H. Evans, unpublished.

2011, 3 March – Pegwell Bay, Kent, England (1 animal, dead stranded).
Length: 45 ft (13.90 m)
Press reports, Deaville 2012.

2011, 2 April – Bovbjerg Fyr, Denmark (seen floating off the coast about 2 weeks prior to stranding).
Length: “11-16 m”.
C.C. Kinze, unpublished.

2011, 31 May – Redcar, Yorkshire, England (1 animal live stranded, died).
Length: 45 ft (13.95 m)
P.G.H. Evans, unpublished; Press reports, Deaville 2012.

2011, 3 November – Hinderplaat off Voorne, the Netherlands (Live stranding, animal escaped).
Smeenk & Camphuysen 2016.

2011, 14 / 15 November – Pellworm, Germany (1 animal, stranded dead).
Length: 15 m.
Press reports.

2011, 14 December – Holbeach, Lincolnshire, England (1 animal, stranded dead)
Press reports, Deaville 2012.

2011, 18 December – Old Hunstanton, Norfolk, England (1 animal, stranded dead).
Length: 55 ft.
Press reports.

2012, 8 February – Heist-aan-Zee, Belgium (1 animal, live stranded, died).
Length: c. 13 m.
Press reports, Haelters et al., this volume.

2012, 5 March – Skegness, Lincolnshire, England (1 animal, seen earlier floating off the coast on 25 February).
Length: 35 ft.
Press reports.

2012, 13 March – Nørre Lyngby, Denmark (decomposed).
Length: 10 m.
C.C. Kinze, press reports.

2012, 15 December – Razende Bol (Noorderhaaks), the Netherlands (1 animal, stranded dead).
Length: 15.1 m.
P. Bonnet / EcoMare, Camphuysen & Smeenk 2016.

2013, 29 July – East point of Terschelling, the Netherlands (1 animal, live stranding, died).
Length: c. 12 m.
Smeenk & Camphuysen 2016.

2014, 11 January – Joppa, Portobello, Scotland (1 animal, stranded dead)
Length: 50 ft (13.95 m).
Press reports.

2014, February – Henne Strand, Denmark (2 animals, 1 live later died).
Length: 14.5 m, 12.5 m.
Hansen et al. 2016, Jensen 2016.

2014, 20 February – Sheerness, Isle of Sheppey, Kent, England (1 animal, live stranding, died)
Length: 15.3 m
P.G.H. Evans, unpublished, Deaville 2015.

2014, 25 June – Scheveningen/Wassenaar, the Netherlands (scattered remains).
Smeenk & Camphuysen 2016.

2014, 17 December – Tain, Highland, Scotland (1 animal, stranded dead).
Length: 14.35 m
Deaville 2015.

2015, 15 January – Harboøre Tange, Limfjord, Denmark (decomposed).
C.C. Kinze, unpublished.

2015, 11 February – Fanø, Denmark (decomposed, earlier floating off Sylt, Germany).
Length: 12 m.
C.C. Kinze, press reports.

2015, 26 June – near Spiekeroog, Germany (1 animal, stranded dead).
A. Schmidt, press reports.

2016, 8 January – Wangerooge, Germany (2 animals stranded, dead).
Length: 13,1 m, 11,8 m.
Clemens et al. 2016, IJsseldijk et al., in press.

2016, 12 January – Eversand, Weser, Germany (1 animal, stranded dead).
Clemens et al. 2016, IJsseldijk et al., in press.

2016, 12 January – Helgoland, Germany (2 animals floating).
Length: 12.0 m, 12.3 m.
Clemens et al. 2016, IJsseldijk et al., in press.

2016, 12 January – Texel, the Netherlands (5 animals live stranded, died).
Live-stranding. died
Length: 9.6 m, 9.7 m, 10.1 m, 10.25 m, 11.1 m
Clemens et al. 2016, Geelhoed et al. 2016, Smeenk & Camphuysen 2016, IJsseldijk et al., in press.

2016, 13 January – Trischen, Germany (restranded Cuxhaven 28 January).
Length: 10.7 m.
Clemens et al. 2016, IJsseldijk et al., in press.

2016, 14 January – Texel, the Netherlands (carcass, not fresh).
Length: 11.5 m.
Clemens et al. 2016, Geelhoed et al. 2016, Smeenk & Camphuysen 2016, IJsseldijk et al., in press.

2016, 23 January – Hunstanton, Norfolk, England (1 live stranded, died; 4-5 escaped).
Length: 13.8 m.
P.G.H. Evans, press reports, Clemens et al. 2016, IJsseldijk et al., in press.

2016, 24 January – Gibraltar Point & Skegness, Lincolnshire, England (3 stranded, 1 died at Gibraltar Point, 2 died at Skegness).
Length: 14.6 m, 14.7 m (Gibraltar Point), 13.5 m (Skegness)
P.G.H. Evans, press reports, Clemens et al. 2016, IJsseldijk et al., in press.

2016, 25 January – Friskney Flats, Wainfleet, Lincolnshire, England (1 stranded dead, 1 escaped).
P.G.H. Evans, press reports, Clemens et al. 2016, IJsseldijk et al., in press.

2016, 31 January – Kaiser-Wilhelm-Koog, Germany (8 animals, 1 live stranded, died; 7 stranded dead).
Length: 10.2 m, 10.5 m, 10.8 m, 11.0 m, 11.2 m, 11.3 m, 11.4 m, 11.7 m
Clemens et al. 2016, IJsseldijk et al., in press.

2016, 2 February – Hemmes de Marck, Calais, France (1 animal, stranded dead).
Length: 13.85 m
Clemens et al. 2016, IJsseldijk et al., in press.

2016, 3 February – Blauortsand, Büsum, Germany (2 animals, stranded dead).
Length: 11.4 m, 12.0 m
Clemens et al. 2016, IJsseldijk et al., in press.

2016, 3 February – Old Hunstanton/Holme-next-the-Sea, England (1 live stranded, died).
Length: 13.6 m
P.G.H. Evans, press reports, Clemens et al. 2016, IJsseldijk et al., in press.

2016, 25 February – Blaavandshuk, Denmark (1 animal, stranded dead, decomposed).
Geelhoed et al. 2016, IJsseldijk et al., in press.

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Samenvatting

Een beredeneerde strandingslijst van potvissen (*Physeter macrocephalus*) rond de Noordzee

Jonge volwassen potvissen maken uitgebreide zwerftochten tot ver in de noordelijke oceanen. Hoewel het hier een uitgesproken oceanische soort betreft, komen er vanuit de oostelijk Noord-Atlantische Oceaan af en toe exemplaren de Noordzee binnen. In de centrale en zuidelijke delen stranden ze dan onveranderlijk op de kusten van noordelijk Europa. Hoewel ze in dit gebied in alle jaargetijden worden waargenomen vinden de meeste strandingen plaats in de periode november-maart. Waarnemingen van potvisstrandingen rond de Noordzee vanaf de dertiende eeuw tot heden worden hier bij elkaar gebracht en gedocumenteerd voor wat betreft datum, vindplaats, aantal individuen en, indien bekend, ook de individuele lengte. Daarnaast wordt per waarneming een lijst van vindplaatsen in de literatuur gepresenteerd. Hoewel de in het verleden opgegeven lengtematen waarschijnlijk onnauwkeurig zijn vastgesteld, zijn er toch wel aanwijzingen dat de grotere (> 16 m lange), oudere individuen zoals waargenomen in het verleden sinds het midden van de jaren 1980 in het gebied van onderzoek zeldzamer zijn geworden.

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Analysis of historical and recent diet and strandings of sperm whales (*Physeter macrocephalus*) in the North Sea

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Abstract: The increasing frequency of sperm whale (*Physeter macrocephalus*) strandings during the winter in the North Sea has resulted in many theories about why this phenomenon occurs. Using a newly updated catalogue of North Sea sperm whale strandings, the possible roles of environmental drivers, which might affect the entry of migrating sperm whales into the North Sea and/or their stranding, were investigated using generalised additive mixed models. Little or no evidence was found of effects of sunspot activity, the North Atlantic Oscillation (NAO) Index or sea surface pressure around Iceland (a component of the NAO) on the occurrence of strandings. Several sea and land surface temperature indices were positively correlated with the occurrence of strandings. There is evidence of changing relationships between strandings and environmental variables during the last three decades and, given the absence of an obvious mechanism by which the temperature-strandings link might operate, it is important to recognise that several different processes may contribute to the strandings, including the recovery of the sperm whale population following the cessation of commercial whaling in the late 20th century. In addition, and since temperature could also be affecting the whales´ prey and changes in prey distribution could explain whale stranding patterns, this paper updates previous studies of diet, confirming the continued dominance of the Boreoatlantic armhook squid *Gonatus fabricii* in stomach contents of sperm whales stranded on North Sea coasts, although remains of small numbers of North Sea species were also found, suggesting some feeding within the North Sea.

Keywords: sperm whale, Boreoatlantic armhook squid, stranding, sea surface temperature, land surface temperature, diet, stomach contents analysis.

Introduction

Sperm whales (*Physeter macrocephalus*) are known to have entered the North Sea and stranded since at least the 13th century. Almost invariably these animals seem to have been males, travelling southwards in the winter from summer feeding grounds in the Arctic (Smeenk 1997, Smeenk & Evans, this volume). The presence – and deaths – of large numbers of sperm whales in a shallow sea area such as the North Sea in the 1990s and the wide year-to-year fluctuation in numbers of whale deaths led to considerable attention and speculation about causes (e.g. the set of papers collected in Jacques & Lambertsen 1997). Possible explanations relate to the distribution, abundance, health and navigational skills of the whales as well as effects of a range of anthropogenic stressors including climate change as well as the possibility that we are documenting rare, random events. It is also important to bear in mind that reasons for sperm whales entering the North Sea may be unrelated to the ultimate cause of death; the explanation for the strandings in the North Sea needs to consider both questions.

The occurrence of feeding migrations in sub-adult and adult male sperm whales is well-documented. The need for the whales to return southwards from Arctic feeding grounds puts them in proximity of the entrance to the North Sea but generally they travel southwards through deep Atlantic waters along the west coast of the UK. Past dietary studies have consistently revealed little evidence of sperm whales feeding within the North Sea; stomach contents of whales stranded on North Sea coasts are usually dominated by the remains of the hard structures (mandibles) of the Boreoatlantic armhook squid *Gonatus fabricii* (e.g. Santos et al. 1999, 2001, 2002, Simon et al. 2003), a species found in Arctic and sub-Arctic waters (Bjørke 2001), and with little evidence of recent feeding.

Gonatus fabricii is the most abundant squid in Arctic and sub-Arctic waters; Bjorke (2001) estimated that it reached a biomass of 1.5 million tonnes in the Norwegian Sea in 1994. As speculated by Santos et al. (1999), it is possible that year to year changes in the distribution and abundance of *Gonatus* influence the likelihood of sperm whales entering the North Sea, for example because the distribution in some years extends closer to the North Sea (e.g. into the Norwegian Deeps). Alternative possibilities are that more sperm whales are present in the Arctic in years of high squid abundance and that a higher proportion of whales migrate southwards in years of low abundance. While few data exist on distribution and abundance of *Gonatus*, there is evidence of substantial year to year variation in its abundance (see Dalpadado et al. 1994).

Sperm whale populations have presumably recovered since the cessation of commercial whaling on this species around 1988 (Whitehead 2002) and increasing whale density may have resulted in more males undertaking feeding migrations to the Arctic. Evans (1997) reported evidence for a higher frequency of younger males among strandings on eastern North Atlantic coasts in recent years and suggested this may have been due increased competition for females on the breeding grounds as populations recovered from the earlier harvesting of the more mature males. Thus we might expect a steady increase in numbers of whales entering the North Sea, although perhaps starting only once a threshold density had been achieved. However, sperm whale population size probably reached an all-time low in the latter half of the 20th century and it is unlikely that abundance has recovered to pre-whaling levels (see hypothetical population trajectories in Whitehead 2002).

Vanselow & Ricklefs (2005) and Vanselow et al. (2009, 2017) have pointed to the possible effect of solar disturbances on sperm whale navigation as a plausible explanation for many strandings, although the statistical support for this is weak. The role of great storms (documented in the North Sea by Lamb (1991)) was investigated by Nielen (2018), who found no apparent relationship. Smeenk (1997) referred to the North Sea as a "sperm whale trap", in which shallow sloping sandy seabeds in coastal waters rendered sperm whale navigation ineffective. The normal migration route of males which have been feeding in the Arctic passes through deep waters to the west of the United Kingdom and it is likely true that a high proportion of sperm whales which enter the North Sea subsequently perish on its coasts. If so, the key question is likely to be why more sperm whales enter the North Sea in some years than in others.

Studies on carcasses of stranded sperm whales on North Sea coasts have revealed high contaminant burdens (Holsbeek et al. 1999) and the presence of significant quantities of plastics in the digestive tracts (Unger et al. 2016). While such findings highlight anthropogenic pressures faced by cetaceans, the pollutants and plastics were not thought to have been responsible for the deaths. Evidently not all sperm whales which strand are healthy animals, and in some cases poor health may contribute to navigational errors, perhaps explaining entry into the North Sea (Hansen et al. 2016). However, in general, even if the North Sea is a sperm whale trap, it seems unlikely that it is also a sperm whale graveyard; it is not a gathering place for ailing and moribund whales. It is worth noting that effects of plastics and PCBs or indeed seismic surveys and naval sonar are modern day threats and could not explain the occurrence of strandings over a half a millennium, nor are they likely to explain the wide year to year variation in numbers of strandings.

Effects of climate variation and change may be suspected, not least due to the known sensitivity of squid (the sperm whale´s main prey) distribution and abundance to changing environmental conditions. However, this suggests only a rather vague general hypothesis. In its favour is a weak but statistically significant positive relationship between occurrence of strandings and sea temperature (Pierce et al. 2007) but the underlying mechanism (if any) remains unclear. Indeed, it is not obvious whether warming would have a positive or negative influence on *Gonatus* abundance. Higher abundance could result in wider distribution of *Gonatus* and draw whales closer to the North Sea while lower abundance could favour more whales undertaking the southward migration rather than remaining in the Arctic.

An obvious question is whether sperm whale strandings in the North Sea are chance events. In some respects, they are obviously not: sub-adult and young adult male sperm whales tend to move around in groups and a stranding of multiple animals cannot be considered as multiple independent events. The likelihood of strandings being reported has probably increased with the density of coastal human populations and in the last century with the emergence of dedicated strandings networks, many of which have become increasingly professional and better funded over the last two or three decades. In addition, publicity likely begets publicity: after a recorded stranding the efficiency with which subsequent strandings are reported may increase. This does not preclude strandings events themselves being essentially random, i.e. whether and how many strandings occur in a given year are independent of what happened in the previous year – something easily tested. Finally, we cannot rule out the possibility that there are multiple causes of the North Sea strandings.

The first two decades of the 21st century have also seen substantial numbers of sperm whale strandings in the North Sea and it is therefore appropriate to revisit evidence about causes. Here we re-examine two specific questions, about the diet of these whales (is there any evidence that they enter the North Sea to feed; has the diet changed over time?) and causes of variation in numbers stranded.

Methods

Diet

We compiled dietary data from our previous publications (which included samples from 1990 to 2004 as well as one from 1937), adding data from stomach contents for four additional individuals stranded in Scotland (UK) during 2002 to 2014 (see table 1). In most cases, only a sample of the stomach contents could be obtained (e.g. samples from Cruden Bay, Aberdeenshire (UK) in 1996 were taken when the carcasses exploded due to buildup of decomposition gases) and the absolute amount of prey remains recovered is not necessarily indicative of stomach fullness. No fresh prey remains were recovered in this

Table 1. Sources of stomach contents samples.

Stranding ID	Date	Season	Location	Area	Event	Age	Sex	Length (cm)	Source
PM1937	23/02/1937	W	Terneuzen NL *	NS	M (2)		Male	1600	2
CN 719	17/11/1990	W	Nymindegab DK	NS	S		Male	1185	1
CN 850	01/12/1991	W	Fanø DK	NS	M (3)		Male	1173	1
M2583/94 3	07/12/1994	W	Orkney UK	NS	M (11)	***	Male	1280	1
M2583/94 6	07/12/1994	W	Orkney UK	NS	M (11)	***	Male	1340	1
M2583/94 9	07/12/1994	W	Orkney UK	NS	M (11)	***	Male	1280	1
M2583/94 11	07/12/1994	W	Orkney UK	NS	M (11)	***	Male	1250	1
M0546/95	23/03/1995	W	Inverness UK	NS	S	23	Male	1370	1
M143/96B	28/01/1996	W	Cruden Bay UK	NS	M (6)		Male	1285	1
M143/96C	28/01/1996	W	Cruden Bay UK	NS	M (6)		Male	1210	1
M143/96D	28/01/1996	W	Cruden Bay UK	NS	M (6)	24	Male	1375	1
M143/96E	28/01/1996	W	Cruden Bay UK	NS	M (6)	19	Male	1365	1
M143/96F	28/01/1996	W	Cruden Bay UK	NS	M (6)		Male	1365	1
1	27/03/1996	W	Rømø DK	NS	M (16)	20	Male	1280	1
5	27/03/1996	W	Rømø DK	NS	M (16)	22	Male	1295	1
8	27/03/1996	W	Rømø DK	NS	M (16)	26	Male	1190	1
12	27/03/1996	W	Rømø DK	NS	M (16)	20	Male	1215	1
1996_009	29/03/1996	W	Tory Island IE	Atl	S		Male	1480	2
PM281197	27/11/1997	W	Wassenaarseslag NL	NS	S		Male	1175	2
Potvis 1	28/11/1997	W	Ameland NL	NS	M (4)		Male	1320	2
Potvis 2	28/11/1997	W	Ameland NL	NS	M (4)		Male	1421	2
Potvis 3	28/11/1997	W	Ameland NL	NS	M (4)		Male	1360	2
M1695/98	06/08/1998	S	Bettyhill UK	Atl**	S		Male	1220	2
M172/02	26/08/2002	S	Lewis UK	Atl	S		Male	1290	4
2004_057	05/05/2004	S	Quilty IE	Atl	S	Calf	Male	580	3
M305/06	10/12/2006	W	Burghead UK	NS	S		Male	1320	4
M133/12	18/05/2012	S	N. Uist UK	Atl	S		Male	1183	4
M11/14	11/01/2014	W	Edinburgh UK	NS	S		Male	1395	4

Seasons: W = winter, S = summer. Location: countries are indicated by two letter codes (DK, IE, DK, UK). Areas: NS = North Sea (east of 4˚W), Atl = Atlantic. Strandings: M = multiple (with number of animals), S = single. Ages of Scottish animals are taken from Mendes et al. (2007). Sources: 1 = Santos et al. (1999), 2 = Santos et al. (2002), 3 = Santos et al. (2006), 4 = this study. Notes: * Smeenk (this volume) records this stranding as occurring at Middelplaat (Westerschelde), just north of Terneuzen, on 24/2/37. ** The location is very close to the boundary at 4˚W. *** Three other animals from this mass stranding, not sampled for stomach contents, had estimated ages of 20-24.

mass stranding or in previous ones or in single animals analysed (at least by us).

Remains consisted principally of cephalopod beaks and fish otoliths, bones and eye lenses, and skate or ray egg capsules. Otoliths, beaks and bones were identified by MBS and GJP to the lowest possible taxonomic level, consulting reference material and relevant guides (e.g. Clarke 1986, Härkönen 1986). Results are expressed in terms of the minimum number of prey individuals represented (for details of stomach analysis methodology and diet quantification, see Santos et al. 1991, 2002).

For the diet analysis, we divided animals into North Sea (east of 4^0 W) and Atlantic (west of 4^0 W) coasts and considered strandings as belonging to winter (November to early April) or summer (the remainder of the year). Note that here we included animals stranded in the Orkney islands along with the North Sea animals although Smeenk (1997), and Smeenk & Evans (this volume) did not include them in the stranding record for the North Sea, since these islands were considered to be outside the North Sea. However, the Orkney islands are on the continental shelf, some distance from the deep waters to the west of the United Kingdom, including the Faroe-Shetland channel, which normally is used by migrating sperm whales. Therefore, we included them here (and they were included in Santos et al. 1999).

Strandings

The strandings series was compiled from Smeenk & Evans (this volume), thus extending (forwards) and updating that used in Pierce et al. (2007). Note that Smeenk & Evans also extended Smeenk´s (1997) series backwards in time from 1563 to the 1250s but this essentially added only one new occurrence record, of three animals stranded during two stranding events in the Netherlands either in 1254 or 1257, hence we retained the previous first record, from 1563, as the first in the series. We first compiled information on the number of sperm whale strandings on North Sea coasts per calendar year, excluding animals which did not strand or live stranded and escaped. Strandings that were described as “insufficiently documented”, e.g. because the species was uncertain, were also excluded. Since strandings normally show a peak between November and March (Smeenk 1997) we also derived an alternative series, with each “year” running from July of the calendar year through to June of the following year. Thus, in the latter case the “1995” strandings refer to July 1995 to June 1996. Since more animals strand in the first six months of the year than in the second (Smeenk 1997), animals for which the month of stranding was unknown were assigned to the first half of the year. Both series of counts were then used to derive occurrence (i.e. presence-absence) series.

The times series of occurrence of strandings were tested for randomness using a non-parametric runs test. Strandings occurrence was then analysed in relation to the following variables (these series extend up to 2016, the last year of the strandings series, unless otherwise stated):

a. Annual (1701-) and winter (1751-) sunspot numbers (as used by Vanselow and co-authors);
b. The NAO index (1825-) and Iceland sea level pressure (i.e. the northern component of the NAO index, 1823-) (data available at https://crudata.uea.ac.uk/cru/data/nao/index.htm, see Jones et al. 1997). The latter index may be more directly relevant to the area in which the whales are found before entering (or not) the North Sea;
c. European (land) surface air temperature (LSAT) reconstructions by Luterbacher et al. (2004, 2006). Here we used winter (December of the previous year to February) and annual series (both 1563-2004);
d. Annual average sea surface temperature (SST) anomaly, available at https://www.eea.europa.eu/ and originating with the UK Meteorological Office´s Hadley Centre. We used global, North Sea and North Atlantic datasets (all 1870-2014).

We initially calculated correlations between the count and occurrence series and each of the environmental series, repeating this for the environmental series lagged by one year. As a way to examine the temporal consistency of the strandings-environment relationships, we plotted correlation “discovery curves”, estimating the correlations after each successive year of data was added. This approach was run forwards from the year in which each environmental series started,

Table 2. Summary of stomach contents. The order of appearance of the whales in this table is the same as in table 1.

Date	Season	Country	Area	Fish					Cephalopods: Squid																Octopus			
				Cho	Lop	Mm	Pv	UK	Arc	Chi	Ga	Gf	Hb	His	Hm	Hr	HtA	Lf	Lg	Ms	Td	Tm	Tp	Ts	Ec	Ha	Oct	UK
23/02/1937	W	NL	NS									7																2
17/11/1990	W	DK	NS									279																
01/12/1991	W	DK	NS									1	1															
07/12/1994	W	UK	NS									4260	3									4				1		
07/12/1994	W	UK	NS									1652	2	1								2				1		
07/12/1994	W	UK	NS									17																
07/12/1994	W	UK	NS									344	1									7						
23/03/1995	W	UK	NS	1								1439	2									60				3		
28/01/1996	W	UK	NS									72										1				1		
28/01/1996	W	UK	NS									207										2				2		
28/01/1996	W	UK	NS					1				1432										2		10	1	1		
28/01/1996	W	UK	NS	1								4631	84					1				31		3		5		6
28/01/1996	W	UK	NS	1								402										1						
27/03/1996	W	DK	NS				1																					
27/03/1996	W	DK	NS									98																2
27/03/1996	W	DK	NS									1																
27/03/1996	W	DK	NS					1				1064	2									5						
27/11/1997	W	NL	NS				1					402	5									4					1	6
28/11/1997	W	NL	NS									1546															1	
28/11/1997	W	NL	NS									160										1		1			17	
28/11/1997	W	NL	NS		1			1				151																
10/12/2006	W	UK	NS			14						20																
11/01/2014	W	UK	NS									3170																
01/04/1996	W	IE	Atl						1	1		14	104						3			13				39		
06/08/1998	S	UK	Atl							1		29	2				1				1	9				1		
26/08/2002	S	UK	Atl									290	1									1						2
04/05/2004	S	IE	Atl								7		2		3	65	405			1		73	1					207
18/05/2012	S	UK	Atl							1		134					6					3				1		
Occurrences				3	1	1	2	3	1	3	1	26	12	1	1	1	3	1	1	1	1	17	1	3	1	10	3	6

Key to species: UK = unidentified fish or unidentified cephalopod. Fish: Cho = chondrithys, Lop = *Lophius* sp., Mm = *Merlangius merlangus*, PV = *Pollachius virens*. Cephalopods: Arc = *Architeuthis* sp., Chi = *Chiroteuthis* sp., Ga = *Galiteuthis armata*, Gf = *Gonatus fabricii*, Hb = *Histioteuthis bonnellii*, His = *Histioteuthis* sp., Hm = *H. meleagroteuthis*, Hr = *H. reversa*, HtA = *Histioteuthis* type A (beak shape consistent with several *Histioteuthis* species including *H. bonnellii* and *H. meleagroteuthis*), Lf = *Loligo forbesii*, Lg = *Lepidoteuthis grimaldi*, Ms= *Mastigoteuthis schmidti*, Td = *Taningia danae*, Tm = *Teuthowenia megalops*, Tp = *Taonius pavo*, Ts = *Todarodes sagittatus*, Ec = *Eledone cirrhosa*, Ha = *Haliphron atlanticus*, Oct = Octopodidae.

and also backwards from the year in which it ended. In both cases, we illustrate the results after excluding the first 10-years of each curve (since results are extremely variable when the series are very short).

Given the non-randomness of the strandings series, we tested them for autocorrelation and partial autocorrelation (PAC). The latter showed autocorrelation values exceeding 0.2 for lags from 1 to 3 or 4 years. Note that with 0-1 data, the confidence intervals generated for AC and PAC are not valid but the plots can still be used as a guide.

Zuur et al. (2012) applied a range of GAM-family modelling approaches to the original strandings and environmental series from Pierce et al. (2007) and all gave rather similar answers. Here, we used binomial GAMMs with an ARMA component to remove autocorrelation in the response variable. In practice, the performance of models accounting for autocorrelation at lag 1 year (corAR1) and for lags of 1 and 2 years (i.e. corARMA(p=2, q=0)) was similar. In both cases autocorrelation was reduced but a few autocorrelation spikes sometimes remained in the residuals, although in the latter the significance of the effect of the explanatory variable was reduced. Hence, we finally used corAR1 and note that some caution is needed in interpreting the results. For all explanatory variables, complexity of smoothers was limited by setting a limit on the number of "knots" (using k=4).

Separate models were fitted for each explanatory variable, for lag 0 and lag 1 year. Note that lag zero does not mean that pairs of points in the strandings and environmental series refer to exactly the same time periods. Thus 1995 winter temperature refers to December 1994 to February 1995 and 1995 July-June strandings refers to July 1995 to June 1996.

Correlations, runs tests, partial autocorrelation and ARMA analyses were carried out using Minitab (Minitab Inc) and Microsoft Excel while GAMMs were fitted using Brodgar (Highland Statistics Ltd) software, which is based on R.

Results

Diet

Diet data were available from 28 individuals stranded in the UK, Ireland, Denmark and the Netherlands between 1937 and 2014, including four animals stranded in Scotland between 2002 and 2014 for which diet results have not previously been published (table 1). All were males, 23 from North Sea coasts (if we include the four animals from Orkney) and five from Atlantic coasts (west Scotland and Ireland).

The main prey species found in stomachs of sperm whales stranded on North Sea coasts in winter (see table 2) was the squid *Gonatus fabricii*, which was present in 22 out of 23 animals, with remains of between 1 and 4600 individual squid recovered. Also frequently occurring, although less numerically important, were the squids *Teuthowenia megalops* (F=12, 1-31 beaks) and *Histioteuthis bonnellii* (F=8, 1-84), and the octopus *Haliphron atlanticus* (F=7, 1-5).

Some evidence of feeding in the North Sea was apparent in the stomach contents, with the appearance of remains of resident fish and cephalopods in stomachs of eight individual whales, including saithe (*Pollachius virens*), whiting (*Merlangius merlangus*), monkfish (*Lophius* sp.), the curled octopus (*Eledone cirrhosa*), and the veined squid (*Loligo forbesii*). Beaks of the latter species were identified only to genus level and assignment of species is based on known squid distribution. Mostly, these remains were of single individual prey specimens, although 28 whiting otoliths were recovered from one whale stomach. Single egg capsules of a shark or ray (Chondrichthyes) were found in three stomachs.

Four of the five individual whales from Atlantic coasts had stranded in summer. The main prey species of three whales from west Scotland were the same as recorded in animals from the North Sea coasts. In the two Irish whales, *Histioteuthis* spp. were the most numerous prey rather than *Gonatus*.

Several cephalopod species were found only in Atlantic samples, namely *Architeuthis* sp., *Chiroteuthis* sp., *Galiteuthis armata*, *Lepidoteuthis grimaldi*, *Mastigoteuthis schmidti*, *Taonius pavo*, *Taningia danae* and two of the

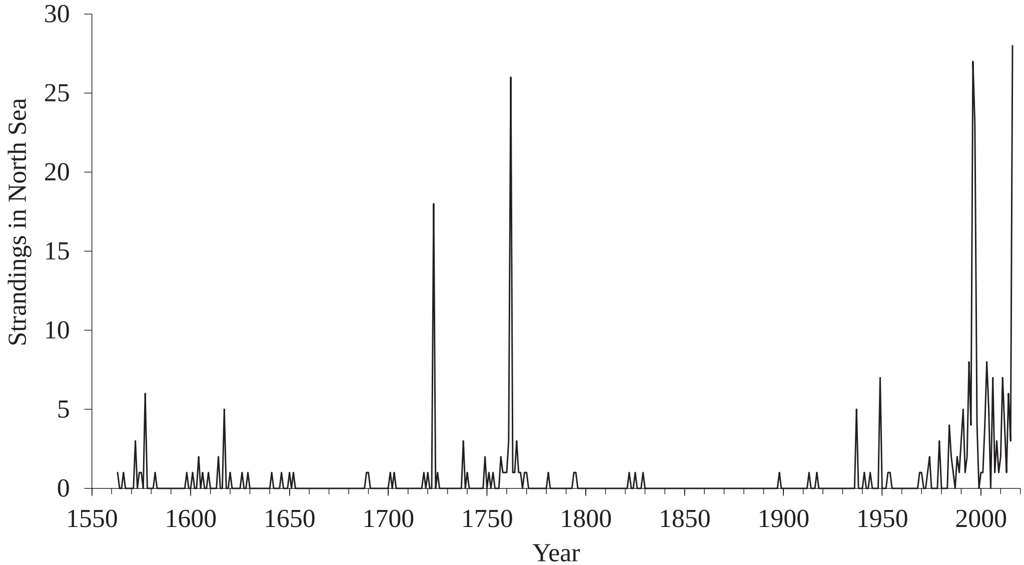

Figure 1. Number of strandings of sperm whales on North Sea coasts per calendar year (data from Smeenk 1997; Smeenk & Evans, this volume).

Histioteuthis species (*H. meleagroteuthis* and *H. reversa*). These samples contained no fish remains.

Strandings

Strandings were recorded in 97 of the 454 calendar years in the series. Twenty-five or more animals were recorded in three years (1762, 1996 and 2016). The series assembled by Smeenk & Evans (this volume) ends in February 2016, by which time it was already the year with most recorded stranded sperm whales (28). The annual number of strandings is illustrated in figure 1. Of 312 stranded whales recorded, more than half (162) have stranded in the last 30 years of the series, a period which includes over a quarter (27) of all the years (since 1563) in which strandings were recorded.

A runs test shows the series of occurrences of strandings per year was clearly more clumped than expected by chance alone ($P<0.0005$) for both calendar years and years running from July to June. Over 454 years, around 154 runs would be expected by chance alone whereas the two series contained just 107 and 105 runs, respectively.

Simple correlations between counts, occurrence, and environmental variables are summarised in table 3. No significant relationships were found between strandings number or occurrence and sunspot numbers. The annual NAO with lag 1 had a weak negative effect on the occurrence of strandings in July-June. Icelandic pressure had a weak negative effect on occurrence of strandings. All strandings variables were positively correlated with all temperature variables; correlations with strandings occurrence were generally higher than those with strandings number and there was little difference between correlations for lags 0 and 1 year. The highest correlations were seen with global SST but this is a relatively short series (145 years). It should be noted that these simple correlations do not account for autocorrelation in the times series, and the significance of correlations may thus be overestimated.

The "discovery curves" of the effect of increasing time series length on the strand-

Table 3. Correlations of standings and environmental variables (SST = sea surface temperature, LSAT = land surface air temperature, NAO = North Atlantic Oscillation, recon = reconstruction).

	n	Count (Cal Year)	Occ (Cal Year)	Count (Jul-Jun)	Occ (Jul-Jun)t
n		454	454	453	453
Lag 0					
Annual sunspots	317	-0.034	0.039	0.000	0.056
Winter sunspots	267	-0.031	0.013	0.001	0.036
Annual NAO	192	-0.072	-0.040	0.008	-0.069
Iceland pressure	194	-0.066	-0.149 *	-0.141 .	-0.178 *
Annual LSAT recon	442	0.186 ***	0.216 ***	0.231 ***	0.227 ***
Winter LSAT recon	442	0.098 *	0.133**	0.152 **	0.164 **
Global SST	145	0.465 ***	0.643 ***	0.473 ***	0.632 ***
N Sea SST	145	0.289 ***	0.431 ***	0.374 ***	0.498 ***
N Atlantic SST	145	0.298 ***	0.362 ***	0.286 ***	0.385 ***
Lag 1					
Annual sunspots	316	-0.002	0.039	0.0006	0.032
Winter sunspots	266	0.006	0.025	0.013	0.003
Annual NAO	191	-0.069	-0.129	-0.098	-0.148 *
Iceland pressure	193	-0.053	-0.072	-0.103	-0.035
Annual LSAT recon	442	0.205 ***	0.174 ***	0.177 ***	0.213 ***
Winter LSAT recon	442	0.148 **	0.138 **	0.097 *	0.167 ***
Global SST	145	0.450 ***	0.651 ***	0.450 ***	0.653 ***
N Sea SST	145	0.268 **	0.465 ***	0.298 ***	0.472 ***
N Atlantic SST	145	0.257 **	0.369 ***	0.246 **	0.397 ***

ings occurrence-environment correlations revealed relatively stable patterns when using the temperature reconstructions and sunspot series (the longest time series available). In the forwards curves (running from 1563 to 2016), these correlations are seen to change in the last 20-30 years of the series. The remaining (shorter) series achieved less stability and again shoe marked changes in the final 20-30 years of the series (figure 2).

GAMM results (table 4) showed no significant relationships between occurrence of strandings and sunspot numbers, NAO or Icelandic air pressure. Some positive relationships were observed with temperature series, the strongest being with the global sea surface temperature series (see also figure 3). However, as noted above, these were the shortest time series (145 years) and, as such, the high correlations with the reconstructed European land surface air temperature series (442 years) is therefore more noteworthy.

Discussion

Diet

Gonatus fabricii is an important resource for many upper level predators in the northeast Atlantic and Arctic (Bjørke 2001) and it has been consistently identified as the main component of prey remains in stomach contents of sperm whales stranded on North Sea coasts (Lick et al. 1995, Clarke 1997, Santos et al. 1999, 2002, Simon et al. 2003).

Comparison with results from northeast Atlantic coasts outside the North Sea is limited by lack of information. Three samples from west Scotland were quite similar to those

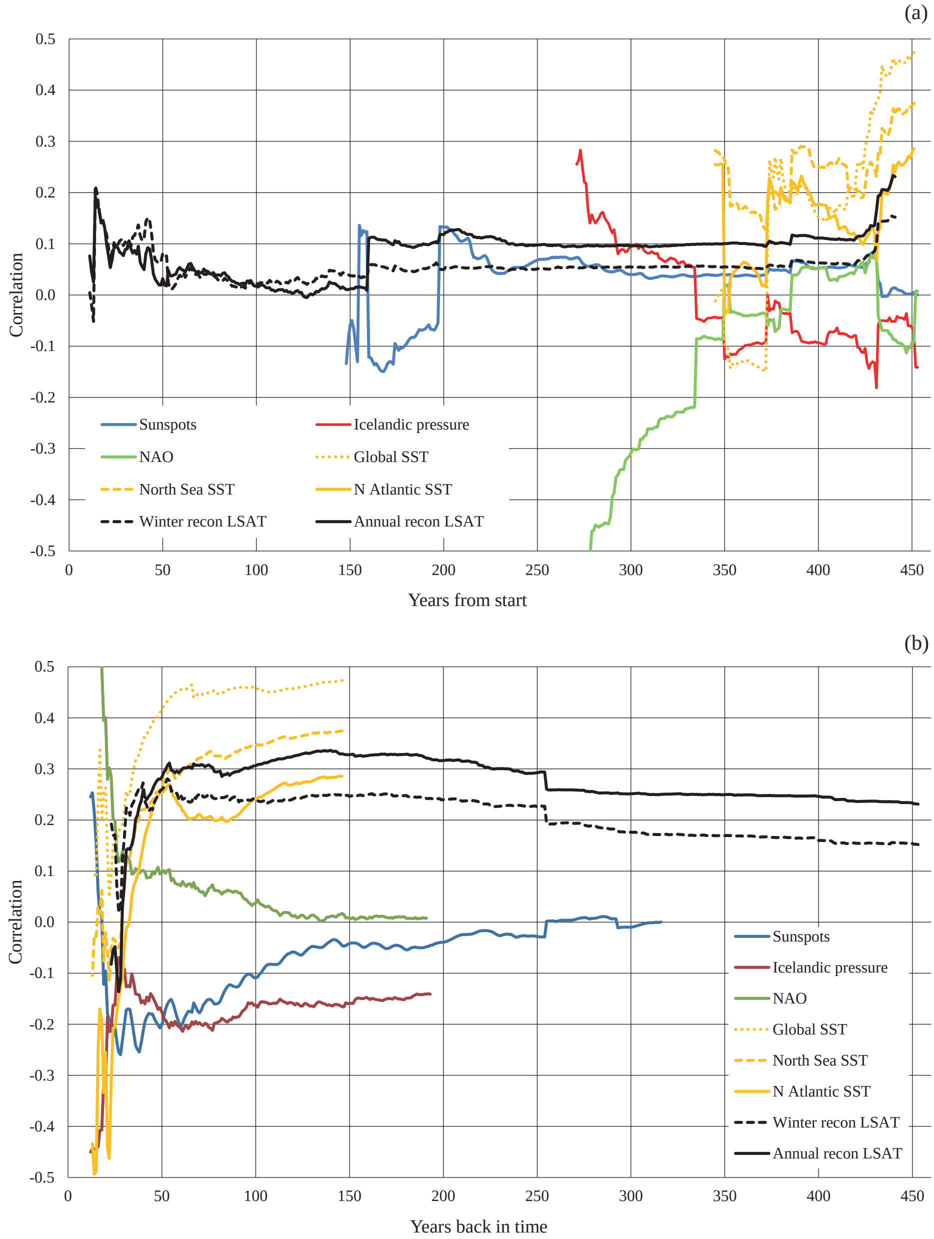

Figure 2. Correlation "discovery curves", running (a) forwards and (b) backwards through time, for occurrence of strandings (July to June) versus selected environmental variables. For each year the correlation refers to the period from when recording of the two variables first coincided through to the year in question. The forwards curves run from the first year of the environmental series towards the present day while the backwards curves start where the series end (i.e. close to the present day) and run backwards through time. The first 10 years of each correlation series are not illustrated (because year to year variation in correlation values is much higher when the series are still very short).

Table 4. GAMM results. For each model the effect of the explanatory variable is described by the degrees of freedom (1 indicates a linear fit, higher values define curves of increasing complexity), probability value (indicating significance) and the direction of the relationship (if significant). Models were fitted using either contemporaneous values of environmental series for each year (lag 0) or values from the previous year (lag 1). All models assume that there is temporal autocorrelation between annual occurrence of strandings and occurrence of strandings in the previous year. (NAO = North Atlantic Oscillation, LSAT = Land Surface Air Temperature, SST = Sea Surface Temperature).

	n	Occ (Cal Year)	Occ (Jul-Jun)
n		454	453
Lag 0			
Annual sunspots	317	1, *P*=0.356	1, *P*=0.409
Winter sunspots	267	1, *P*=0.785	1, *P*=0.570
Annual NAO	192	1, *P*=0.713	1, *P*=0.666
Iceland pressure	194	1, *P*=0.396	1, *P*=0.0540
Annual LSAT recon	442	1.536, *P*=0.0018, +	1.595, *P*=0.0017, +
Winter LSAT recon	442	1, *P*=0.0653	1, *P*=0.0282, +
Global SST	145	1, *P*<0.0001, +	1, *P*<0.0001, +
N Sea SST	145	1.972, *P*=0.0470, +	1, *P*=0.0001, +
N Atlantic SST	145	1.479, *P*=0.0868	1, *P*=0.0146, +
Lag 1			
Annual sunspots	316	1, *P*=0.865	1, *P*=0.686
Winter sunspots	266	1, *P*=0.542	1, *P*=0.954
Annual NAO	191	1, *P*=0.376	1, *P*=0.224
Iceland pressure	193	1, *P*=0.742	1, *P*=0.213
Annual LSAT recon	442	2.116, *P*=0.0032, +	1.005, *P*=0.0025, +
Winter LSAT recon	442	1.629, *P*=0.0695	1, *P*=0.0142, +
Global SST	145	1, *P*<0.0001, +	1, *P*<0.0001, +
N Sea SST	145	1, *P*=0.0041, +	1, *P*=0.0011, +
N Atlantic SST	145	1, *P*=0.0103, +	1, *P*=0.0022, +

from the North Sea while two from Ireland showed greater differences, containing few or no *Gonatus* and including several cephalopod species not recorded from North Sea strandings. The stomach of a juvenile (length 700 cm) sperm whale stranded in Galicia NW Spain on 4 March 1993 contained a few beaks of *Histioteuthis* sp., *Mastigoteuthis* sp., *Chiroteuthis* sp., *Teuthowenia megalops* and *Octopus vulgaris* (Gonzalez et al. 2004) – all but the last of these also occurred in stomach contents of individuals stranded on the west (Atlantic) coast of Ireland (outside the distribution range of *Octopus vulgaris*) (Santos et al. 2002, 2006).

One notable difference between North Sea and Atlantic samples in the present study, albeit again based on a small sample size, was the presence of fish and coastal cephalopod species only in the North Sea samples, suggesting that feeding on such species is unusual, perhaps occurring *in extremis* in animals "trapped" in the shallow North Sea. However, although studies on sperm whale diet based on stranded animals almost invariably indicate them to have fed mainly on cephalopods, it is worth remembering that studies undertaken during the whaling era found evidence of extensive predation on fish (e.g. Martin & Clarke 1986).

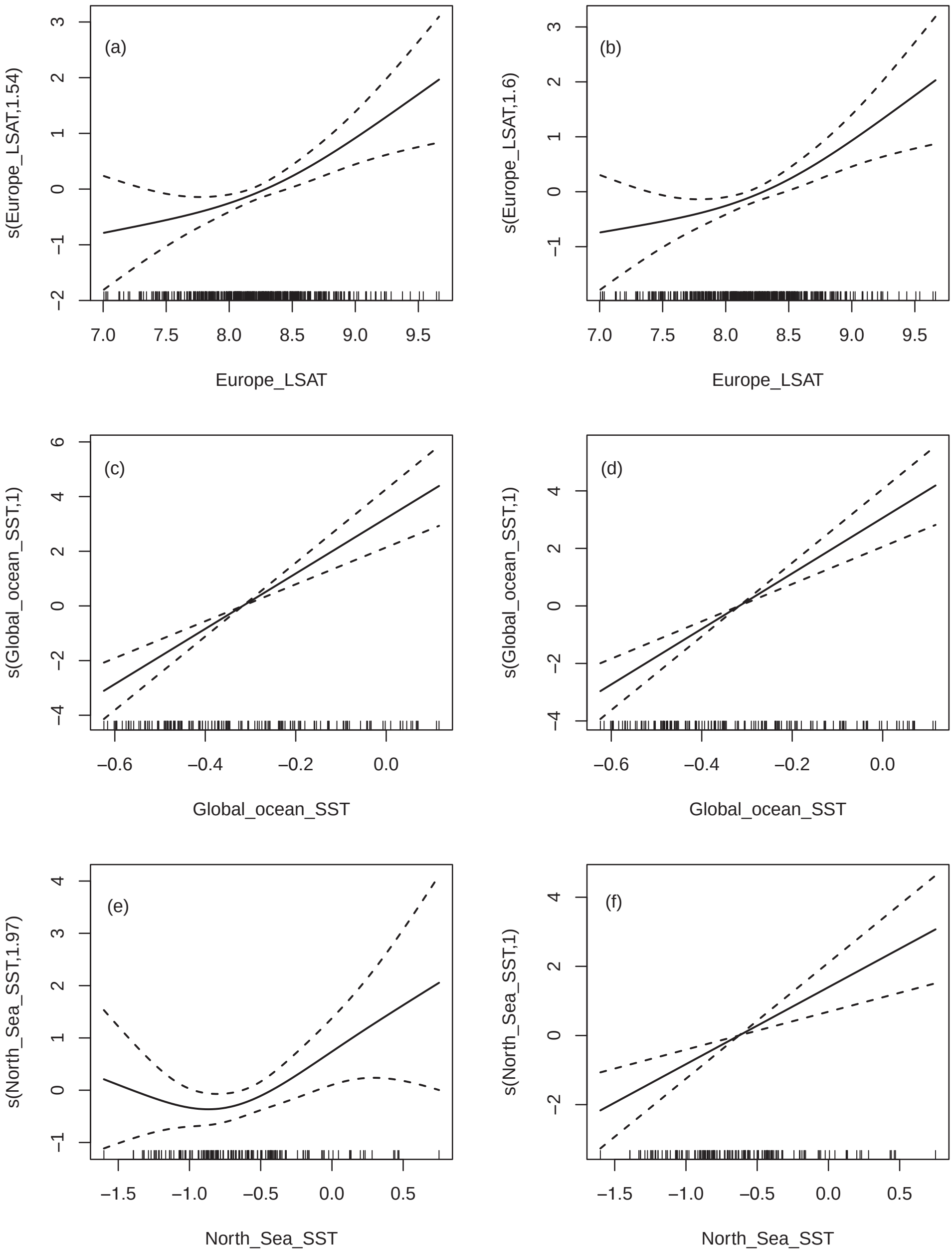

Figure 3. Plots of GAMM smoothers illustrating modelled effects of temperature variables on the occurrence of sperm whale strandings in the North Sea, per calendar year (a,c,e) and per year from July to June (b,d,f): reconstructed annual European land surface air temperature (LSAT) to 2004 (a, b), global sea surface temperature (SST) 1870-2014) (c, d) and North Sea SST 1870-2014 (e,f). In all case the upward slope of the relationhip indicates a positive effect of temperature on the occurrence of strandings. Results are shown for time-lag zero. The "rug plot" of lines along the x-axis indicates the variation of data density as a function of the value of the x-axis variable. Sample sizes associated with each plot are given in table 3.

Strandings

Since we published on this topic in 2007, the strandings series has obviously been extended by another decade. However, the only "environmental" data series available for the entire 450-year period are those for sunspots. As previously, statistical modelling carried out in this paper revealed no relationship between strandings and numbers of sunspots.

Positive relationships were again found with temperature series, relatively weak with reconstructed (land surface air) temperature in Europe over the majority of the study period but stronger for (sea surface) temperature in the last 150 years. One problem with this finding is that, at least in the most recent part of the series, we are looking at unidirectional change in the incidence of strandings, i.e. a phenomenon that appears to be increasingly frequent. Thus, other phenomena that are also continuously increasing will appear to be related, making it harder to avoid coincidental relationships. The marked increase in the incidence of strandings over the last 20-30 years suggests a superficial parallel to the famous "hockey stick" fit to long-term temperature records (Mann et al. 1998). What is evident from the correlation discovery curves is that what has happened with strandings over the last few decades, differs from what has gone before. Our new analysis again suggests that there is a relationship with the sea and land surface temperature signals but the underlying mechanism, if this relationship is indeed non-coincidental, is unclear.

It is tempting to ascribe the increased frequency of strandings in the last 30 years to the recovery of the North Atlantic sperm whale population. However, a longer-term perspective casts doubt on this interpretation. Whitehead´s (2002) reconstruction of global sperm whale numbers suggests that whaling mortality led to only a gradual decline from 1700 to around 1950, when the unprecedented catches achieved by the modern whale hunting (peaking in 1964; Rice 1989) caused a sharp decline in abundance. In the North Atlantic, catches reached a peak between 1952 and 1981, and Hiby & Harwood (1981) suggest that numbers declined continuously from 1905 to 1979, especially from 1940 onwards. The cessation of whaling should have allowed some recovery. The global population trajectory proposed by Whitehead (2002) indicates that the population in 2000 would still have been well below the 1950 abundance level and it seems likely that this would also be true in the North Atlantic. Thus, the only part of this story apparent in the strandings record is the increase in strandings in the last three decades as abundance rose from a historical low point.

In conclusion, it is perhaps most likely that multiple phenomena are at work and the functioning of the North Sea sperm whale trap does not have a single simple explanation.

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Samenvatting

Analyses in heden en verleden van het voedsel en de strandingen van potvissen (*Physeter macrocephalus*) in de Noordzee

Het toenemende aantal strandingen van potvissen gedurende de winter in de Noordzee heeft geleid tot veel speculatie over de oorzaken van dit fenomeen. Onder gebruikmaking van een onlangs bijgewerkte lijst van strandingen van de potvis in de Noordzee werd met behulp van zogenoemde *generalised additive mixed models* (statistische technieken waarmee o.a. de ontwikkeling van een populatie kan worden voorspeld) onderzocht wat de mogelijke rol is van diverse milieuomstandigheden die effect zouden kunnen hebben op het binnenzwemmen van de Noordzee door potvissen en/of op hun strandingen rond de Noordzee. Het optreden van zonnevlekken, de *North Atlantic Oscillation* (NAO – een weerfenomeen waarbij gelet wordt op de luchtdrukverschillen op zeeniveau tussen IJsland en de Azoren) index of alleen de luchtdruk op zeeniveau rond IJsland bleken nauwelijks tot geen invloed te hebben. Diverse indexen voor de temperatuur op zee en land vertonen een positieve correlatie met het

optreden van strandingen.

Echter, er zijn daarnaast aanwijzingen voor het optreden van veranderingen gedurende de afgelopen dertig jaar in de correlatie tussen strandingen en milieuvariabelen en, gezien het ontbreken van een duidelijk mechanisme waarmee de relatie tussen de temperatuur en de strandingen kan worden verklaard, is het van belang om in te zien dat verschillende processen kunnen bijdragen aan de veranderingen in de strandingen. Bovendien moet rekening worden gehouden met het herstel van de potvissenstand na het stoppen van de commerciële walvisvangst aan het eind van de 20ste eeuw. Temperatuurveranderingen kunnen namelijk ook invloed hebben gehad op de prooidiersoorten van potvissen en hierdoor veroorzaakte veranderingen in het voorkomen van deze soorten kunnen óók een verklaring opleveren voor veranderingen in het patroon van de potvisstrandingen. Daarom wordt in dit artikel eerder voedselonderzoek herhaald onder gebruikmaking de oorspronkelijke gegevens, aangevuld met nieuw verzamelde gegevens. Hieruit komt naar voren dat de diepzee-inktvis *Gonatus fabricii* (een soort die voorkomt in de noordelijke delen van de Atlantische Oceaan, zoals ook de Engelse naam - *Boreoatlantic armhook squid* - aangeeft) in de maaginhouden van rond de Noordzee gestrande potvissen blijft overheersen. Hierbij wordt opgemerkt dat er ook restanten van in de Noordzee levende soorten inktvissen, zij het in kleine hoeveelheden, werden aangetroffen, op basis waarvan mag worden aangenomen dat er ook sprake is van enig foerageren in de Noordzee zelf. De conclusie wordt getrokken dat er geen sprake is van één verklaring voor het verschijnsel dat de Noordzee als een fuik voor potvissen functioneert maar dat we hierbij zeer waarschijnlijk te maken hebben met een combinatie van oorzaken.

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Cetacean stranding records along the Danish coastline: records for the period 2008-2017 and a comparative review

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Abstract: For the period 2008-2017, finds of stranded cetaceans along the Danish coastline are listed and reviewed in comparison to the preceding 40-year period (1968-2007). The harbour porpoise (*Phocoena phocoena*) was by far the most commonly stranded species with a total of 1177 individuals for the period 2008-2017. Of these, 62.4% (*n*=735) originated from the North Sea and Skagerrak coastlines, i.e. the outer Danish waters (ODW), 37.0% (*n*=435) from the Kattegat and Belt Sea, i.e. the inner Danish waters (IDW), and 0.6% (*n*=7) from the waters around Bornholm (WAB), i.e. the Baltic Sea proper. Due to the large number and the amount of information for these records only a summary is given. In addition, 90 strandings of twelve other cetacean species occurred between 2008-2017. These comprise 49 white-beaked dolphins (*Lagenorhynchus albirostris*), three white-sided dolphins (*Leucopleurus acutus*), seven common dolphins (*Delphinus delphis*), a striped dolphin (*Stenella coeruleoalba*), a Risso's dolphin (*Grampus griseus*), four long-finned pilot whales (*Globicephala melas*), a killer whale (*Orcinus orca*), a Sowerby's beaked whale (*Mesoplodon bidens*), six sperm whales (*Physeter macrocephalus*), 14 minke whales (*Balaenoptera acutorostrata*), two fin whales (*Balaenoptera physalus*) and a humpback whale (*Megaptera novaeangliae*). During the last 50 years (1968-2017) five additional cetacean species have stranded on the Danish coasts: bottlenose dolphin (*Tursiops truncatus*) in 1968, 1975 and 1976, beluga (*Delphinapterus leucas*) in 1976 and 1987, northern bottlenose whale (*Hyperoodon ampullatus*) in 1969 and 1998, Bryde's whale (*Balaenoptera brydei*) in 2000, and sei whale (*Balaenoptera borealis*) in 1980. The cetacean fauna around Denmark falls into the following categories: 1. native species such as the harbour porpoise, white-beaked dolphin, and minke whale; 2. resilient visitors, i.e. species such as common dolphin, fin whale and humpback whale that during their occurrences adapt well to altered environmental conditions encountered; and 3. erratic stragglers of oceanic, pelagic origin failing to adapt, such as long-finned pilot whale, Sowerby's beaked whale and sperm whale.

Keywords: cetaceans, strandings, Denmark, comparative review.

Introduction

Cetacean strandings constitute one of the most important sources for the study of regional and temporal cetacean diversity and the retrieval of basic population parameters, and hence nature management and conservation measures. The first comprehensive review covering the waters around Denmark and the period 1575-1992 was provided by Kinze (1995) with subsequent compilations and reviews covering the periods 1993-1997 (Kinze et al. 1998) and 1998-2007 (Kinze et al. 2010). For the most common species, the harbour porpoise (*Phocoena phocoena*), comparable quantitative data were not collected before the year 2008 and are therefore not available for an analysis. This article presents a detailed overview of cetacean strandings for the entire Danish coastline covering the period 2008-2017 and provides a comparative analysis with the preceding four decadal periods (1968-2007).

Material and methods

Although a formal stranding network for rare sea creatures was set up in Denmark as early as 1885, for many years specimens were not collected systematically and compilations of records rather restricted to summarising accounts (Tauber 1880, Winge 1899, 1908, Degerbøl 1935). Bondesen (1951, 1977) published popular overviews of cetacean strandings including records dating back to the 17th century, but collecting efforts were continuously hampered by the lack of funds, and for the more common species also the lack of attention. Only in 1980, the Zoological Museum of Copenhagen (now the Natural History Museum of Denmark) began to register cetacean strandings systematically and to collect as many non-phocoenid specimens as possible. These efforts provided the basis for the Danish Contingency Plan which was launched in 1993, and has been in operation ever since as a co-operative network between the Natural History Museum of Denmark, the Fisheries and Maritime Museum, Esbjerg and the Danish Environmental Protection Agency. Recently, also the Department of Bioscience at University of Aarhus and DTU Vet National Veterinary Institute became partners. Annual or biannual reports have been published since 2003 (Thøstesen 2018). Having no dedicated personnel to patrol the beaches, the records rely strongly on observations by the public and

Table 1. Summary of harbour porpoise strandings for the period 2008-2017 divided by zoo-geographical region outer Danish waters (ODW), inner Danish waters (IDW) and the waters around Bornholm (WAB)

	Zoo-geographical region			
Year	ODW	IDW	WAB	Total
2008	149	75	0	224
2009	49	84	1	134
2010	73	46	0	119
2011	97	50	1	148
2012	66	52	3	121
2013	102	34	0	136
2014	78	43	0	121
2015	9	13	1	23
2016	57	19	1	77
2017	55	19	0	74
Total	735	435	7	1177

local game wardens and numbers thus constitute a minimum. For several cases, strandings were preceded by sightings near the stranding location, in which case the date of the observation was retained in the record.

The present study summarises the cetacean strandings for the period 2008-2017 and compares with four preceding decadal periods (1968-2007) – for each species and in a zoogeographical context.

Results and review

Harbour porpoise (*Phocoena phocoena*)

The harbour porpoise is regarded as the only native cetacean species occurring in all waters around Denmark, i.e. both along the North Sea and Skagerrak coastlines (ODW=outer Danish waters), the Kattegat and Belt Sea coastlines (IDW =inner Danish waters), and the waters around Bornholm (WAB part of the Baltic Sea proper). In contrast to other national compilations in adjacent countries, in Denmark harbour porpoise stranding data were not systematically collected and compiled before 2008. Dedicated schemes during

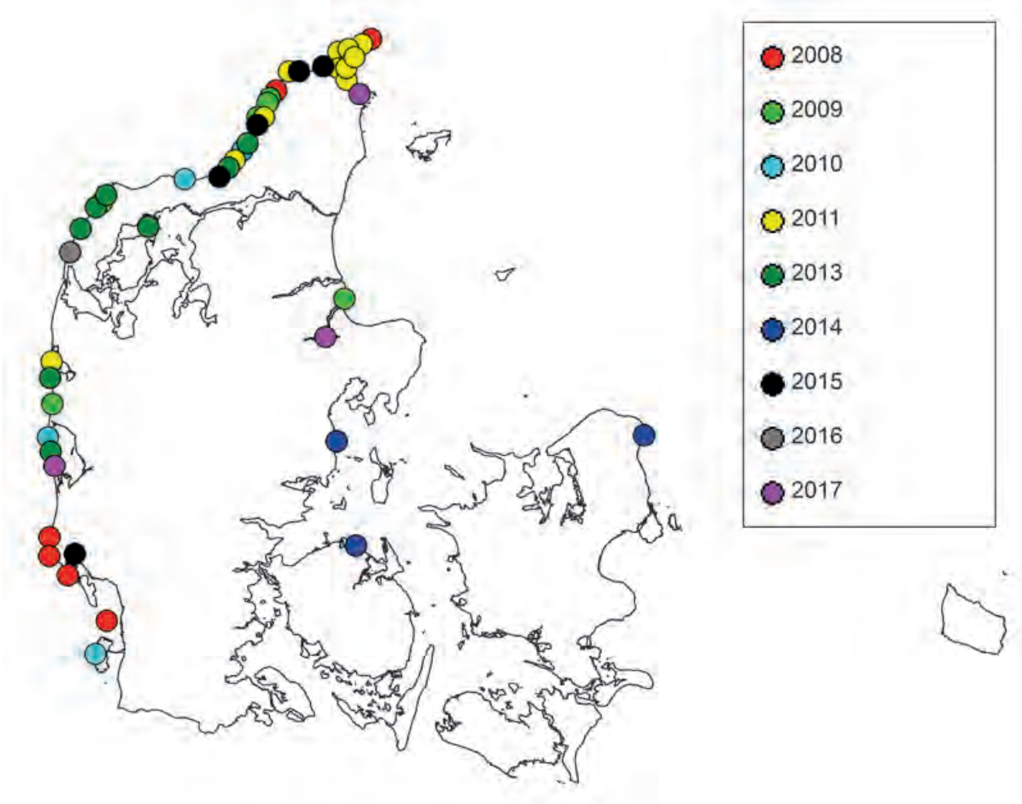

Figure 1. Strandings of white-beaked dolphin recorded between 2008-2017.

certain periods collected larger numbers of specimens, such as *Projekt Marsvin* (1983-1990; Kinze 1990) and *Fokus på Hvaler i Danmark* (2000-2003; Kinze et al. 2003).

For the years 2008-2017 a total of 1177 animals was documented (table 1). Geographically subdivided, they fall into 735 (62.4%) animals from the ODW, 435 (37.0%) from the IDW, and just 7 (0.6%) from the WAB. While the ODW and the WAB exhibit relatively straight coastlines of 606 km and 158 km, respectively, the inner Danish waters constitute an archipelago of islands, straits and peninsulas with a total coastline approaching 8000 km in length. Thus, stranding figures from this latter region are certainly underestimated.

For 2015-2017, figures are not comparable to the preceding years due to a break in the reporting effort. Between 2008 and 2014, figures fluctuated between 121 and 224 records per year.

White-beaked dolphin (*Lagenorhynchus albirostris*)

Once considered a rare northern species, the white-beaked dolphin now is regarded as native to the outer Danish waters, i.e. the Skagerrak and the north-eastern North Sea (figure 1). It is by far the most frequent non-phocoenid cetacean in the stranding record (table 2, figure 2). The most recent period from 2008-2017 yielded 49 individuals, the second highest total after the preceding 10-year period. Noteworthy is that the year 2012 did not yield a single specimen. Just four individuals (8% of the total) originated from the inner Danish waters south of Skagen. The comparable figures for the period 1998-2007 for the inner Danish waters were 8 out of 69 animals (11.6%) and 6 out of 41 animals (14.6%) for 1988-1997.

Table 2. Summary of cetacean strandings along the Danish coastline over a 50-year period from 1968 to 2017.

Species	Abbreviation	First record	1968-1977	1978-1987	1988-1997	1998-2007	2008-2017	Total
White-beaked dolphin	WBD	1845	6	19	41	69	49	184
White-sided dolphin	WSD	1942	1	0	2	6	3	11
Common dolphin	CMD	1865	0	1	0	8	7	16
Striped dolphin	STD	1998	0	0	0	1	1	2
Bottlenose dolphin	BND	1844	4	0	0	0	0	4
Long-finned pilot whale	LFP	1863	0	2	8	4	4	18
Killer whale	KIW	1679	1	1	2	1	1	6
Risso's dolpin	RID	1938	0	0	0	0	1	1
Beluga	BEW	1903	1	1	0	0	0	2
Sowerby's beaked whale	SBW	1880	1	0	1	0	1	3
Bottlenose whale	NBW	1838	1	1	1	0	0	3
Sperm whale	SPW	1572	1	4	39	1	7	51
Minke whale	MIW	1824	3	5	6	18	14	43
Bryde's whale	BRW	2000	0	0	0	1	0	1
Sei whale	SEW	1955	0	1	0	0	0	1
Fin whale	FIW	1603	0	0	0	0	2	2
Humpback whale	HUW	1806	0	0	0	0	1	1
Total			19	35	100	109	90	349

Two pregnant females were documented; their foetuses measured 43 cm (18 January) and 35 cm (27 November), adding to the rather limited knowledge of reproduction in this species.

White-sided dolphin (*Leucopleurus acutus*)

The white-sided dolphin, formerly known as *Lagenorhynchus acutus*, has a more pelagic habitat than the white-beaked dolphin. Surprisingly therefore, it was documented for the first time in Denmark in the inner Danish waters in 1942 (Isefjord, Sealand; Degerbøl 1943). Between 1988 and 2007 finds mirror the general distribution of the species in the adjacent deeper parts of the North Sea along the North Sea and Skagerrak coastlines since all strandings have hitherto taken place here. In the present period, two strandings have been documented from the North Sea coastline and, interestingly, also one from the inner Danish waters (figure 3). Overall, this is a decline in comparison to the preceding 10-year period and the same figure as for 1988-97 (table 2).

Common dolphin (*Delphinus delphis*)

The first documented common dolphin specimen from Denmark originates from the year 1865 (Kinze 1995). It is a shelf species usually inhabiting warmer and more southerly waters than the seas around Denmark. During certain times, however, an influx has been noted with individuals taking residence for longer periods. Sightings of small schools and individual animals have been reported since about 1990, and strandings occurred almost every year (Jensen & Kinze 2005) (table 2). For the years 2008-2017, individuals were found both in ODW and IDW (figure 3; appendix).

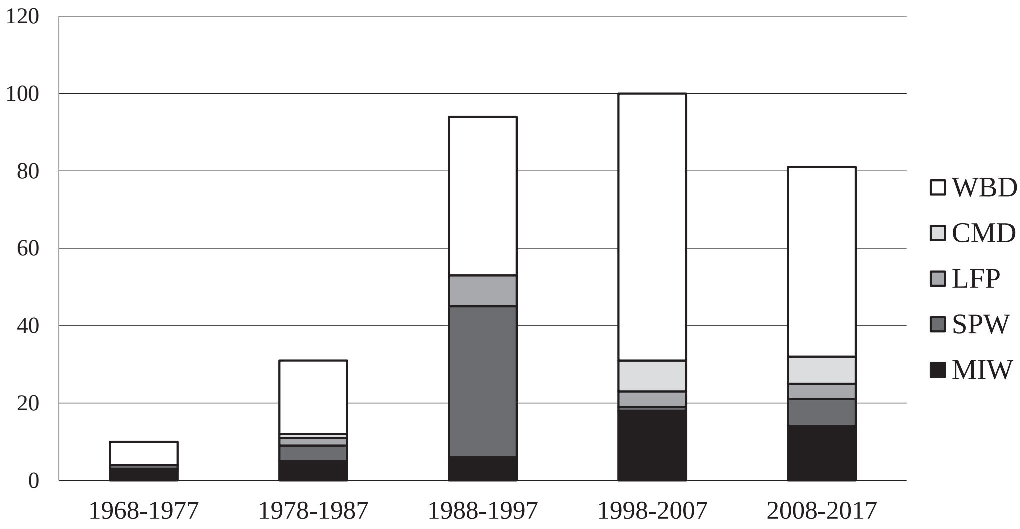

Figure 2. Number of recorded strandings in Denmark during 1968-2017 summarised for the five most common non-phocoenid species; white-beaked dolphin (WBD, 52%), sperm whale (SPW, 15%), minke whale (MIW, 12%), long-finned pilot whale (LFP, 5%) and common dolphin (CMD, 4%).

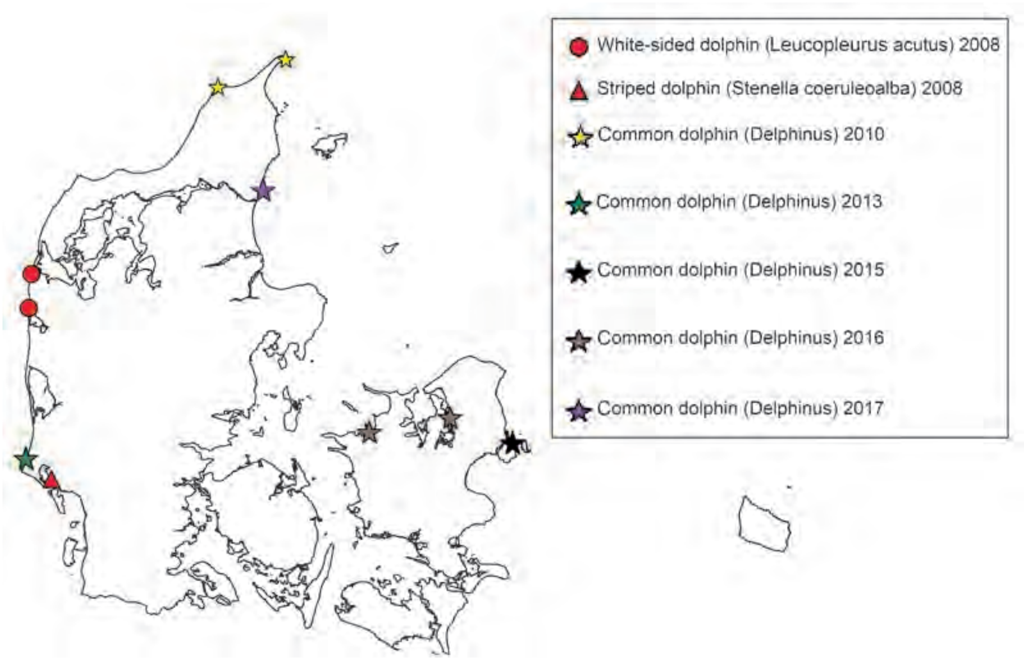

Figure 3. Strandings of white-sided dolphin, common dolphin and striped dolphin recorded between 2008-2017.

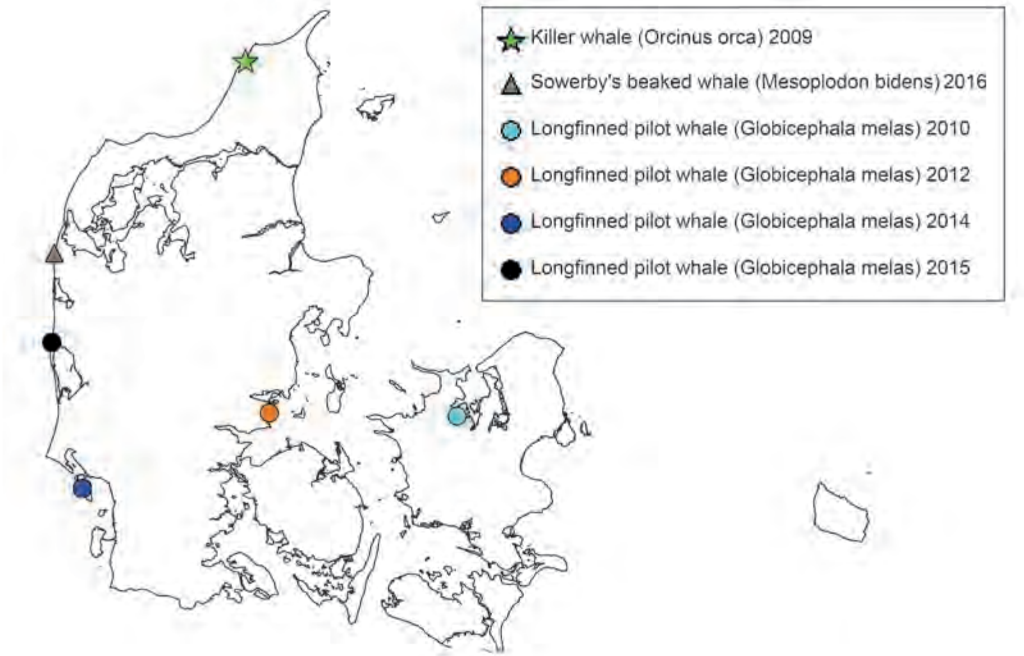

Figure 4. Strandings of killer whale, long-finned pilot whale and Sowerby's beaked whale recorded between 2008-2017.

Striped dolphin (*Stenella coeruleoalba*)

The striped dolphin is a tropical and subtropical pelagic species, only recorded from the Danish coasts twice, in 1998 and 2008 (Kinze et al. 2000, Thøstesen et al. 2009) (table 2, figure 3). Additionally, a single individual was sighted in 2000 near the island of Anholt (Kinze 2007).

Bottlenose dolphin (*Tursiops truncatus*)

The bottlenose dolphin has a long history of occurrence in the North Sea, yet there are rather few recorded strandings from the Danish North Sea coast (table 2). There are only two confirmed records, from Manø in 1957 and from Trans Strand in 1968, and in addition a dubious record from Blåvandshuk in 1847 for which verification has not been possible (Kinze 1995). The first record of this species from in the inner Danish waters was documented in 1844 when a small school was killed at Frederiksgave near Assens in the Little Belt (Kinze 1995). In 1870, there was a large influx into the Baltic Sea, yielding 49 individuals at the porpoise catch site at Gamborg Fjord, and in the 1940s and 1970s, there were periodical occurrences. In 1998, a specimen was found in the Baltic proper on the border between Lithuania and Latvia. Most recently, in 2015-2016, a small school entered the Baltic Sea, with one female stranding on the island of Öland, Sweden, and three live males observed at various localities in the inner Danish waters (Kinze & Thøstesen 2016).

Long-finned pilot whale (*Globicephala melas*)

The long-finned pilot whale is a pelagic, primarily squid eating boreal species rather commonly occurring in the Skagerrak. The first documented find originated from the Isefjord area (Reinhardt 1864). Quite commonly, there are sightings in the deeper parts of the Skagerrak have been reported, hence most strandings have taken place along the Skagerrak coasts, with occasional records further south along the Danish North Sea coastline. For the period 2008-2017, two records originated from the inner Danish waters and two from the North Sea coast of Denmark (figure 4, table 2).

Killer whale (*Orcinus orca*)

The killer whale used to share with the minke whale the position of third most common cetacean species along the Danish coasts. However, the fifty-year period 1968-2017 produced six specimens (including one record between 2008 and 2017; figure 4), slightly less than the preceding periods 1868-1917 and 1918-1967, each providing nine records (Kinze 1995; table 1). Taking into account the increased effort and hence possibility of detection, we regard this as an indication for a decline in occurrence.

Risso's Dolphin (*Grampus griseus*)

The Risso's dolphin is a rare visitor to the inner Danish waters where it has been encountered only three times: twice in 1938 (Degerbøl 1939) and once in 2007 (Kinze et al. 2010; table 1). Due to its teuthophagic habit, it should be considered an erratic species. Likewise, there are few records of the species from adjacent waters, with a single find from the Swedish Kattegat coast in 1927 (Lepiksaar 1966) and two German records from the North Sea coast, both for the year 1873 (Möbius 1873).

Beluga (*Delphinapterus leucas*)

The beluga is an arctic species with a preference for coastal habitats, but extra-limital occurrences in adjacent temperate waters are not infrequent. Jensen et al. (1987) and Kinze (1988) reviewed the occurrences in Danish waters, describing several historic intrusions of belugas through Danish straits into the Baltic Sea proper in 1841, 1869, 1884 and from 1903-1908 (Kinze et al. 2011). More recently, the species has been sighted in 1995 and 2012 in Danish waters, and in 2016 in adjacent Swedish waters (Kinze 2007, Jensen 2012, Lysen 2016). Due to its great resilience to cope with even complex coastal conditions, individual belugas may often survive their beaching and get free, and in contrast to almost all other cetacean species, belugas may be underrepresented in the stranding record (considering strandings as an indicator of occurrence), because sightings may occur much more frequently than fatal strandings. For instance, during the fifty-year period from 1968-2017 only three dead corpses have been recorded (in 1964, 1976 and 1987), all originating from incidental catches in fishing gear (Kinze 1995) (table 2).

Sowerby's beaked whale (*Mesoplodon bidens*)

Sowerby's beaked whale is an oceanic species encountered irregularly along the Danish coasts, mostly when entering from the deeper parts of the Skagerrak. The period 2008-2017 only yielded a single specimen, a young male and presumably the youngest individual so far encountered along the Danish coastline (table 1, figure 4). During 2015, another individual swam undetected through the Danish straits and was first sighted off the German Baltic coast. It was eventually found dead near Karlskrona on the Swedish Baltic Sea coast (Dähne 2015, Lyrholm 2015).

Bottlenose whale (*Hyperoodon ampullatus*)

The bottlenose whale is a North Atlantic oceanic species with infrequent occurrence in

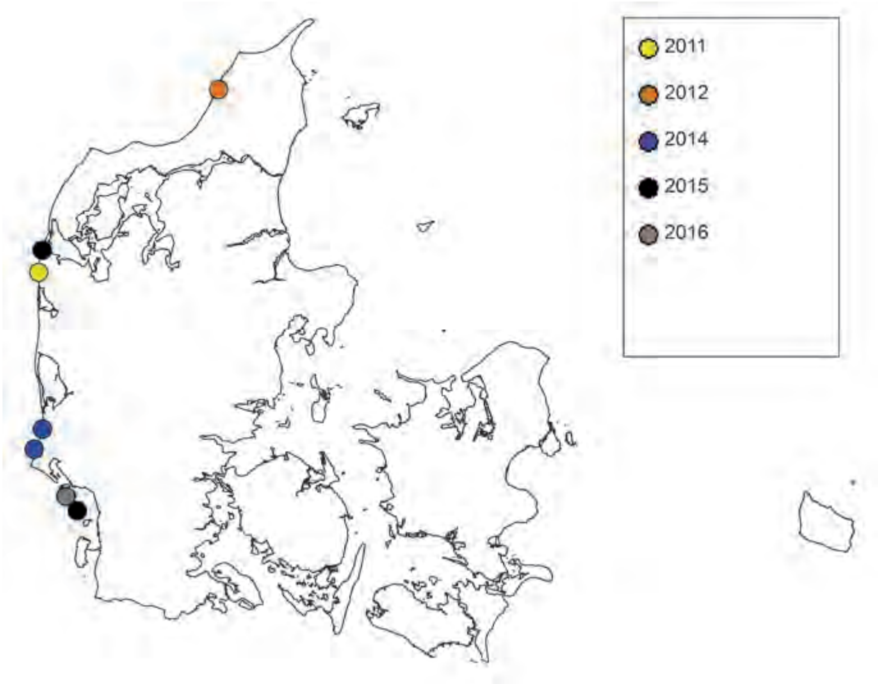

Figure 5. Strandings of sperm whale recorded between 2008-2017.

Danish waters. The latest stranding took place in the inner waters on the island of Tåsinge in 1998, while in 2000 there was a live stranding near Hundested at the entrance of the Isefjord on the island of Sealand (table 2). A rescue operation prevented a fatal stranding. The occurrence of this species in Danish and adjacent waters can be traced back in time to at least 1661, with a catch in the harbour of Aabenraa, Little Belt coast of Jutland (Kinze et al. 2011), and possibly even to 1634 in the Flensborg Fjord (Kinze 1995).

Sperm whale (*Physeter macrocephalus*)

The present period (2008-2017) yielded five single strandings of sperm whales as well as a stranding of two individuals (table 2, figure 5, Hansen et al. 2016). Records from the inner Danish waters are very rare, but in 2016, an individual was sighted in the northern Sound and Kattegat at several localities, and it is believed that it eventually escaped these unfamiliar waters.

It is obvious that during the present period, a relatively large number of strandings occurred when compared with the preceding ten-year period. However, the figure is still very low in comparison to the period before that (1988-1997), totalling 69 individuals with several mass strandings - in particular on the island of Rømø in April 1996 (16 individuals) and December 1997 (13 individuals) (Jensen & Tougaard 1997, 1998, Tougaard & Kinze 1999; table 2). Sperm whale strandings along the Danish North Sea and Skagerrak coast have been documented back to the year 1572 and fit the general North Sea scenario, i.e. all males stranding, and mainly from November through April (Smeenk 1997, Smeenk & Evans, this volume). It is noteworthy that only a single specimen was documented from the Danish west coast in the aftermath of the North Sea mass-stranding event of 2016 (Ijsseldijk et al. 2018).

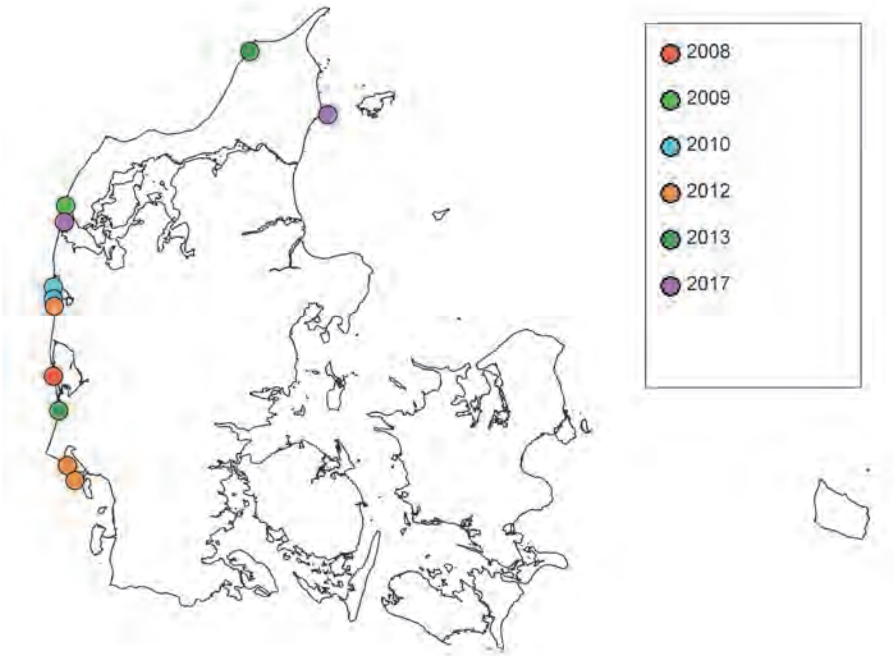

Figure 6. Strandings of minke whale recorded between 2008-2017.

Minke whale (*Balaenoptera acutorostrata*)

The minke whale is to be considered a native species in the central and northern North Sea and hence the outer Danish waters. During 2008-2017, 14 specimens were recorded (16%; *n*=89) (figure 6), further establishing the species as the third most common cetacean species in Danish waters (table 2, figure 2). Corresponding figures for earlier periods are 26% (1998-2007; *n*=69), 15% (1988-1997, *n*=41), 20% (1968-1977, *n*=35), and 16% (1968-1977, *n*=19). The species was not encountered in the inner Danish waters during the period 2008-2017, but several individuals were found stranded on the German and Swedish Baltic coasts as well as sighted in the area (M. Dähne, personal communication, www.valar.se). Earlier ten-year periods yielded five (1998-2007), one (1988-1997), two (1978-1987) and two (1968-1977) individuals.

Bryde's whale (*Balaenoptera brydei*)

This subtropical and tropical pelagic species was documented from the inner Danish waters in 2000 (Kinze 2006; table 2). In addition, there is a likely preceding occurrence from the German Baltic coast in 1944 (Kinze et al. 2011), but, otherwise, the species is extremely rare in northern Europe.

Sei whale (*Balaenoptera borealis*)

This pelagic species was encountered in 1955 for the first time in Danish waters on the island of Tåsinge, inner Danish waters, and again in 1980 on the northern shore of the island of Als, when a heavily decayed whale corpse could be identified as sei whale, based on skeletal features (Kinze 1995). Remarkably, the type specimen of the species originates from a 1819 stranding in the Baltic Sea (Grömitz, Schleswig-Holstein, Germany).

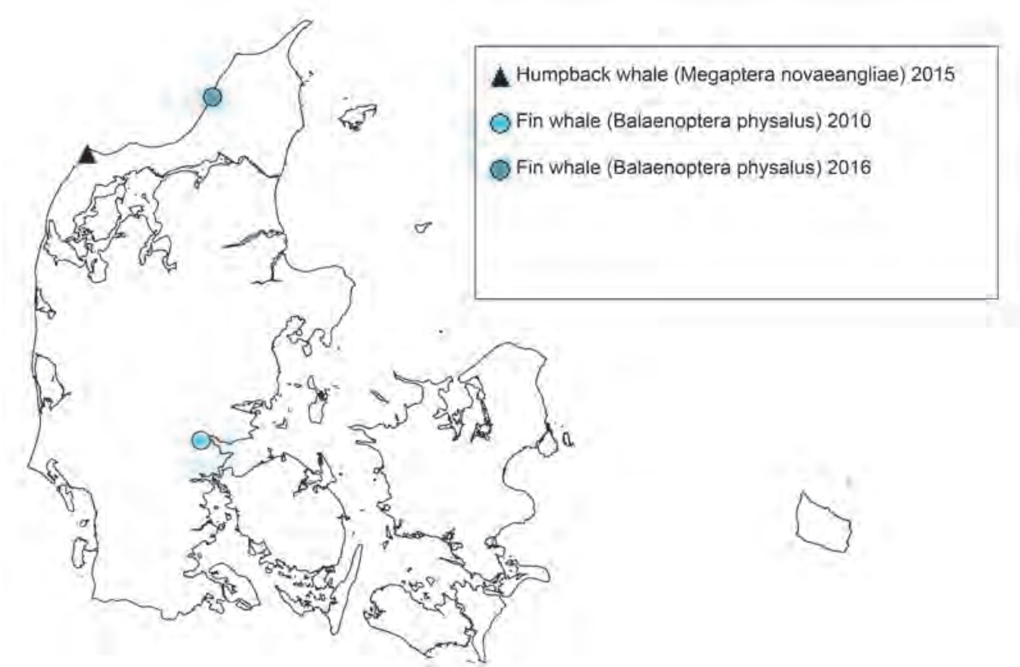

Figure 7. Strandings of fin whale and humpback whale recorded between 2008-2017.

Fin whale (*Balaenoptera physalus*)

Fin whales were found stranded on two occasions: in 2010 and 2016, in the inner Danish waters and on the Skagerrak coastline, respectively (table 2, figure 7). The species had last been recorded stranded in 1958. Both specimens were about 17 m long, but of very different age. The 2010 individual was very old (120 years, according to Nielsen et al. 2012), but of relatively small size, while the 2016 individual was a maturing and much younger male (Jo et al. 2017). Since 2003, one or two fin whales have been sighted regularly in the inner Danish waters (Jensen et al. 2004, Jensen & Kinze 2010) and three individuals have been found dead on the German and Polish Baltic coasts (Harder et al. 2011). Fin whale intrusions into the Baltic proper have been documented over the last centuries and maybe should not be regarded erratic occurrences, but rather trips exploring new feeding areas since individuals have appeared and reappeared at the same localities to prey on shoaling fish (Jensen & Kinze 2011).

Humpback whale (*Megaptera novaeangliae*)

The humpback whale is a piscivorous baleen whale, but unlike the fin whale, it seems to be an opportunistic feeder without 'fixed' feeding localities (Harder et al. 2011). The humpback whale has rarely been encountered stranded along the Danish coasts. The first record was an animal killed in 1806 near Bornholm in the Danish Baltic Sea (Harder et al. 2011). The second record is from 1905, a stranding on the Skagerrak coast (Kinze 1995). In 2015, only the third stranding was recorded - also in the Danish North Sea, in the Skagerrak (table 2, figure 7). During the present period (in 2008, 2012 and 2014), several sightings of the species have been documented on return trips to and from the Baltic proper (Kinze & Jensen 2015). Earlier periods had also yielded sightings of the species in 1978-1979, 2004, and 2006. A single stranding of a young male occurred in 2003 on the German Baltic seaboard (Harder et al. 2011).

Diversity over time and in space

Species origins

According to Kinze et al. (2001), cetaceans encountered in Danish waters have three "waters of origin" in geographical terms: northerly, native and southerly waters, which climatologically can be classified into subtropical, temperate, and subarctic-arctic waters. In ecological terms, three categories should also be differentiated: coastal and riverine species, shelf species and pelagic species. The first category consists of native species, the second comprises species that appear capable of adapting to the waters around Denmark (referred to here as "resilient"), while the third includes all remaining erratic species. Whether a species is termed "resilient" or "erratic" hence depends on how well it adapts to or copes with altered abiotic and biotic environmental conditions. As discussed in the following text, several species have exhibited increased stranding frequencies in Danish waters, which may reflect range shifts due to climate change or changes in prey abundance, range expansions due to increase in cetacean populations, increased disease prevalence due to pathogens or contaminants, and/or increased attention and recording of stranded animals (table 3).

Table 3. Occurrence of selected cetacean species in the three zoo-geographical regions of Denmark

	Zoo-geographical region		
Species	ODW	IDW	WAB
HBP	N	N	N
WBD	N	R	R
MIW	N	R	E
CMD	R	R	R
BND	R	R	R
KIW	R	R	R
HUW	R	R	R
BEW	R	R	R
FIW	R	R	E
SPW	E	E	E
SBW	E	E	E
WSD	E	E	E
LFP	E	E	E

N = Native, R = Resilient visitors, E = Erratic

Temporal patterns in stranding records

For the period 2008-2017, a total of 90 non-phocoenid cetacean specimens representing ten species have been documented by strandings and a further two species only by sightings, bringing the total to twelve species recorded in Danish waters (table 2; appendix). None of them were new to the Danish fauna list, and three of them – the harbour porpoise, white-beaked dolphin and minke whale – are considered native to Danish waters (Kinze 2007).

During the last 50 years, 18 different cetacean species, including the harbour porpoise, have been encountered, while five species previously recorded in Denmark have remained absent. Species only encountered before 1968 include the narwhal (*Monodon monoceros*), only recorded once in 1960, pygmy killer whale (*Feresa attenuata*) recorded once in 1944, blue whale (*Balaenoptera musculus*), last recorded in 1936, false killer whale (*Pseudorca crassidens*), last recorded in 1935, and northern right whale (*Eubalaena glacialis*), only known from 1838 (Kinze 1995, 2007, 2013).

Zoo-geographical subdivision

In terms of hydrography, the Danish national waters include outer Danish waters forming part of the North Sea and Skagerrak regime, the inner Danish waters consisting of the Kattegat, Belt Sea and Sound, and the waters around Bornholm as an integral part of the Baltic Sea proper. These regions differ in their average water depth, as well as in their distance to the open Atlantic Ocean, leading to an expected gradual decline in number of species recorded from the outer Danish waters via the inner Danish waters to the waters around Bornholm (table 3).

Outer Danish waters

With the exception of the shallow Wadden Sea region dominated by strong tidal fluctuations, the outer Danish waters are characterised by depths greater than 30 m, with deeper waters in particular in the Danish part of the Norwegian Trench within the Skagerrak. The outer Danish waters are home to three cetacean species: the harbour porpoise, white-beaked dolphin and minke whale which have all-year presence in the region (Kinze 2007; table 3). In addition, despite their oceanic habit, five other species (all odontocetes) have been frequently encountered in this area. The white-sided dolphin occurs commonly in the deeper parts of the Skagerrak i.e. the Norwegian Trench, and scattered records of the species exist from the west coast of Jutland. In contrast, the long-finned pilot whale, Sowerby's beaked whale, bottlenose whale and sperm whale all are deep-water specialists that only occur sporadically, perhaps being (mis)guided by the deep Norwegian Trench into the shallower Danish waters. There is a lengthy time series of sperm whale strandings, especially along the west coast of Jutland, and in particular within the shallow Wadden Sea region. When entering the North Sea, described by Smeenk (1997) as a sperm whale trap, male groups or singletons apparently rarely find food (see Pierce et al., this volume, and references therein) and most eventually perish on beaches (Smeenk 1997, Smeenk & Evans, this volume). Sometimes dead specimens get re-floated and are washed ashore elsewhere.

Inner Danish waters and waters around Bornholm

The only native species to this region is the harbour porpoise, while both white-beaked dolphins and minke whales are considered regular visitors (table 3). The minke whale of the North Atlantic is a piscivorous species with a rather frequent occurrence in the inner Danish waters. It is vulnerable to the large numbers of static nets in this area. Common dolphin, killer whale, beluga, fin whale and humpback whale are regarded as periodical or seasonal visitors and can often survive quite well in these waters exhibiting *resilience* to altered environmental conditions.

The common dolphin has probably always had a background occurrence in Danish waters, but since 1990 a marked increase in sightings as well as strandings. However, the species is challenged in particular during winter time due to the occasional formation of sea ice. The bottlenose dolphin only appeared in the stranding records during the period 1968-1977, but in most recent years has been sighted in Danish and inner Baltic waters, possibly as a consequence of increased influx of warm Atlantic water. In earlier times, until about 1975, the source of these occurrences was the southern North Sea. The recent reappearance is instead believed to consist of individuals originating from the Scottish coasts, whose range nowadays extends well beyond the Moray Firth (e.g. Stockin et al. 2006). Potentially, further range expansion could bring about entire schools taking up new residence and lead to the formation of entirely new populations.

The killer whale occurs in habitats of widely different salinity, bathymetry and food availability, but as top predator also is very sensitive to environmental pollution (Jepson et al. 2016). In recent years, the species has become less frequent in the Danish stranding record, possibly supportive of a general lack of reproduction reported in a community from the western British Isles in recent decades (Jepson et al. 2016).

Beluga visits to the inner Danish waters are not infrequent and individuals fare well even in the complicated coastal environments of the Danish archipelago and the Baltic proper. Genuine strandings of the species are rare and corpses encountered should rather be regarded as by-catch casualties. In the early 1900s, several individuals swam through the Danish straits and subsequently survived in the upper Baltic Sea for years - a phenomenon perhaps to be re-interpreted as a colonisation attempt rather than a mistaken attempt to return to Artic waters by entering the cul-de-sac of the Bay of Bothnia.

Fin whales exhibit great flexibility in feeding, breeding, and navigational skills. Although several individuals have been found dead, frequent sightings during the last 15 years indicate an adaptability potential to exploit food resources in the inner Danish waters. Individuals seemingly seek and find so-called "food stations" where they prey on shoaling fish, and they have been documented to migrate between such stations (Jensen & Kinze 2011). The slight increase in occurrence in Danish waters may reflect the general recovery of this species from whaling, in its natural habitat. This is probably also the case for the humpback whale, which is increasingly observed in Danish and neighbouring waters, and has been documented during 2008, 2012 and 2014 on return trips into the Baltic proper (Kinze & Jensen 2015).

Finally, five odontocete species have, despite their oceanic habitat, been encountered with some frequency in inner Danish waters. While the white-sided dolphin is native to the deeper parts of the Skagerrak adjacent to the outer Danish waters, intrusions into the inner Danish waters and waters around Bornholm are very rare (Kinze et al. 2010) but have repeatedly occurred, in 1984 (Sweden) in 2006 (Poland), and in 2013 in Denmark (Kinze et al. 2011). The long-finned pilot whale, Sowerby's beaked whale, and bottlenose whale seemingly fit into this general scheme. However, the latter two species are known to have performed long distance erratic intrusions into the Baltic proper. For Risso's dolphin, the most recent find dates from 2007 when a male individual strayed into the Isefjord inlet on the island of Sealand and eventually starved to death here.

Concluding remarks

The present cetacean stranding record constitutes an important source for understanding long term trends in regional and temporal cetacean diversity in Denmark and neighbouring regions, and hence nature management and conservation measures. The past 50 years have seen an increase in strandings and observations of several species, which are currently not considered native to Danish waters but may in time adapt to local conditions and establish permanent or seasonal populations. Successful management of native and putative new species will require national prioritisation to support continuous efforts to register live and stranded cetaceans in Danish waters.

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Samenvatting

Strandingen van walvisachtigen op de Deense kust: waarnemingen in de periode 2008-2017, alsook een vergelijking met waarnemingen in het verleden

Vondsten van walvisachtigen op de Deense kust gedurende 2008-2017 zijn bij elkaar gebracht en worden hier gepresenteerd. Deze waarnemingen worden vergeleken met waarnemingen uit de afgelopen 50 jaar (1968-2017). De bruinvis (*Phocoena phocoena*) was verreweg de meest voorkomende soort (1177 individuen in de periode 2008-2017). Daarvan werd 62,4% (*n*=735) waargenomen langs de

Noordzee en het Skagerrak - ‘the outer Danish waters’ -, 37,0% (*n*=435) langs het Kattengat, de Grote Belt en de Kleine Belt en 0,6% (*n*=7) rond Bornholm - de beide laatste categorieën vormen tezamen ‘the inner Danish waters’. Gezien dit grote aantal waarnemingen en de grote hoeveelheid daaraan gerelateerde informatie wordt op deze plaats alleen een samenvatting van deze waarnemingen van de bruinvis gepresenteerd. Verder werden in de periode 2008-2017 twaalf andere soorten waargenomen, verdeeld over 90 waarnemingen: 49 witsnuitdolfijnen (*Lagenorhynchus albirostris*), drie witflankdolfijnen (*Leucopleurus acutus*), zeven gewone dolfijnen (*Delphinus delphis*), een gestreepte dolfijn (*Stenella coeruleoalba*), een gramper (*Grampus griseus*), vier grienden (*Globicephala melas*), een orka (*Orcinus orca*), een gewone spitssnuitdolfijn (*Mesoplodon bidens*), zes potvissen (*Physeter macrocephalus*), 14 dwergvinvissen (*Balaenoptera acutorostrata*), twee gewone vinvissen (*Balaenoptera physalus*) and een bultrug (*Megaptera novaeangliae*). In de periode 1968-2017 werden daarnaast nog vijf andere soorten waargenomen: de tuimelaar (*Tursiops truncatus)* in 1968, 1975 en 1976, de beloega (*Delphinapterus leucas*) in 1976 en 1987, de butskop (*Hyperoodon ampullatus*) in 1969 en 1998, de Brydevinvis (*Balaenoptera brydei*) in 2000, en een noordse vinvis (*Balaenoptera borealis*) in 1980. De walvisachtigen in de wateren rond Denemarken kunnen gezien hun oorspronkelijke habitat worden gerekend tot de volgende drie categorieën: 1. *inheemse soorten*: bruinvis, witsnuitdolfijn en dwergvinvis; 2. *flexibele bezoekers,* dat wil zeggen die gedurende hun verblijf in deze wateren opgewassen zijn tegen andere leefomstandigheden dan waar ze normaal gesproken mee te maken hebben, zoals gewone dolfijn, gewone vinvis en bultrug; en 3. *dwaalgasten*, afkomstig uit de diepe wateren van de oceaan die zich niet kunnen aanpassen, zoals griend, gewone spitssnuitdolfijn en potvis.

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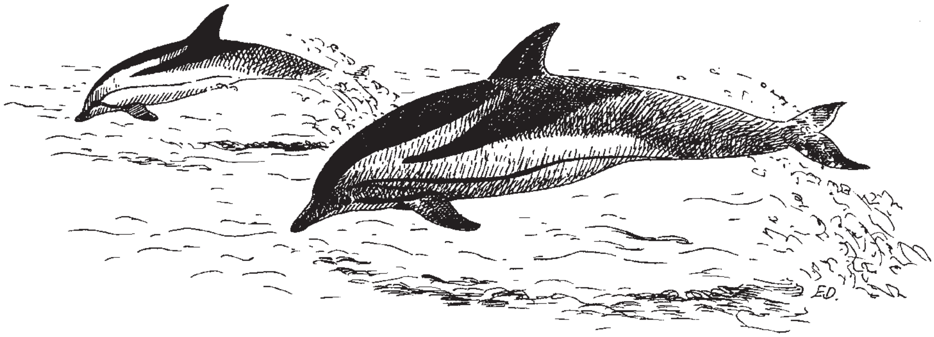
Appendix. Complete list of all reported cetacean strandings in Denmark in the period 2008-2017, excluding the harbour porpoise. FIMUS = Fishery and Maritime Museum, Esbjerg, ZMUC = Zoological Museum University of Copenhagen, DET NC = species determined but not collected, TL = total length, TW= total weight, pr = pregnant. ODW = outer Danish waters, IDW = inner Danish waters.

White-beaked dolphin (*Lagenorhynchus albirostris*)

Date	Locality and sea area	Specimen / determination	Sex	TL cm	TW kg
15-01-2008	Skagen, ODW	ZMUC MCE1595	F	252	230
02-03-2008	Mandø, ODW	FIMUS C 265	M	266	287
17-06-2008	Vejers, ODW	FIMUS C 268	M	221	-
17-06-2008	Skallingen, ODW	FIMUS C 269	M	245	-
28-08-2008	Ferring Sø, ODW	DET NC	U	-	-
20-10-2008	Nørlev Strand, ODW	DET NC	U	-	-
19-02-2009	Lønstrup, ODW	FIMUS C274	M	250	176
06-03-2009	Mårup Kirke, ODW	DET NC	U	-	-
11-03-2009	Mårup Kirke, ODW	DET NC	U	-	-
29-03-2009	Hovvig /Husby, ODW	ZMUC M 1691	M	177	57.5
13-05-2009	Lønstrup Strand, ODW	DET NC	U	-	-
15-11-2009	Sødringholm, IDW	FIMUS C314	F	260	-
13-03-2010	Vester Thorup, ODW	DET NC	U	-	-
31-05-2010	Blokhus-Løkken, ODW	ZMUC	U	-	-
04-06-2010	Nr. Lyngvig Fyr, ODW	FIMUS C318	U	230	-
07-06-2010	Lakolk, Rømø, ODW	FIMUS C319	F	179	-
25-05-2011	Gammel Skagen, ODW	DET NC	U	-	-
28-05-2011	Kandestederne, ODW	FIMUS C325	M	193	-
30-05-2011	Kandestederne, ODW	FIMUS C326	M	280	-
30-05-2011	Klitmøller, ODW	FIMUS	U	-	-
12-06-2011	Skagen, ODW	DET NC	U	-	-
12-06-2011	Højen (Gammel Skagen), ODW	ZMUC	U	257	-
17-06-2011	Højen, ODW	ZMUC	U	-	-
17-06-2011	Højen S, ODW	ZMUC	U	-	-
17-06-2011	Rødhus Blokhus, ODW	ZMUC	M	275	-
17-06-2011	Thorsminde/Husby, ODW	FIMUS C327	F	254	-
18-07-2011	Lønstrup, ODW	DET NC	U	-	-
29-09-2011	Hirtshals, ODW	DET NC	U	210	-
08-02-2013	Klitmøller, ODW	DET NC	U	250	-
19-03-2013	Thorsminde, ODW	FIMUS C340	F	239	-
07-06-2013	Saltum, ODW	FIMUS C342	M	218	-
07-07-2013	Blokhus, ODW	FIMUS C344	U	280	-
12-08-2013	Skarehage, IDW	FIMUS C339	F	200	-
07-12-2013	Hvide Sande, ODW	FIMUS C347	M	260	239.6
10-12-2013	Stenbjerg, ODW	FIMUS C348	F	242	227.2
31-12-2013	Klitmøller, ODW	DET NC	U	285	
18-01-2014	Fuglsang/Fyn, IDW	FIMUS C349	F pr	262	200.3
29-01-2014	Snekkersten, IDW	ZMUC M 1643	F	254	280
03-03-2014	Ejstrup strand, ODW	ZMUC M 1668	U	275	-

23-05-2015	Marbæk Strand, Esbjerg, ODW	FIMUS C361	F	251	-
24-05-2015	Mouth of Uggerby Å, ODW	FIMUS C360	F	223	-
30-05-2015	Rødhus; ODW	ZMUC M1688	U	-	-
30-05-2015	Nr. Lyngby Løkken, ODW	ZMUC M 1689	F	260	-
01-06-2015	Kjul Hirtshals, ODW	FIMUS C365	U-	-	-
19-06-2016	Lodbjerg Fyr, ODW	FIMUS C377	M	269	-
09-01-2017	Strandby, IDW	ZMUC 1679	F	182	84.5
24-01-2017	Uggelhuse Randers Fjord, IDW	ZMUC 1680	F	262	223
21-06- 2017	Haurvig, ODW	DET NC	U	-	-
27-11-2017	Skagen, ODW	ZMUC M08-1690	F pr	246	240
White-sided dolphin (*Leucopleurus acutus*)					
11-04-2008	Bøvling Klit, ODW	FIMUS C267	M	290	-
22-11-2008	Vrist, ODW	FIMUS C273	F	204	100
24-09-2013	Asnæs Nordstrand, Kalundborg Fjord, IDW	ZMUC	M	235	135.5
Common dolphin (*Delphinus delphis*)					
03-10-2010	Skagen, ODW	ZMUC M1639	F	c150	-
01-11-2010	Hirtshals, ODW	FIMUS C322	M	c177	-
03-11-2013	Vejers, ODW	FIMUS C343	F	149	43
26-02-2015	Amager, IDW	ZMUC M1665	F	165	53
13-03-2016	Havnsø, IDW	ZMUC M06-1672	F	152	
05-09-2016	Lejre Vig, Roskilde Fjord, IDW	ZMUC M08-1673	M	158	27
17-10-2017	Hou /Hals, IDW	ZMUC M08-1686	F	200	-
Striped Dolphin (*Stenella coeruleoalba*)					
06-03-2008	Hjerting. ODW	FIMUS C266	M	189	65
Long-finned pilot whale (*Globicephala melas*)					
25-05-2010	Tusenæs, IDW	ZMUC M08-1598	SEX	416	-
17-10-2012	As Vig, IDW	FIMUS C333	M	435	680
27-10-2014	Fanø, ODW	FIMUS C356	M	446	-
20-09-2015	Søndervig, ODW	FIMUS C369	M	270	240
Killer whale (*Orcinus orca*)					
06-05-2009	Nørlev Strand, ODW	FIMUS C276	M	550	-
Sowerby's beaked whale (*Mesoplodon bidens*)					
07-11-2016	Ferring Sø, ODW	ZMUC M08-1677	M	271	240.5
Sperm whale (*Physeter macrocephalus*)					
02-04-2011	Bovbjerg Fyr, ODW	FIMUS C324	M	1400	-
12-03-2012	Nr. Lyngby, ODW	FIMUS C330	M	1280	-
16-02-2014	Henne Strand, ODW	ZMUC MCE 1644	M	1450	-
16-02-2014	Henne Strand, ODW	ZMUC MCE 1645	M	1283	-
16-01-2015	Harboøre, ODW	FIMUS C358	M	-	-
11-02-2015	Sønderho, ODW	FIMUS C359	M	1510	-
22-05-2016	Fanø, ODW	DET NC	M	-	-
Minke whale (*Balaenoptera acutorostrata*)					
30-06-2008	Hvide Sande, ODW	FIMUS	U	400	-
30-09-2009	Agger Tange Høfte 85/84, ODW	FIMUS C280	M	500	-
02-08-2010	Thorsminde Tange, ODW	FIMUS	U	-	-
05-08-2010	Fjand, ODW	DET NC	U	-	-

04-07-2011	Ferring Sø, ODW	ZMUC	F	510	-
21-10-2011	Klitmøller, ODW	FIMUS C329	U	c750	-
12-12-2011	Hvide Sande, ODW	DET NC	U	600	-
18-08-2012	Skallingen, ODW	FIMUS C335	F	755	3330
16-09-2012	Husby, ODW	DET NC	U	900	-
18-10-2012	Skallingen, ODW	DET NC	U	700	-
03-07-2013	Tornby, ODW	DET NC	U	630	-
19-07-2013	Houstrup, ODW	FIMUS C337	U	770	-
14-06-2016	Skagen, ODW	FIMUS C 379	F	542	900
03-01-2017	Thyborøn, ODW	DET NC	U	-	-
Fin whale (*Balaenoptera physalus*)					
20-06-2010	Vejle Fjord, IDW	ZMUC M08-1507	M	1728	23680
23-02-2016	Løkken, ODW	ZMUC M08-1671	M	1720	-
Humpback whale (*Megaptera novaeangliae*)					
30-06-2015	Stenbjerg, ODW	ZMUC M08-1666	U	c700	-



Strandings of cetaceans in Belgium from 1995 to 2017

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Abstract: It is a tradition that regular overviews are published of strandings of cetaceans. The last overviews for Belgium covered the period 1975 to 1989 and 1990 to 1994. This overview deals with strandings between 1995 and 2017. Along the short Belgian coastline, and in Belgian marine and inland waters, 1401 dead or dying cetaceans of twelve species were found between 1995 and 2017. Most of these (*n*=1364) were harbour porpoises (*Phocoena phocoena*), a species that made a remarkable return to the southern North Sea after a virtual absence since the 1950s. Numbers of stranded harbour porpoises quickly rose since the end of the 1990s, and have remained relatively high since then, with on average almost 100 strandings per year between 2005 and 2017. The only other species currently considered as indigenous to the southern North Sea is the white-beaked dolphin (*Lagenorhynchus albirostris*), with 17 records of dead animals in Belgium between 1995 and 2017. Between 1995 and 2017, also a number of species not indigenous to the southern North Sea, or having become extirpated in this area, were recorded. This was the case for Atlantic white-sided dolphin (*Lagenorhynchus acutus*) (*n*=1), bottlenose dolphin (*Tursiops truncatus*) (2), common dolphin (*Delphinus delphis*) (2), striped dolphin (*Stenella coeruleoalba*) (1), long-finned pilot whale (*Globicephala melas*) (1), narwhal (*Monodon monoceros*) (1), sperm whale (*Physeter macrocephalus*) (2), minke whale (*Balaenoptera acutorostrata*) (3), humpback whale (*Megaptera novaeangliae*) (1), fin whale (*Balaenoptera physalus*) (5) and an unidentified dolphin. The two washed ashore bottlenose dolphins, as well as the pilot whale and one of the common dolphins, had probably drifted in from distant areas. Two of the fin whales were brought to port on the bow of an ocean-going vessel, while two other cases concerned finds of recent lower jaws. The stranding of a narwhal was by far the most remarkable one: of this Arctic species only ten stranding records are known for the whole of the North Sea. During the period considered, identified anthropogenic causes of death were incidental catch, ship collision and plastic ingestion.

Keywords: strandings, cetaceans, Belgium, North Sea.

Introduction

It is a tradition that strandings of cetaceans in the Netherlands and Belgium are regularly reported, with most of the reports published in this journal. Especially in the Netherlands the tradition dates back from many decades ago, with almost yearly reports published by Antonius Boudewijn van Deinse (1933, van Bree 1970), an effort continued by Peter Johannes Hendrikus van Bree (1978, 1982) and Chris Smeenk (van Bree & Smeenk 1978, 1983, Smeenk 1986, 2003). Dutch strandings from 2008 to 2014 were reported by Keijl et al. (2016). In Belgium, Wim De Smet (1974) published the first overview of strandings. He made a huge effort – pre-Internet - to include all known cases, some dating back centuries, from the river Scheldt and from the 'Flemish coasts', ranging from Zeeland (the Netherlands) to Northern France. He published new cases (1969-1975) and additional older cases of strandings in 1981 (De Smet 1981). Subsequently, veterinarian and keen naturalist John Van Gompel (1991, 1996) reported strandings in Belgium from 1975 to 1989 and from 1990 to 1994.

In Belgium, prior to the early 1990s, scientific investigations of stranded animals were mainly conducted on a voluntary and ad hoc basis. This changed after the establishment of a legal framework, with commitments made in international fora. In 1991 ASCOBANS (Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas; now […] of the Baltic, North-East Atlantic, Irish and North Seas) was concluded under the auspices of the Convention on Migratory Species (CMS or Bonn Convention). With the aim of meeting specific obligations which the government had accepted in the framework of ASCOBANS, Belgium established a multidisciplinary intervention and research network in 1992. The network, coordinated by the Royal Belgian Institute of Natural Sciences (RBINS), is responsible for scientific investigations of marine mammals washed ashore or bycaught in Belgium. Cetaceans are protected under the Habitats Directive of the European Commission (92/43/EEC), and Belgium implemented aspects of this Directive through legislation on the protection of the Marine Environment (Law of 20 January 1999) and more specifically on the protection of marine species (Royal Decree of 21 December 2001).

Since 1994, yearly overviews on stranded cetaceans were only published in the annual reports of Belgium to ASCOBANS, and from 2014 onwards as stand-alone RBINS reports (Haelters et al. 2016a, 2016b, 2017, 2018a). Efforts are made to report all marine mammal strandings in an online database (www.marinemammals.be), with more detailed data recorded in a database managed by the RBINS. Accounts of particular cases of harbour porpoise and other cetacean strandings were published on an ad hoc basis in several journals.

In this contribution we continue the tradition of publishing accounts of stranded cetaceans, and cover the period from 1995 to 2017.

Material and methods

This contribution covers the short Belgian coastline (65 km), the part of the North Sea over which Belgium has jurisdiction and internal waters, including the Belgian part of the river Scheldt and its tributaries. We include not only stranded animals, but also bycaught animals delivered by fishermen, carcasses recovered at sea, animals found dead in the river Scheldt, ship-struck whales that were transferred to Belgium on the bulb of ships and a few recent remains of cetaceans found in fishermen's nets. We do not include sightings of cetaceans, although this was very tempting in one case: an entangled bowhead whale (*Balaena mysticetus*) very close inshore on 31 March and 1 April 2017, probably the first record of this species in the North Sea (Haelters 2017). In most cases, heavily entangled baleen whales die due to emaciation and starvation, or due to systemic infection arising from damage to tissues (Cassoff et al. 2011, Barratclough et al. 2014), and as such, entangled animals should be considered as lost to the population.

Due to the commitments of the government, the cooperation of coastal community services and technical advances, such as the availability of digital cameras and social media, the reporting of strandings can currently be considered as nearly complete, and certainly fast and efficient.

The interventions by the Belgian state in case of strandings of protected species have been agreed in a coastguard framework (Haelters et al. 2013). In case of a marine mammal stranding, a representative of the RBINS is usually informed very quickly, after which the most appropriate intervention is decided. This can be the collection of the carcass, the release for destruction in case it represents a common animal in an advanced state of decomposition, or autopsy at the stranding location in case of large animals. Small stranded cetaceans, such as harbour porpoises, were in most cases submitted to an external examination, with a description and documentation of characteristics and lesions, after which they were frozen for a later autopsy. Photographs were stored in a database for possible later evaluation of lesions. Most of the stranded animals were investigated by a pathologist of the Department of Morphology and Pathology, Faculty of Veterinary Medicine, University of Liège, with recently also an involvement of veterinarians of the Department of Morphology, Faculty of Veterinary Medicine of the University of Ghent. The investigations follow standardised protocols (Kuiken & García Hartmann 1991, Jauniaux et al. 2002a). The decomposition codes (DCC) presented are: (1) live animal; (2) very fresh; (3) slightly decomposed; (4) very decomposed and (5) mummified or skeletal remains.

Relatively small live stranded animals were usually transported, using dedicated equipment, to a rehabilitation facility in the Netherlands.

Given the large number of records of stranded harbour porpoises (*Phocoena phocoena*), these are not listed on a case-by-case basis, as is done for the other species, but summarised. For the harbour porpoise we provide information on short- and long-term temporal patterns in strandings, sex ratio, age and cause of death.

Results and discussion

Harbour porpoise (*Phocoena phocoena*)

The harbour porpoise is the most common cetacean in Belgian waters, and currently it is probably always present in these waters. In comparison to the previous report (Van Gompel 1996), a remarkable increase in strandings of harbour porpoises has occurred. Where traditionally only three to five strandings were reported in the early 1990s, this number increased dramatically, with on average almost 100 animals per year since 2005 (figure 1), and with a maximum of 148 animals in 2013. In total, 1364 animals were considered, including those found at sea and collected (n=9), found (dead) in fish-

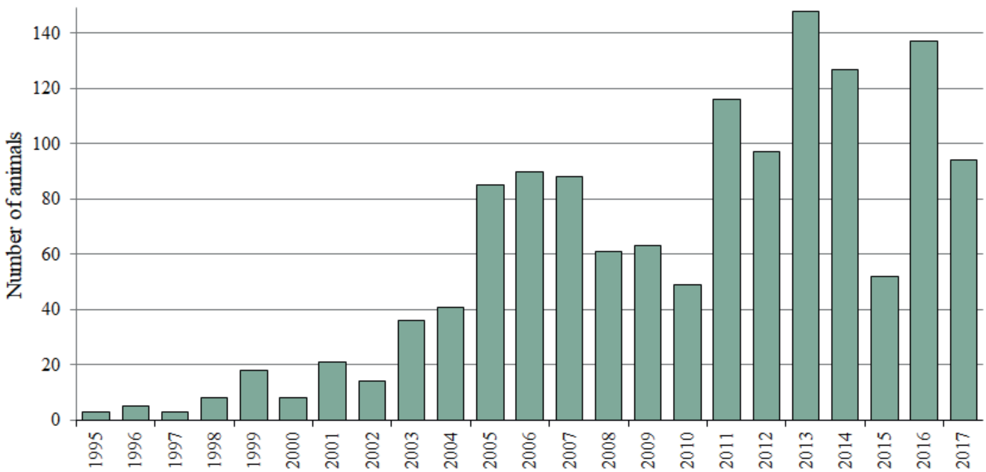

Figure 1. Number of harbour porpoises stranded, bycaught and collected, or found in harbours or in waterways in Belgium between 1995 and 2017 (data RBINS).

	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
Jan	0	0	0	1	0	2	0	1	4	1	3	1	2	1	6	2	3	4	3	3	2	1	1
Feb	0	0	0	0	3	0	4	1	0	1	5	2	9	3	2	2	2	4	7	4	2	4	5
Mar	0	0	1	1	3	1	3	1	4	8	4	20	8	11	6	4	6	18	11	23	5	31	7
Apr	1	0	1	0	3	1	4	0	7	9	19	17	14	9	5	6	25	13	39	14	6	23	6
May	0	1	0	2	1	0	5	2	4	6	18	16	14	7	5	7	10	11	26	7	7	14	5
Jun	0	1	0	1	1	1	2	2	1	2	7	8	4	7	4	4	4	2	20	18	8	6	9
Jul	1	1	1	1	1	2	0	1	2	7	3	1	4	5	3	2	16	9	13	14	6	14	19
Aug	0	0	0	1	0	1	1	2	8	5	13	13	13	4	10	8	25	7	6	9	3	5	13
Sep	0	2	0	0	0	0	1	4	2	0	5	5	12	3	12	5	7	18	7	24	5	17	5
Oct	0	0	0	1	0	0	0	0	1	0	4	1	4	8	8	4	5	5	12	5	5	12	13
Nov	0	0	0	0	4	0	1	0	2	1	2	3	4	3	1	3	5	1	2	0	3	6	5
Dec	1	0	0	0	2	0	0	0	1	1	2	3	0	0	1	2	8	5	2	6	0	4	6

Figure 2. Strandings of harbour porpoises per month and per year between 1995 and 2017.

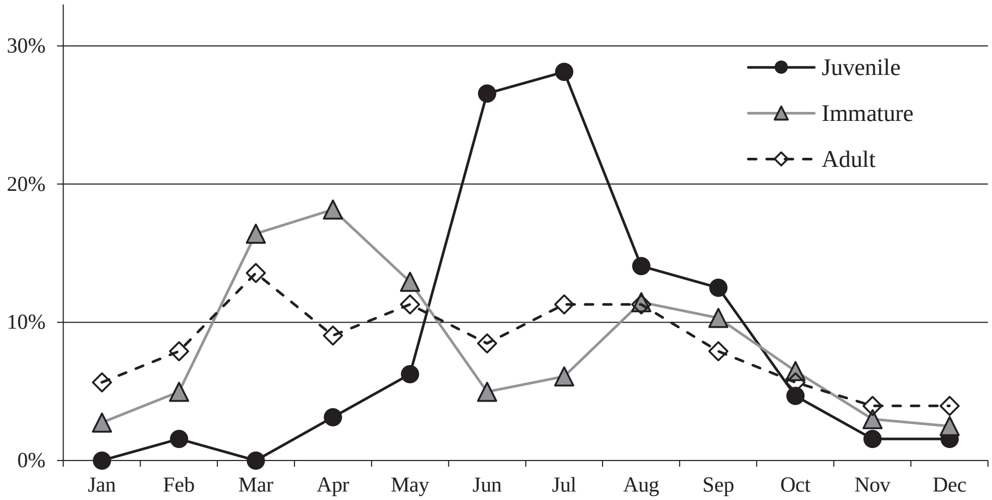

Figure 3. Distribution over the year of the strandings of juvenile harbour porpoises, immatures and adults (as percentage of the monthly total number of strandings).

ing nets on the beach or at sea and collected (*n*=9), live stranded, and died on the beach or taken to a rehabilitation facility (*n*=36), and found in a harbour (*n*=28) or an inland waterway (*n*=33). Excluded were live stranded animals that were returned to sea immediately (*n*=10), bycaught animals that survived and were released immediately (*n*=2) and animals found at sea that remained uncollected (as these could have washed ashore later, and would thus be counted twice).

In the early years of the series considered here, most strandings occurred in late winter and spring (March to May), but during the last ten years the number of stranded animals in summer and autumn (July to October) has increased, with a relatively high number of stranded animals in summer, especially in 2009, 2011, 2014 and 2017 (figure 2). The months with the lowest number of stranded animals were generally November to February.

We can roughly estimate the approximate age of a harbour porpoise using its length; we consider it as adult when longer than 1.3 m, immature when between 0.9 and 1.3 m and juvenile or neonate when shorter than 0.9 m (in accordance with Keijl et al. (2016)). Most of the harbour porpoises that washed ashore were immatures (77% of the animals for which this could be estimated). There were more males (55%) than females (45%), due to a

Table 1. Age classes of harbour porpoises (approximation based on length): percentage of total known per sex (and number).

Sex / Age class	Female (%; *n*)	Male (%, *n*)	Unknown (%, *n*)	Total
Juvenile	7% (25)	4.5% (20)	9% (19)	6% (64)
Immature	72% (273)	79.5% (361)	80.5% (170)	77% (804)
Adult	21% (81)	16% (74)	10.5% (22)	17% (177)
Unknown	(4)	(4)	(311)	(319)
Total	45% (383)	55% (459)	(522)	1364

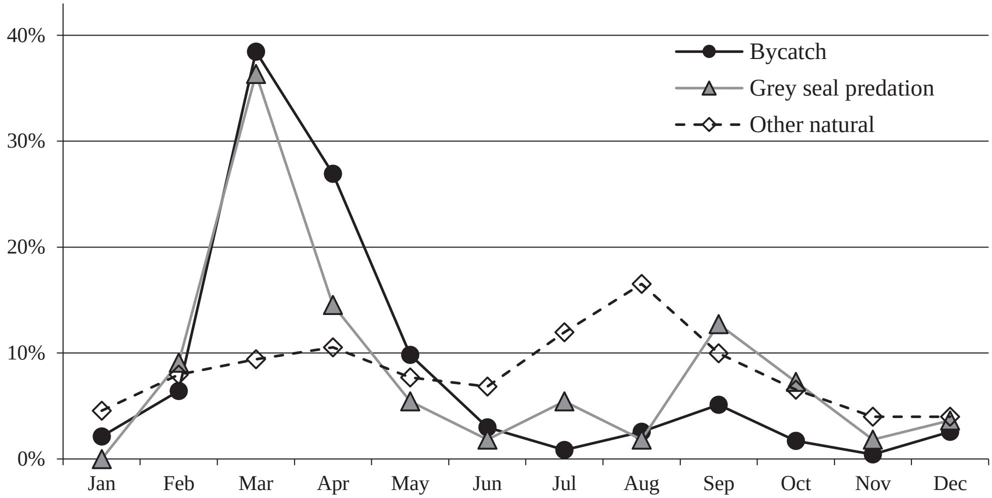

Figure 4. Distribution of the cause of death of stranded harbour porpoises over the year (as percentage of the total per cause of death).

higher number of immature males vs. females (*n*=361 vs. 273; table 1). A peak in the stranding of juveniles occurs from June to September, as can be expected, given that the majority of births of harbour porpoises in the North Sea take place between May and August (Sørensen & Kinze 1994, Lockyer 2003, Hasselmeier et al. 2004). The stranding of immatures shows a peak from March to May and (a lower one) in August and September (figure 3).

Of the 81 females considered as adult, twelve were pregnant and three were lactating (but not all could be investigated).

We could assess a likely cause of death for 640 animals (47%), in many cases using expert judgement and exclusion of other possible causes of death. Of the 640 animals, 36.5% (*n*=234) had (probably) been bycaught, while 63.5% (*n*=406) had probably died due to natural causes. Of the natural causes, predation by grey seals (*Halichoerus grypus*) accounted for 55 cases (14% of the total number of animals that died from natural causes), with the other important natural causes being infectious disease and emaciation (Jauniaux et al. 2002b; national reports to ASCOBANS – see www.ascobans.org). As is the case with strandings, also causes of death were not distributed evenly over the year (figure 4), and there were long-term trends in the causes of death.

The first case of grey seal predation in Belgium was recorded in 2010 (based on a retrospective analysis of available photographs taken from 1995 onwards; own data, unpublished), while 17 and 11 cases were recorded

Figure 5. The harbour porpoise that live stranded on 15 February 2014 on the day of the stranding (left; *photo*: *Jan Haelters*) and after rehabilitation (right; *photo: SOS Dolfijn*).

Figure 6. Harbour porpoise that died due to the (partial) ingestion of unsuitable prey (10 March 2016). *Photo: Jan Haelters*.

in 2016 and 2017 respectively. In 2015 (Anonymous 2015) the Government of Flanders took the decision to prohibit the recreational use of different types of gill and trammel nets on the beach as a protective measure for marine mammals in the intertidal zone. Until then, this recreational fishery had been responsible for a number of harbour porpoise bycatch cases every year (Haelters & Camphuysen 2009).

Remarkable harbour porpoise strandings

On 30 December 2006 a harbour porpoise died on the beach at Blankenberge. Its cause of death was assessed as accidental due to its presence in a heavy surf in shallow water. The animal presented completely healed (unpigmented) scars which were probably inflicted during interaction with white-beaked dolphins (*Lagenorhynchus albirostris*; Haelters & Everaarts 2011).

In September 2011, two harbour porpoises washed ashore that had died shortly before. Both presented extensive lesions, with large parts of skin and blubber missing. Similar lesions had been described from neighbouring countries, however without a valid explanation of their origin. Eventually, male grey seals were identified as the prime suspects for having caused the death of both harbour porpoises (Haelters et al. 2012). Afterwards, predation events were observed in the field (Bouveroux et al. 2014), and DNA of grey seals was found in harbour porpoise lesions (Jauniaux et al. 2014a, van Bleijswijk et al. 2014).

On 15 February 2014, a live harbour porpoise was found on the beach at Koksijde. The animal had many fresh injuries, including missing parts of the left pectoral fin and fluke (figure 5). It was concluded that the injuries had been caused by scavenging foxes (*Vulpes vulpes*) (Haelters et al. 2016c). The animal was transported to a rehabilitation facility in the Netherlands (SOS Dolfijn, Harderwijk). As it was not fit for release, it was taken to Seamarco (Zeeland, the Netherlands) where it was used in non-invasive research. It died due to pneumonia on 27 December 2017.

On 10 March 2016, a very fresh 1.06 m long male harbour porpoise washed ashore that had suffocated due to swallowing a tub gurnard (*Chelidonichthys lucerna*), a scorpaeniform fish (Scorpaeniformes) with a solid head and firm spines (figure 6). This species is not a common prey species for harbour porpoises – and apparently not a suitable one. Asphyxiation due to fish blocking the airways has been described in a number of cetacean species, with mostly spiny fish or flatfish involved (IJsseldijk et al. 2015).

White-beaked dolphin (*Lagenorhynchus albirostris*)

Together with the harbour porpoise, this is the only cetacean regularly observed in Belgian waters. In total, 17 white-beaked dolphins stranded or were found at sea (and taken to port) between 1995 and 2017 (table 2, figure 7; see also IJsseldijk et al., this volume). Given the state of decomposition, not all animals were collected for autopsy. Ten of the cases were recorded between November and January, and four animals had stranded alive.

Atlantic white-sided dolphin (*Lagenorhynchus acutus*)

An Atlantic white-sided dolphin stranded alive at Knokke-Heist (figure 8) on 4 February 1999. It was a male of 2.47 m long that weighed 167 kg. The animal was transported to Harderwijk, where it died the day after. The autopsy revealed that it was emaciated, and that it had died due to pneumonia.

Bottlenose dolphin (*Tursiops truncatus*)

The remains of a very decomposed (DCC 4) bottlenose dolphin washed ashore at Oostende on 26 April 2016. The animal, a male of 3.19 m long, was not further investigated.

The remains of a very decomposed (DCC 5) bottlenose dolphin washed ashore at Middelkerke on 7 October 2017. The length of the animal was estimated at 2.5 to 3 m, and the remains weighed approximately 200 kg. While all of the skin and part of the intestines were missing, we recovered a full stomach. It contained, amongst other species, the remains of fish either not usually present or uncommon in the southern North Sea: conger eel (*Conger conger*) and sea bream spp. (Sparidae), suggesting a westerly origin.

Common dolphin (*Delphinus delphis*)

A live male common dolphin stranded at Heist on 26 February 1996; it was taken to Harderwijk where it died on 25 August 1997. At the time of the stranding, it weighed 120 kg and measured 2.1 m (Haelters 1996).

A very decomposed common dolphin (DCC 4) was found on the banks of the river Scheldt (community of Hemiksem) on 30 April 2016. It was a male of 1.62 m.

Striped dolphin (*Stenella coeruleoalba*)

On 6 May 2009 and the days after, a live dolphin was observed in and around the port of Antwerp (Verrebroekdok and Scheldt near Zwijndrecht). Images taken on the 18th of May clearly showed that it concerned a striped dolphin. On 21 May it was found dead on the banks of the Doeldok, port of Antwerp (Haelters & Verbelen 2009). The animal was a male of 1.50 m, and it weighed 38 kg. Its skin was in a very bad condition, with many lesions and algal growth (figure 9). It was very emaciated.

Long-finned pilot whale (*Globicephala melas*)

A very decomposed pilot whale washed ashore at De Haan on 21 March 1995. The remains measured 4.1 m and weighed 413 kg. Most of the intestines had disappeared. The autopsy revealed a

Table 2. White-beaked dolphins between 1995 and 2017 (DCC: decomposition code; L: length; M: weight; N/A: not available/unknown).

Date	Circumstances	Location	Comments	DCC	Sex	L (m)	M (kg)
10/01/1995	Washed ashore	Nieuwpoort		4	♂	2.82	330
14/01/1995	Live stranded	Oostende	Died at Harderwijk on 16/1/1995	1	♂	1.61	45
2/12/1997	Bycaught	At sea	Bycaught close to shore (2 miles off Westende) by otter trawl	2	♀	2.55	215
24/04/1998	Live stranded	Bredene	Died at Harderwijk on the same day	1	♀	2.4	230
25/07/2000	Washed ashore	De Haan		4	N/A	2.42	250
24/11/2004	Washed ashore	Zeebrugge		4	♀	2.2	N/A
18/12/2004	Washed ashore	Oostduinkerke		4	♀	2.52	N/A
10/05/2005	Found at sea	At sea	Skull with fleshy remains from fishermen; found near Buitenratel sandbank	5	N/A	N/A	N/A
27/12/2005	Washed ashore	De Panne	With lesions possibly due to fox scavenging; empty stomach; possibly bycaught	2	♂	1.67	55
12/08/2006	Washed ashore	Wenduine	Very decomposed and parts missing; the remains weighed 15kg	4	♂	1.1	N/A
17/12/2006	Washed ashore	Knokke-Heist	No lesions, probably bycaught	2	♂	2.5	250
7/09/2007	Washed ashore	Knokke-Heist		4	♀	2.2	N/A
2/12/2008	Live stranded	Oostende	Died on beach; very emaciated (figure 7)	1	♀	2.55	200
17/12/2011	Live stranded	Oostduinkerke	Euthanised; with lesions probably due to fox scavenging	1	♀	2.11	240
25/03/2012	Found in harbour	Nieuwpoort harbour	Taken to destruction facility	4	♂	2.49	N/A
12/05/2013	Washed ashore	Blankenberge		3	♂	2.24	N/A
29/11/2017	Washed ashore	Oostduinkerke	Rope around tail, probably attached by fishermen putting the animal overboard; bycaught	2	♀	2.52	267

fish head-down in the oesophagus, which could point at bycatch as the cause of death.

Narwhal (*Monodon monoceros*)

On 27 April 2016 a dead narwhal was found on the bank of the river Scheldt at Bornem, 92 km from the river mouth. The male animal was 3.04 m long and its remains weighed 290 kg (figure 10). Due to its decomposition, the results of the autopsy remained inconclusive, but it is probable that the animal had died due to a long process of starvation (Haelters et al. 2018b). In the stomach a large number of small litter items were found that were probably ingested while the animals was dying. The animal had already been observed (but not identified at that moment) on 30 March 2016 in the river Scheldt at Bazel, probably shortly before it died.

Dolphin sp.

The remains of a 2.5 m long unidentified dolphin were removed from the beach of Middelkerke on 22 June 2009. The weight of the remains was estimated at 200 kg. It was taken to a destruction facility.

Figure 7. White-beaked dolphin that died immediately after stranding (Oostende, 2 December 2008). *Photo: Jan Haelters*.

Figure 8. The first Atlantic white-sided dolphin recorded in Belgium (Knokke-Heist, 4 February 1999). *Photo: Norbert Minne*.

Sperm whale (*Physeter macrocephalus*)

The very decomposed (DCC 4-5) remains of a 13 m long sperm whale washed ashore at Koksijde on 26 February 2004. A month before, the remains of this very animal had been observed at Holme (UK), and on 28 January it had washed ashore at Thornham (Norfolk, UK), where its lower jaw was removed. Due to adverse weather conditions, the carcass had

Figure 9. Striped dolphin in the port of Antwerp (21 May 2009). *Photo: Jan Haelters*.

Figure 10. Narwhal upon arrival at the University of Ghent (28 April 2016). *Photo: Jan Haelters*.

not been removed from the beach in the UK. By 15 February the sea had reclaimed it, until it finally washed ashore at Koksijde.

A live, 13.5 m long male sperm whale washed ashore at Heist on 8 February 2012. It died approximately 8 hours after its stranding. Its weight was estimated at 32 tons. Some plastic was found in its stomach (figure 11), next to a large number of cephalopod beaks and the skeletons of at least two large cod (*Gadus morhua)*. From the blood of the animal the bacterial pathogen *Edwardsiella tarda* was isolated. The sepsis could have lead directly or indirectly to the stranding, which in turn caused the death of the animal (Cools et al. 2013).

Fin whale (*Balaenoptera physalus*)

A very fresh fin whale (DCC 2) washed ashore at Oostende on 1 November 1997. It was a juvenile, emaciated female with a length of 13 m (Haelters & Rappé 1997). The autopsy revealed a severe parasitism by nematodes, which had

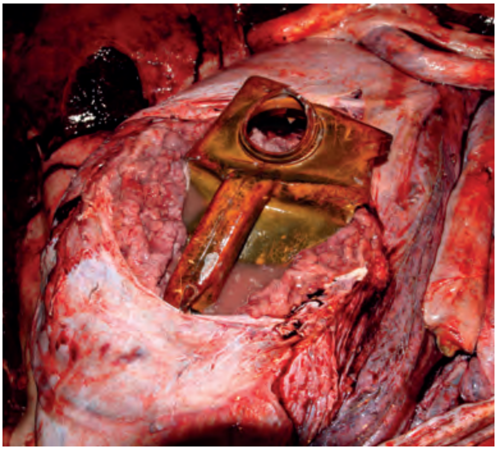

Figure 11. Parts of a jerrycan in the stomach of a sperm whale (Heist, 8 February 2012). *Photo: Jan Haelters*.

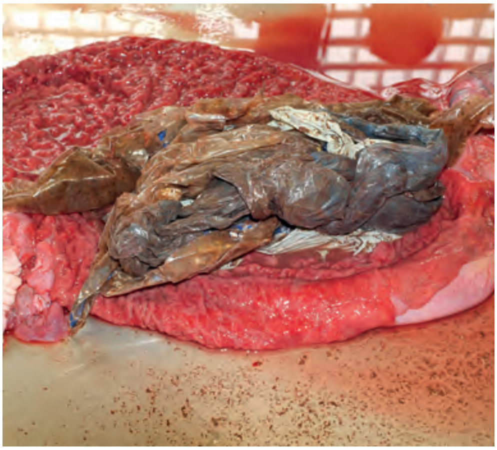

Figure 13. Plastic bags in the stomach of a minke whale (Nieuwpoort, 10 March 2013). *Photo: Jan Haelters*.

Figure 12. Fin whale on the bulb of a vessel (Port of Ghent, 9 November 2015). *Photo: Jan Haelters*.

caused a chronic and massive thrombus in the portal vein (the probable cause of death). The parasitism and lesions were associated with a morbillivirus infection, and from this animal, for the first time, specific lesions and antigen presence of morbillivirus infection were reported for a baleen whale (Jauniaux et al. 1998a, 2000).

A relatively recent jawbone of an adult fin whale (animal estimated at 18 to 20 m length) was found by fishermen in Belgian waters on 16 December 2008.

A 19.9 m long female fin whale was brought into the port of Antwerp on 22 September 2009, on the bow of the ship Summer Flower (Nassau, Bahamas; 169 m long, cruising speed 22.5 kts), after a journey from Santa Marta (Colombia). The animal had been dead already for a couple of days. The autopsy revealed it had died due to the ship-strike that probably had taken place in the Bay of Biscay or off the Spanish or Portuguese coast (Haelters & Kerckhof 2010).

In 2011 we received a relatively recent jawbone of an adult fin whale (estimated at 20 m) from a fisherman. He had found the bone in his nets in Belgian waters 'a couple of years earlier'. It did not match with the find of 2008.

An 11.6 m long male fin whale was found on the bulb of the ship Premium do Brazil (204 m long, cruising speed 20 kts), that had arrived at the port of Ghent on 9 November 2015 after a journey from Porto de Santos (Brazil) (figure 12). Different haemorrhages confirmed that the cause of death was traumatic and associated with the ship strike that had probably taken place in the Bay of Biscay or the (western?) Channel. The crane lifting the remains from the water registered a weight of around 10 tons, but some of the bodily fluids and part of the throat tissue were missing. The animal was heavily infested with the nematode *Crassicauda boopis* (Lempereur et al. 2017).

Northern minke whale (*Balaenoptera acutorostrata*)

On 14 December 2004 a dead minke whale was found at sea, a few km off Nieuwpoort. The female was in a very fresh condition (DCC 2) and was 4.2 m long. Although it was judged to be very emaciated, its stomach was filled with clupeids. The animal presented several lesions that pointed at bycatch.

A very emaciated male minke whale washed ashore at Nieuwpoort on 10 March 2013. It was very fresh, and had possibly stranded alive. It measured 3.40 m. It had died due to plastic ingestion: its stomach was completely blocked by several plastic bags (Figure 13; Jauniaux et al. 2014b). The inscriptions on one of the bags suggested a Scottish origin.

The remains of a dead minke whale were observed floating north of the Westhinder anchorage area on 23 March 2017. The carcass was observed a few times afterwards, and it finally washed ashore on 16 April in Zeeland, the Netherlands. It is possible that it was shipstruck.

Humpback whale (*Megaptera novaeangliae*)

A floating carcass of a large cetacean was observed on 28 February 2006 in French waters. On 1 March it was observed a few miles off Calais (France). This was probably the humpback whale that was found on the beach of Nieuwpoort on 5 March 2006. Although from the outside it seemed fairly fresh, with still living barnacles and whale lice, internally it was relatively decomposed (DCC 3 to 4). The female of 10.5 m long showed signs of a ship strike, with internal haemorrhages and broken bones.

General discussion

Most of the finds of dead or dying cetaceans in Belgium between 1995 and 2017 were harbour porpoises (97%; *n*=1364). The results of two large-scale summer sightings surveys, respectively in 1994 and 2005 (Scans-II 2008, Hammond et al. 2002, 2013) concluded that there had been a large-scale southward shift in the harbour porpoise population of the North Sea between 1994 and 2005. The return of the species to the very southerly part of the North Sea, since its virtual disappearance in the 1950s, was recorded at an early stage in the Netherlands (Camphuysen & Leopold 1993, Camphuysen 1994, Witte et al. 1998, Addink & Smeenk 1999), implying that the distribution shift had started already prior to the first SCANS survey. From 1997 onwards, a remarkable increase in strandings (and sightings) of this species occurred also in Belgium and northern France (Kiszka et al. 2004, Haelters & Camphuysen 2009, Haelters et al. 2011).

Strong yearly fluctuations in the number of stranded harbour porpoises could be due to changes (on a relatively small geographical scale for the species) in their distribution related to changes in prey distribution and abundance, the presence of grey seals or underwater noise generated by piling offshore wind farm foundations (Haelters & Geelhoed 2015). Bycatch of harbour porpoises predominantly occurred in March and April, coinciding both with the main season for bottom set gillnet fisheries for flatfish (Pouvreau & Morizur 1995) and the period with the highest density of harbour porpoises in coastal waters (Haelters et al. 2011). The highest level of grey seal predation (almost 40% of all cases) occurred in March, probably coinciding with relatively large numbers of adult male grey seals in coastal waters of the southern North Sea (Vincent et al. 2018) and a high density of harbour porpoises close inshore.

The second most common species in strandings, indigenous to the southern North Sea, is the white-beaked dolphin (*n*=17). The numbers of white-beaked dolphins in Belgian waters vary, with periods during which observations are common and periods during which hardly any are observed (RBINS, unpublished data). White-beaked dolphins occur on average further offshore than harbour porpoises, and they are more common in the central and northern North Sea than in the southern part (Reid et al. 2003, Hammond et al. 2017, IJsseldijk et al., this volume). Their periodic occurrence in southerly waters might be food-related. Live or very fresh animals (DCC 1 or 2) were found only between November and January (*n*=7), with the exception of one live animal in April. One of the animals, a decomposed male of around 1.1 m length, washed ashore in August, was a calve. Length-at-birth is estimated at 110 to 120 cm, and births take place in summer (Galatius et al. 2013).

The Atlantic white-sided dolphin is an oceanic species that does not occur in the southern North Sea or the Channel. The stranding reported here was the first record of this species in Belgium (Kerckhof & Haelters 1999).

A population of the bottlenose dolphin existed in the southern North Sea (northern France to the north of the Netherlands) up to around half a century ago (Kompanje 2001, Camphuysen & Peet 2006, Camphuysen & Smeenk 2016). One of the main reasons for its disappearance in this area could have been pollution: the species, being a long-lived cetacean, is vulnerable to the effects of persistent organic pollutants, with high levels potentially inhibiting reproduction (Jepson et al. 2016). Bottlenose dolphins that are currently observed in the southern North Sea probably originate from populations in the northern North Sea, the Channel or the adjacent Bay of Biscay. The two stranded animals were very decomposed, and had drifted at sea for a long time. The indication of a possible origin (more westerly waters) can only be provided for the animal of 2017, thanks to the analysis of its stomach contents.

Common dolphins rarely wash ashore in Belgium. However, it is a species that we could expect more frequently in the southern North Sea in the near future, due to the increasing abundance of favoured prey species such as anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*), perhaps under the influence of climatic changes (Petitgas et al. 2012, Montero-Serra et al. 2015). During the last few years, bluefin tuna (*Thunnus thynnus*) were recorded again in the North Sea. This iconic fish had disappeared from these waters in the 1960s, and its return (Bennema 2018) could be partly the consequence of an increase in temperature and the increase in favoured prey. Like the bluefin tuna (Mackenzie & Meyers 2007, Bennema 2017), common dolphins have not always been rare in the North Sea: Camphuysen & Peet (2006) describe a slow disappearance of the common dolphin from the 1950s, and stated that in more westerly and southerly waters it is often associated with bluefin tuna.

The striped dolphin prefers warmer water, and occurs more to the west and south of the North Sea (Reid et al. 2003, Hammond et al. 2017). Strandings are extremely rare in Belgium.

Long-finned pilot whale strandings are very rare in Belgium. The species occurs in deeper waters around or beyond the shelf ridge (Reid et al. 2003, Rogan et al. 2017). On rare occasions, such as in November 2014 (IJsseldijk et al. 2015), pods of tens of animals are observed close inshore, and the possibility of mass-strandings (such as in northern France in 2015; Jauniaux et al. 2017) should not be excluded.

The narwhal record (sighting and stranding) was the first ever of this Arctic species in Belgium, and the most southerly one in Europe. For the North Sea, only ten other strandings are known, the oldest one dating back to 1588 (Haelters et al. 2018b).

Groups of male sperm whales occasionally enter the North Sea, probably from the north (De Smet 1997, Evans 1997, Smeenk 1997, Pierce et al., this volume). The shallow waters in its southern part are not a suitable habitat for this species, which is used to foraging in deep waters (Jacques & Lambertsen 1997, Jauniaux et al. 1998b). Strandings of sperm whales in the North Sea have been documented since the 16th Century (Smeenk 1997, Smeenk & Evans, Pierce et al., this volume) and seem to be on the rise over the last few decades. Especially in 2016 a high number of animals stranded, many of which had litter in their stomach (probably unrelated to their stranding or death; Unger et al. 2016). Hypotheses for increased numbers of stranded sperm whales are, amongst others, alterations in habitats and prey distribution due to climatic changes and an increase in the sperm whale population since the cessation of whaling during 1979-1987, with accompanying range extensions (Evans et al. 2005, Hobbs et al. 2007, Rødland & Bjørge 2015, Pierce et al., this volume).

Although minke whales are indigenous to the North Sea, they are very rare in its southern part. There are indications that minke whale distribution shifted slightly towards the south in the North Sea between 1994 and 2005 (Hammond et al. 2013, 2017), but sightings and strandings in Belgium remain exceptional. The death of the two minke whales that were investigated was related to a human activity.

Fin whales are not indigenous to the North Sea. They prefer deeper water beyond the continental shelf edge in the Atlantic Ocean (Reid et al. 2003). Strandings in Belgium are rare. The species is vulnerable to ship-strikes, and animals that enter port on the bulb of ships undoubtedly only represent part of the total mortality due to ship-strikes (Rockwood et al. 2017).

Until 2006, the humpback whale had only been recorded once in Belgium, in 1751 (a floating carcass) (Haelters et al. 2010). The first record of a dead humpback whale in the Netherlands even dates back only to 2003 (Camphuysen & Peet 2006). In the North-Atlantic the humpback whale was hunted almost to extinction, until it was protected in 1955. Since then, numbers have increased, and sightings have risen in the North Sea, including in its southern part (Camphuysen 2007, Leopold et al., this volume). The stranding of the humpback whale in 2006 can be placed in that context. 'European' Humpback whales move between feeding grounds in the north, and breeding locations off the Cape Verde Islands as well as the West Indies (Jann et al. 2003, Stevick et al. 2003, Wenzel et al. 2009), although there might be, or have been, more than two stocks in the North Atlantic, including one using a non-tropical breeding ground (Punt et al. 2007). Threats to the species in the southern North Sea include entanglement and ship collisions (as in the case of the 2006 record).

The study of stranded cetaceans can help identify changes in their ecology and distribution, and is important to assess causes of death, in particular anthropogenic ones. It is useful to, from time to time, publish an overview of strandings, which however should also be analysed and interpreted on a wider scale, especially for Belgium with its very short coastline.

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Samenvatting

Strandingen van walvisachtigen in België van 1995 tot 2017

Het laatst gepubliceerde overzicht van strandingen van walvisachtigen in België dateert reeds van de periode 1990-1994. Hier behandelen we de aansluitende periode: 1995 tot en met 2017. Langs de korte Belgische kustlijn, en in het Belgische zeegebied en inlandse wateren, werden tussen 1995 en 2017 in totaal 1401 dode of stervende walvisachtigen, behorend tot twaalf soorten, aangetroffen. De meeste stran-

dingen (1364) betroffen bruinvissen (*Phocoena phocoena*), een soort die na een afwezigheid van vele decennia weer algemeen voorkomt in de zuidelijke Noordzee. Tussen 2005 en 2017 registreerden we jaarlijks gemiddeld bijna 100 strandingen van dit dier. Van de witsnuitdolfijn (*Lagenorhynchus albirostris*), de enige andere soort die momenteel als inheems kan beschouwd worden in de zuidelijke Noordzee, werden 17 strandingen of vondsten op zee genoteerd. Verder registreerden we een witflankdolfijn (*Lagenorhynchus acutus*), de eerste stranding voor deze soort in België, twee tuimelaars (*Tursiops truncatus*), twee gewone dolfijnen (*Delphinus delphis*), een gestreepte dolfijn (*Stenella coeruleoalba*), een gewone griend (*Globicephala melas*), een narwal (*Monodon monoceros*), twee potvissen (*Physeter macrocephalus*), een bultrug (*Megaptera novaeangliae*), drie dwergvinvissen (*Balaenoptera acutorostrata*), vijf gewone vinvissen (*Balaenoptera physalus*) en een niet-geïdentificeerde dolfijnachtige. De twee tuimelaars, de griend en één van de gewone dolfijnen verkeerden in verregaande staat van ontbinding en zijn vermoedelijk gestorven in een gebied op relatief grote afstand van Belgische wateren. Eén van de dwergvinvissen was langzaam verhongerd, doordat enkele plastic zakken de maag van het dier volledig geblokkeerd hadden. De bultrug was gestorven door een aanvaring. Twee van de gewone vinvissen werden binnengebracht in een haven op de voorsteven van een schip, en waren vermoedelijk aangevaren in de Golf van Biskaje of de aanpalende Atlantische Oceaan. Twee andere meldingen van gewone vinvissen betroffen recente skeletdelen die door vissers in Belgische wateren gevonden zijn. De meest opmerkelijke walvisachtige in België was een narwal, die eerst levend gezien werd in de Schelde, en een maand later in ontbonden toestand aan de oevers gevonden werd. Het was niet enkel de eerste narwal voor België, maar het was ook bijna 70 jaar geleden dat deze Arctische soort in de Noordzee geregistreerd was.

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Abundance of harbour porpoises (*Phocoena phocoena*) on the Dutch Continental Shelf, aerial surveys 2012-2017

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Abstract: The harbour porpoise (*Phocoena phocoena*) is the most abundant marine mammal species in Dutch waters. Aerial surveys along predesigned track lines in 2012-2017 provided density and abundance estimates for the Dutch Continental Shelf (DCS) in spring (Mar/Apr 2012, 2013) and summer (Jul 2014, 2015, 2017). The abundance estimates in spring (*n*=63,408-66,685) were in the same order of magnitude as summer (*n*=41,299-76,773). Distribution patterns of porpoises differed between seasons and years, but a band of higher densities from the southern part of the DCS to the area north of the western Wadden Isles was visible in all seasons. Calves were only seen in July. The total abundance estimates in spring and summer correspond to a maximum of 17-21% and 7-23% of the southern North Sea population respectively, which implies that a large part of the North Sea population resides in Dutch waters during both seasons.

Keywords: abundance, aerial survey, distance sampling, distribution, harbour porpoise, Dutch Continental Shelf, North Sea, *Phocoena phocoena*, population size.

Introduction

The harbour porpoise (*Phocoena phocoena*) is the most abundant marine mammal species on the Dutch Continental Shelf. After it almost disappeared in the first half of the 20th century, the occurrence of harbour porpoises on the Dutch Continental Shelf has increased significantly in the last decades (Camphuysen 2011). This is probably a result of a southward shift in distribution as shown by a series of three large-scale dedicated cetacean surveys (SCANS, SCANS II and SCANS III) in the summers of 1994, 2005, and 2016 (Hammond et al. 2002, 2013, 2017). The reasons for this shift that occurred between the 1990s and 2000s, are not clear. Changes in prey species distribution, abundance and availability are a likely cause (Camphuysen 2004), although this remains a matter of debate (MacLeod et al. 2007).

The fore mentioned SCANS surveys resulted in abundance estimates of harbour porpoises in European shelf waters, but the survey design did not allow for national abundance estimates. Systematically collected survey data on harbour porpoise abundance and distribution in Dutch waters were virtually lacking until a decade ago. Since May 2008, dedicated aerial surveys were conducted in parts of the Dutch Continental Shelf (Scheidat et al. 2012). In 2010-2011 dedicated surveys of the entire Dutch Continental Shelf were conducted for the first time, in three different seasons (Geelhoed et al. 2013). Since then, surveys have been undertaken almost annually in spring or in summer, and once in autumn.

The objective of this paper is to present the distribution, density and abundance of the harbour porpoise on the entire Dutch Continental Shelf resulting from dedicated aerial surveys conducted in 2012-2017.

Methods

Study area, survey design and data acquisition

Aerial line transect surveys were conducted on the Dutch Continental Shelf, which was divided into four areas (figure 1): A (Dogger Bank; 9615 km²), B (Offshore; 16,892 km²), C (Frisian Front; 12,023 km²) and D (Delta; 20,797 km²). The areas were surveyed by aircraft along predesigned track lines ensuring equal coverage probability. The design of the track lines was parallel in 'near shore' areas C and D and zigzag in offshore areas A and B (figure 1). Two sets of track lines were designed per area. Surveying one set allows for a robust abundance estimate. The direction of transects in areas C and D followed depth gradients in order to minimise potential variance in encounter rate within transect lines caused by depth (Buckland et al. 2001). The zigzag design of the offshore areas aimed at maximising the endurance of the plane and cover as large an area as possible.

The surveys were conducted using distance sampling methodology (Buckland et al. 2001, Buckland et al. 2004). Surveys were conducted by a team of three people, using a high-winged twin-engine airplane, the *Partenavia 68*, equipped with so-called bubble windows (allowing observations directly under the plane). The plane flew at an altitude of 183 m (600 feet) with a speed of ca. 186 km.h^{-1} (ca. 100 knots). Every four seconds, time and the aircraft's position were recorded automatically onto a Toughbook laptop connected to a GPS. Details on environmental conditions were entered in a database by the so-called navigator at the beginning of each

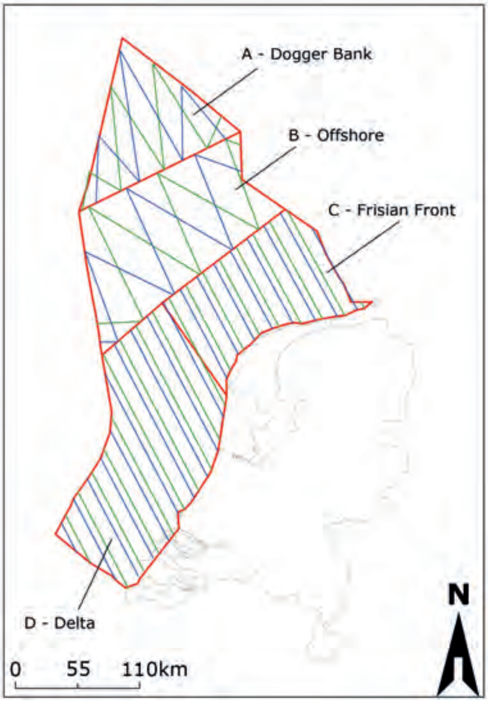

Figure 1. Map of the Dutch Continental Shelf with the planned track lines in study areas A - Dogger Bank, B - Offshore, C - Frisian Front and D - Delta. Colours indicate sets of track lines.

transect and whenever conditions changed. Observations were made by two dedicated observers each seated at the bubble windows on the left and right side of the aircraft. For each observation, the observers acquired data that were entered in real time into a database by the navigator using VOR-software. Observation data included species (all cetaceans and seals), declination angle measured with an inclinometer from the aircraft abeam to the individual or group, group size, presence of calves, behaviour, swimming direction relative to the transect, detection cue, whether the individual or group was above or below the sea surface when abeam, and reaction to the survey plane. Environmental data included sea state (Beaufort scale), turbidity (assessed by visibility of objects below the sea surface), cloud cover (in octaves), glare (observation area covered and strength) and subjective sighting conditions. These sighting conditions represent each observer's subjective view of the likelihood that the observer would see a harbour porpoise within the search area should one be present. These conditions could be good, moderate or poor. Furthermore, a category X "not possible to observe" is used. Sighting conditions could differ between the left and right side of the plane.

Surveys were undertaken in weather conditions safe for flying operations (no fog or rain, no chance of freezing rain, visibility >3 km) and suitable for porpoise surveys (sea state ≤3 Beaufort).

Data analysis

The survey data were collected using distance sampling techniques (Buckland et al. 2001, Buckland et al. 2004). The collected sightings and effort were used to calculate densities and abundance estimates, and to produce distribution maps. Line-transect distance sampling allows for obtaining estimates of absolute densities, i.e. the number of animals/km² with the associated 95% confidence interval (CI) and coefficient of variation (CV; Buckland et al. 2001). Animal abundance in each stratum v (i.e. area A, B, C and D) was estimated using a Horvitz-Thompson-like estimator (Buckland et al. 2001, Buckland et al. 2004) as follows:

$$\hat{N}_v = \frac{A_v}{L_v}\left(\frac{n_{gsv}}{\hat{\mu}_g} + \frac{n_{msv}}{\hat{\mu}_m}\right)\bar{s}_v$$

where Av is the area of the stratum, L_v is the length of transect line covered on effort in good or moderate conditions, n_{gsv} is the number of sightings that occurred in good conditions in the stratum, n_{msv} is the number of sightings that occurred in moderate conditions in the stratum, $\hat{\mu}_g$ is the estimated total effective strip width (ESW) in good conditions, $\hat{\mu}_m$ is the estimated total effective strip width in moderate conditions and $\bar{s}_v$ is the mean observed school size in the stratum.

The effective strip width is the distance at which the number of animals detected outside the strip width equals the number of animals missed inside the strip width. The ESW is corrected for the proportion of animals missed on the track line by a factor called g(0). For the current surveys, the g(0) values obtained in a similar German study (Scheidat et al. 2008) were applied. These g(0) values are 0.37 for good conditions and 0.14 for moderate conditions, resulting in effective strip widths of 153 m and 54 m, respectively.

Group abundance by stratum (areas A, B, C and D) was estimated by:

$$\hat{N}_{v(\text{group})} = \hat{N}_v / \bar{s}_v.$$

Total animal and group abundances of the entire study area were estimated by

$$\hat{N} = \sum_v \hat{N}_v \text{ and } \hat{N}_{(\text{group})} = \sum_v \hat{N}_{v(\text{group})}$$

respectively. Densities were estimated by dividing the abundance estimates by the area of the associated stratum. Average group size across strata was estimated by

$$\hat{E}[s] = \hat{N} / \hat{N}_{(\text{group})}.$$

Coefficients of variation (CV) and 95% confidence intervals (CI) were estimated by a non-parametric bootstrap (999 replicates) within strata, using transect segments as the sampling units. The variance due to estimation of ESW was incorporated using a parametric bootstrap procedure assuming the ESW estimates to be normally distributed random variables. More details on this method can be found in Scheidat et al. (2008, 2012).

Distribution maps

The distribution of harbour porpoises is shown as densities represented spatially on a 1/9 ICES grid. This grid has latitudinal rows at intervals of 10' and longitudinal columns

Table 1. Total survey days, effort (surveyed distance), sighting conditions (g – good, m – moderate, p – poor, x – not possible to observe) and harbour porpoise sightings during the aerial surveys. Calves are included in the number of individuals. Navigator sightings are excluded.

Survey	Effort (km)	Sighting conditions (%)			Harbour Porpoise sightings (*n*)		
		g	m	p/x	Sightings	Individuals	Calves
Mar 2013 (18, 19, 21)	950	20.9	69.7	9.4	76	87	-
Apr 2013 (6, 7, 21, 22)	2496	10.2	70.1	19.7	121	136	-
Mar 2012 (6, 13-15, 17)	3666	25.3	70.2	4.5	232	285	-
Jul 2017 (7-10, 17, 18)	2362	18.9	61.6	19.5	230	299	21
Jul 2015 (13-16, 20)	2333	0.7	95.2	3.9	144	172	13
Jul 2014 (11-13, 15, 16)	2791	20.0	72.7	7.3	229	273	20
Nov 2012 (14, 16, 18)	1157	0	82.9	17.1	28	35	-
Total	15,755	15.2	74.0	10.8	1060	1287	54

at intervals of 20'. Within the DCS, this corresponds to approximately 20x20 km grid cells, with areas ranging from 388 to 409 km^2. Densities per 1/9 ICES grid cell were calculated by dividing the total number of animals observed during good and moderate conditions by the total surveyed area. The surveyed area is the distance travelled multiplied by the effective strip width (ESW). Grid cells with low effort, such as grid cells extending outside the borders of the surveyed area, tend to be less reliable. Therefore, grid cells with an effort less than one km^2 were omitted from the maps (but the estimated numbers in these grid cells were used for the abundance estimates).

Results

Effort and sightings of harbour porpoises

Surveys were conducted in spring (2012, 2013), summer (2014, 2015, 2017) and autumn (2012), with a total of 15,755 km on effort (table 1). The spring surveys had the best coverage with 7122 km on effort. During both spring surveys, some track lines could be surveyed twice to ensure they were flown in moderate or good conditions. Even though yearly effort was lower in summer (7486 km), one set of track lines in areas A-D could be surveyed during the three survey periods. The survey effort in autumn 2012 was very low (1157 km), and apart from a complete set of track lines in area C – Frisian Front, only a proportion of the track lines in areas A-B and no track lines in area D – Delta could be surveyed. The coverage of the DCS and the number of sightings in autumn 2012 were too low to warrant sensible densities and abundance estimates.

In total, 1060 sightings of 1287 harbour porpoises were collected. Average group size for all surveys combined was 1.21 animals. Average group size was 1.18 (CV 0.36) animals in spring, and 1.25 (CV 0.51) animals in summer and autumn. The largest group size was a pod of eight animals in July. In all seasons over 80% of the sightings consisted of single animals. Calves were sighted during the summer surveys only (*n*=54), comprising 7.3% of the sighted individuals (*n*=744). The group size for sightings in July without calves was 1.14 animals.

Density and abundance of harbour porpoises

Tables 2 and 3 give an overview of density (animals/km^2) as well as abundance (number of animals) per survey area and survey period.

The overall DCS density in summer ranged from 0.70 to 1.29 animals/km^2 annually. Den-

Table 2. Density and abundance estimates and the associated 95% confidence intervals (CI) and coefficients of variation (CV) of Harbour Porpoises obtained in spring 2012 and 2013.

March-April 2013	Density (animals/km^2)	C95% CI	Abundance (*n* animals)	95% CI	CV
Area A – Dogger Bank	0.47	0.18-1.20	4492	1768–11,505	0.49
Area B – Offshore	1.44	0.47–3.48	24,268	7856–58,820	0.51
Area C – Frisian Front	0.59	0.31-1.24	7046	3663–14,907	0.36
Area D - Delta	1.32	0.66–2.83	27,602	13,815-58,987	0.36
Total DCS	1.07	0.55–2.17	63,408	32,478–128,588	0.35
March 2012					
Area A – Dogger Bank	1.44	0.69-2.72	13,860	6601-26,156	0.36
Area B – Offshore	0.70	0.25-1.51	11,877	4285-25,557	0.42
Area C – Frisian Front	0.94	0.33-2.09	11,252	4023–25,079	0.48
Area D - Delta	1.42	0.77-2.91	29,696	15,992–60,810	0.35
Total DCS	1.12	0.63-2.20	66,685	37,284-130,549	0.33

Table 3. Density and abundance estimates and the associated 95% confidence intervals (CI) and coefficients of variation (CV) of harbour porpoises obtained in summer 2014, 2015 and 2017.

July 2017	Density (animals/km^2)	C95% CI	Abundance (n animals)	95% CI	CV
Area A – Dogger Bank	0.14	0.01-0.29	1325	167–2833	0.46
Area B – Offshore	1.28	0.55-2.92	21,584	9229–49,331	0.44
Area C – Frisian Front	0.53	0.08-1.53	6360	991-18,402	0.64
Area D - Delta	0.85	0.41-1.66	17,631	8595–34,552	0.37
Total DCS	0.79	0.41–1.86	46,902	24,389–93,532	0.35
July 2015					
Area A – Dogger Bank	1.12	0.43-2.25	10,748	4113–21,676	0.39
Area B – Offshore	0.80	0.17-1.20	13,573	7 002–26,606	0.35
Area C – Frisian Front	0.44	0.20-0.98	5304	2354-11,798	0.43
Area D - Delta	0.56	0.41-1.58	11,674	3542-24,958	0.45
Total DCS	0.70	0.36-1.34	41,299	21,194-79,256	0.33
July 2014					
Area A – Dogger Bank	3.08	1.50-6.45	29,689	14,375–61,995	0.37
Area B – Offshore	0.37	0.00–1.21	6297	0–20,509	0.96
Area C – Frisian Front	1.83	0.97–4.11	22,010	11,623–49,439	0.39
Area D - Delta	0.90	9.46–1.84	18,778	9548–38,167	0.36
Total DCS	1.29	0.73–2.60	76,773	43,414-154,265	0.34

sities per area showed more variation, ranging from 0.14 to 3.08 animals/km^2. The overall DCS density in spring ranged 1.07-1.12 animals/km^2. For the areas A-D, the lowest density was 0.47 and the highest density 1.44 animals/km^2.

Absolute abundance of harbour porpoises on the Dutch Continental Shelf in summer was estimated at a minimum of 41,299 (CI: 21,194-79,256) in 2015 and a maximum of 76,773 (CI: 43,141–154,265) in 2014. The abundance estimate in 2017 numbered 46,902 (CI: 21,194-79,256) animals. The abundance estimate in March comprised 63,408 (CI: 34,478-128,588)

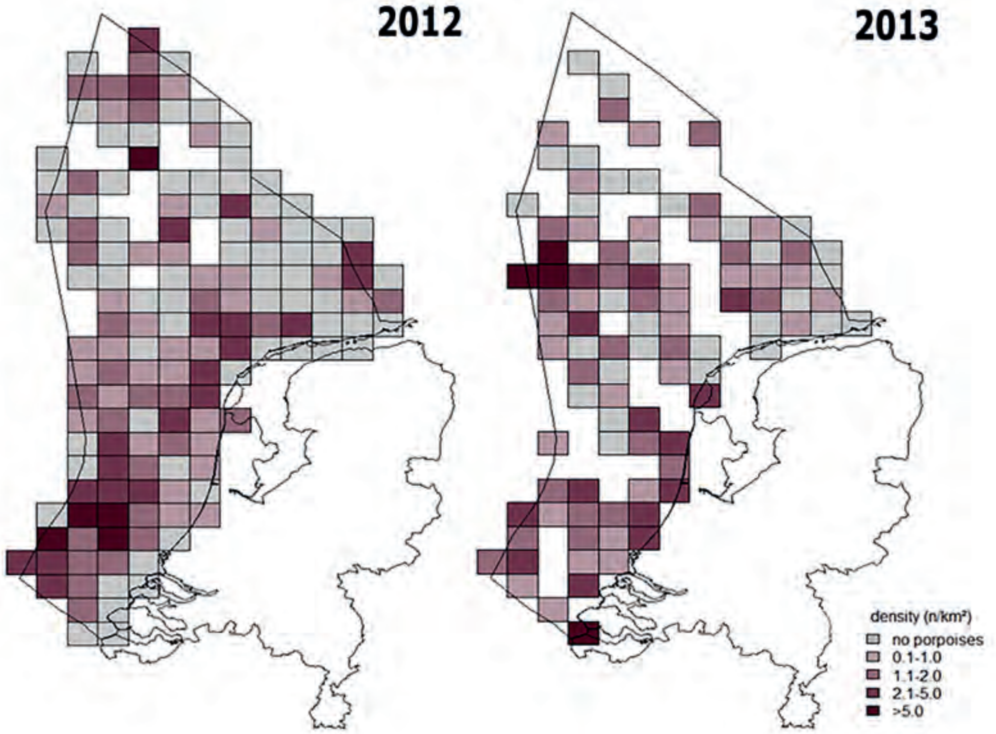

Figure 2. Density distribution of harbour porpoises (animals/km²) per 1/9 ICES grid cell, spring 2012 and 2013. Grid cells with low effort (<1 km²) are omitted.

and 66,685 animals (CI: 37,284-130,549) in 2013 and 2012 respectively (tables 2 and 3).

Distribution of harbour porpoises

Figures 2-3 show densities of porpoises (animals/km²) per 1/9 ICES grid cell. In spring, the distribution (figure 2) was homogeneous in the southern part of the DCS, from area D – Delta extending north of the Wadden Isles in area C – Frisian Front and B – offshore. In the eastern part of the latter areas, and further north in area A – Dogger Bank, the distribution was more heterogeneous, with low densities in bigger areas, especially in 2012. The summer distribution (figure 3) showed a consistent broad band of high(er) densities from area D – Delta to area C – Frisian Front north of the Wadden Isles in all three summers. In 2014, and to a lesser extent in 2015, this band of high densities continued to the German border in areas B – offshore and C – Frisian Front, whereas this area contained virtually no porpoises in 2017. In 2015 and 2017, high densities were present in large areas of area B – offshore, whereas densities in area A – Dogger Bank were lower. In 2014, however, densities in this area were the highest ever recorded.

Discussion

The results show distinct differences in densities, abundance and distribution of harbour porpoises between surveys. The summer densities for the years 2014-2017 varied between 0.14-3.08 animals/km² in the areas A-D, highlighting that the density between the sub-

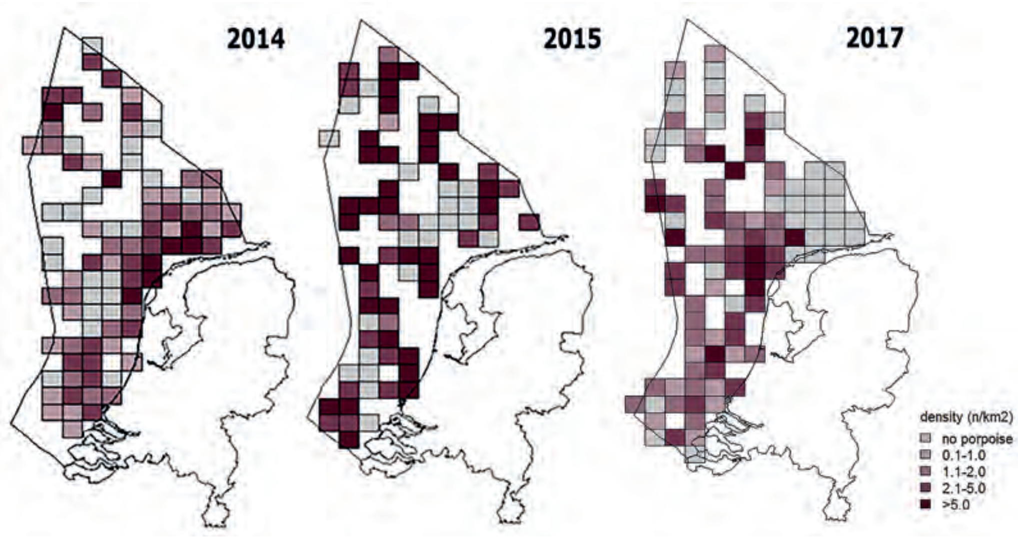

Figure 3. Density distribution of Harbour Porpoises (animals/km²) per 1/9 ICES grid cell, summer 2014, 2015 and 2017. Grid cells with low effort (<1 km²) are omitted.

areas is highly variable. The spring densities in 2012-2013 showed less variation (0.47-1.44 animals/km²), and fell within the range of the 2011 spring survey. In March 2011, the estimated densities of harbour porpoises on the Dutch Continental Shelf ranged from 0.90–2.98 animals/km², whereas the densities in summer 2010 ranged from 0.34–0.48 animals/km² (Geelhoed et al. 2013).

Based on the results of (aerial) surveys in Belgium, the Netherlands, Germany, Denmark, and the entire North Sea and the wider Dogger Bank region, Gilles et al. (2016) calculated an average density of 0.88 and 0.91 animals/km² in spring and summer, 2005-2013 respectively.

Despite inter-annual differences in abundance estimates for the DCS, the spring and summer numbers in 2012-2017 were of the same order of magnitude, whereas the numbers in spring 2010-2011 were three times as high as the numbers in summer and autumn (Geelhoed et al. 2013). The 2012-2017 spring and summer numbers are consistent with North Sea wide model-based abundance estimates, using SCANS II data and national surveys 2005-2013. These spring (*n*=372,167; CI: 260,658-531,380) and summer (*n*=361,000; CI: 243,827-534,913) estimates were similar, whereas the abundance estimate in autumn (*n*=228,913; CI: 159,264-329,022) was lower (Gilles et al. 2016).

Harbour porpoise in the Atlantic can be divided into several populations or management units (MUs). Evans et al. (2009) assessed these for the north-eastern Atlantic, and concluded that the North Sea should be divided into two MUs along an arbitrary line running NNW–SSE from northern Scotland to Germany-Denmark. The 'Dutch porpoises' would belong to the MU south of this line: the south-western North Sea and the eastern Channel MU. The boundaries of this MU are not well defined and an abundance estimate for this MU is lacking.

The wider North Sea, however, was surveyed during the summers of 2005 and 2016 (SCANS-II and SCANS-III), resulting in abundance estimates of 355,000 (CV 0.22) or 345,000 (CV 0.18) individuals respectively (using effective strip widths of 138 m for good conditions and 109 m for moderate conditions Hammond et al. 2017, revised from Hammond et al. 2013). Using EWS's of 170 m for good conditions, and 67 m for moderate conditions, Gilles et al. (2016) estimated the population size as numbering 361,000 individuals in summer 2005-2013. Smaller EWS's result in relatively high abundance estimates. With this in mind, however, these estimates indicate that a maximum of 7-21% of the North Sea population can be present on the Dutch Continental Shelf in summer (this study, and Geelhoed et al. 2013). In spring, the population size in the North Sea is estimated at 372,000 animals (Gilles et al. 2016). This corresponds to a proportion of at maximum 17-23% on the Dutch Continental Shelf (this study, and Geelhoed et al. 2013). At least part of the year, a substantial proportion of the porpoise population in the southern North Sea and the eastern Channel utilises the Dutch Continental Shelf.

Conclusions

By correcting for biases in the detection probability, aerial surveys provided un-biased abundance estimates of harbour porpoises on the Dutch Continental Shelf in spring and summer, 2012-2017. The results show that there is a strong seasonal and annual variation in density and abundance. In 2010-2011, the spring densities of porpoises were threefold higher than in summer. The recent results show that the summer occurrence of porpoises on the Dutch Continental Shelf increased and densities are now in the same order of magnitude as in spring. This higher number of porpoises, as well as the regular presence of mother-calf pairs, confirms that the Dutch Continental Shelf is of growing importance for porpoise reproduction.

Although the abundance estimates may show (large) variability, at least in spring and summer, a substantial proportion of the harbour porpoise population in the southern North Sea and the eastern Channel utilises the Dutch Continental Shelf. This emphasises the importance to fulfil requirements of the EU Habitats Directive and the EU Marine Strategy Framework Directive, to achieve and maintain a favourable conservation status for the harbour porpoise in Dutch waters. As recommended in the Dutch Harbour Porpoise Conservation Plan (Camphuysen & Siemensma 2011), repeated aerial surveys of the Dutch Continental Shelf have been conducted, providing information to assess trends and seasonal distribution patterns of harbour porpoises. However, as 'Dutch' porpoises belong to the southern North Sea and the eastern Channel population, transboundary surveys with larger spatial coverage should be conducted on a regular basis as well. A combination of six-yearly North Sea wide SCANS-type surveys and more frequent (national) smaller scale surveys would fulfil the fore mentioned requirements. Using such data in combination with a model based approach (e.g. Gilles et al. 2016) would allow predictions on how anthropogenic activities impact porpoises. This information is necessary to develop and implement management and protection measures in relation to anthropogenic activities for harbour porpoises in the North Sea.

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Samenvatting

Het voorkomen van bruinvissen (*Phocoena phocoena*) op het Nederlands Continentaal Plat: vliegtuigtellingen in de jaren 2012-2017

De bruinvis (*Phocoena phocoena*) is de algemeenste zeezoogdiersoort in Nederlandse wateren. In voorjaar, zomer en najaar 2012-2017 werden vliegtuigtellingen langs vooraf ontworpen *track lines* uitgevoerd op het Nederlands Continentaal Plat (NCP). Met deze gegevens was het mogelijk dichtheden en aantalsschattingen van bruinvissen op het

NCP te berekenen voor voorjaar en zomer. Het was niet mogelijk om dichtheden en aantalsschattingen voor het najaar te berekenen. De aantallen in het voorjaar (*n*=63.408-66.685) lagen in de zelfde ordegrootte als in de zomer (*n*=41.299-76.773). Het verspreidingspatroon verschilde per telperiode, maar gedurende alle telperioden was een strook met hogere dichtheden aanwezig van het zuidelijk deel van het NCP tot een gebied ten noorden van de westelijke Waddeneilanden. In juli werden kalfjes gezien, hetgeen een bevestiging vormt dat bruinvissen zich regelmatig in Nederlandse wateren voortplanten. De aantalsschattingen voor het voorjaar en de zomer corresponderen met respectievelijk maximaal 17-21% en 7-23% van de populatie in de zuidelijke Noordzee; een groot deel van de Noordzeepopulatie verblijft in die periode in Nederlandse wateren.

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Feeding behaviour of harbour porpoises (*Phocoena phocoena*) in the Ems estuary

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Abstract: Passive acoustic monitoring (PAM) was used to study the occurrence and distribution of feeding behaviour of harbour porpoises (*Phocoena phocoena*) in the Ems estuary, on the border between the Netherlands and Germany. Occurrence was expressed as detection positive hours (DPH) per month or station, and feeding behaviour was described as feeding buzz ratio (FBR). Three types of analyses were undertaken: 1. A year-round analysis of FBR and DPH for one PAM station close to the Ems harbour; 2. An analysis of FBR and DPH for 10 PAM stations in the Ems estuary in March and September 2010; and 3. A comparison of porpoise clicks and fish density in the area for September/October of 2010. The year-round analysis results showed a variable seasonal pattern of porpoise occurrence, with in general lower values in April–July, and higher values in August–December. FBR and DPH per station differed between March and September 2010. The March data shows an increase of DPH when moving from the Wadden Sea into the estuary, with at the same time an increase in FBR. In September 2010, DPH decreased from outside to inside the Ems estuary, coinciding with an increase in feeding behaviour. Fish density was analysed for 5 potential prey taxa (smelt, whiting, goby, flounder and herring) at sampling stations in 4 areas along the estuary. Flounder and smelt increased in occurrence towards the inner estuarine waters. Smelt is an anadromous fish that is a known prey species for porpoise. The results of this study suggest that while feeding activity and occurrence of porpoises is observed all along the estuary and throughout the whole year, the presence of a preferred prey might be the reason for porpoises to move far into the Ems estuary at specific times. The Ems is highly used by humans and some activities, such as construction work and intense shipping, could have potential harmful consequences to the locally occurring porpoises. As this study has only covered a short time frame, the results should be considered preliminary. Future studies on the investigation of fish and porpoise occurrence in this area would allow a more in-depth understanding of this relationship and would be of high relevance for conservation and management actions.

Keywords: harbour porpoise, *Phocoena phocoena*, C-POD, feeding buzzes, behaviour, Ems estuary, smelt, anadromous fish.

Introduction

Ranking amongst the smallest of cetaceans in the world, harbour porpoises (*Phocoena phocoena*) are usually found in coastal seas and estuaries in temperate northern climes (Perrin et al. 2002). With a short nursing period (usually less than a year) and reaching sexually maturity at three years, the resting period between pregnancies is brief (Santos & Pierce 2003). The consequence of this feature, plus their small size, is that they cannot store much energy, which makes them highly dependent on year-round food availability (Brodie 2001).

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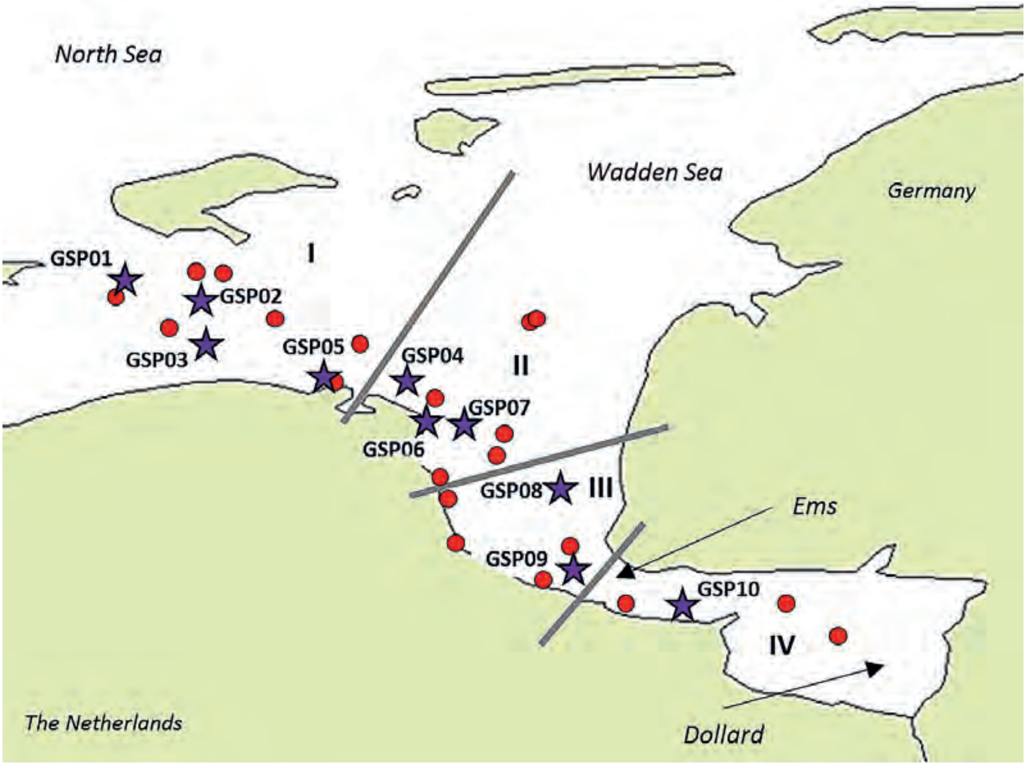

Figure 1. Location of C-PODs (stars; GSP01 to GSP10) in the study area in the Ems-Dollard estuary. The fish sampling stations are represented as dots. The roman numbers (I-IV), indicate the areas used for comparing acoustic and fish sampling data.

According to Brodie (2001), the distribution of this species may strongly reflect the distribution and energy density of their prey.

Harbour porpoise is also the most abundant cetacean species found in Dutch North Sea waters (Hammond et al. 2002, 2013, Geelhoed et al. 2013). Aerial surveys conducted on the Dutch Continental Shelf in 2010 and 2011 showed distinct differences in abundance and distribution between seasons (Geelhoed et al. 2013). Highest densities were found in March, with almost threefold higher values than during summer and autumn (Geelhoed et al. 2013). This observed pattern fits the general seasonal occurrence seen along the Dutch coast during systematic land-based observation (Camphuysen 2011, Camphuysen & Siemensma 2011). Surveys in the Dutch Continental Shelf conducted from 2012-2017, however, suggest that the numbers in summer can be much higher than in spring (Geelhoed & Scheidat 2018).

Harbour porpoises consume a wide variety of fish and cephalopods, and their main prey items appear to vary regionally and seasonally as well as between individuals (Leopold 2015). Several years ago, Santos & Pierce (2003) found the main food source of porpoises in the Netherlands to be whiting (*Merlangius merlangus*), making up around 34% of the total reconstructed prey weight. More recent studies have shown that whiting is still important in the diet of porpoises along the Dutch coast and that herring (*Clupea harengus*), cod (*Gadus morhua*), sprat (*Sprattus sprattus*), gobies (Gobiidae) and lesser sand eel (*Ammodytes* sp.) (Jansen et al. 2013, Leopold 2015) are further key prey.

From mid-2009 to 2014, the effect of construction activities in and around the Ems estuary on harbour porpoise occurrence was studied (Brasseur et al. 2010, Lucke et al. 2011, 2012, Kirkwood et al. 2014). Acoustic data loggers were used to investigate their relative abundance on both temporal and spatial scales (Brasseur et al. 2010, 2011, Lucke et al. 2012). For this paper, we have re-analysed this dataset to specifically investigate acoustically detectable behaviour associated with foraging in the Ems estuary. We explore whether there is a seasonal pattern and geographic variation in feeding behaviour and if any observed patterns can be explained by fish distribution.

Material and Methods

Study site

The Ems-Dollard area is one of the two last open, natural estuaries in the Netherlands (figure 1). It is defined as the semi-enclosed body of water that stretches from the island of Borkum to the end of the range of tidal influence at the flood defence weir in Herbrum (Talke et al. 2006, Bos et al. 2012). The prevailing physical forces that affect the estuary are the tides, wind (both waves and shear), and the freshwater inflow from both the Ems River and the Westerwoldse Aa (Talke et al. 2006, Baptist 2017).

Acoustic monitoring

Harbour porpoises produce distinctive signals, lasting about 50–150 microseconds, with the main part at around 132 kHz within a narrow band between 120–150 kHz (e.g. Au et al. 1999, Teilmann et al. 2002, Madsen et al. 2010). This makes them ideal for automatic detection as most other sounds in the sea, barring some boat sonars, are broadband or lower energy frequencies and can thus be filtered out during post-processing of data (Tregenza 2012). Porpoise click trains are recognisable by a gradual change of click intervals and amplitudes throughout a click sequence, whereas boat sonars and echo sounders have highly consistent inter-click intervals (Tregenza 2012).

C-PODs (Continuous-Porpoise Detectors, Chelonia Ltd., Mousehole, UK) are acoustic data loggers widely used to study porpoises and other odontocetes that are producing high frequency clicks (e.g. Brasseur et al. 2010, Scheidat et al. 2006, 2012, Tougaard et al. 2006, 2009, Castellote et al. 2012). They consist of a polypropylene casing with hydrophone housing at one end, and a removable lid on the other. Contained within the housing is an amplifier, a digital waveform analyser, a data-logger that continuously logs echolocation click-activity and 10 D-cell batteries. A summary of click features is logged, such as time, duration, dominant frequency, bandwidth and amplitude, and stored on a secure digital flash card (SD).

Ten C-POD locations were chosen between the island of Borkum and Dollard (Brasseur et al. 2010, 2011; see figure 1). The water depth at the C-POD locations ranged from 8 to 15 metres (Brasseur et al. 2010). The devices were anchored to a weight and attached to a light buoy equipped with an alarm, the C-POD itself positioned about a metre above the bottom. Every 8–10 weeks, the C-PODs were retrieved to offload the data, replace batteries and for general maintenance (Brasseur et al. 2010). Data were collected from April 2009 until January 2011. Because of icy conditions, and the related risk of damage and loosening of the buoys attached to the C-PODs, the buoys and associated C-PODs GSP 07, GSP 08 and GSP 09 were retrieved on 23 December 2010; the GSP 10 C-POD was lost (Brasseur et al. 2011).

Feeding behaviour

Harbour porpoise use their narrowband high frequency echolocation clicks to communi-

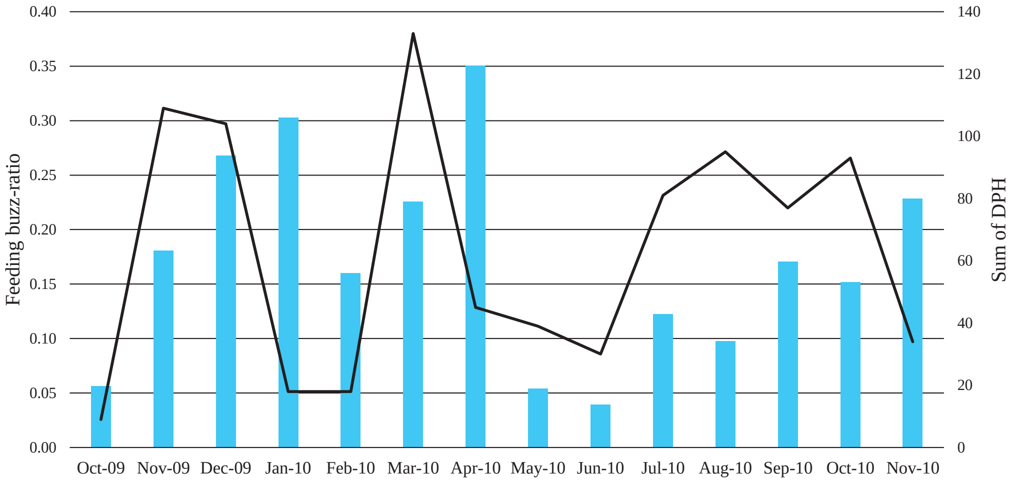

Figure 2. Feeding buzz-ratios (FBR) per month (blue bars) versus acoustic activity expressed as the summation of detection positive hours (DPH) per month (black line) for C-POD location GSP03.

cate, navigate and hunt (Verboom & Kastelein 1995, 1997, Au et al. 1999, Teilmann et al. 2002, Madsen et al. 2010). To find their prey, they emit high-powered, directional clicks and subsequently receive and process the returning echoes (Madsen et al. 2010). A number of studies have investigated how the varying interclick interval (ICI) between clicks may be used to distinguish different acoustic behaviours (Koschinski et al. 2008, Verfuss et al. 2009, Miller et al. 2010). During foraging, after a stable ICI of 50–60 ms (the initial part of the approach phase), the interval decreases progressively (Miller et al. 2010). When closing in on prey, the ICI drops sharply from roughly 50 ms to below 20 ms. Within the last one metre, the click train ends with a “buzz”, with an ICI below 2 ms, indicating prey capture (Carlström 2005, Verfuss et al. 2009, Miller et al. 2010, Nurminen 2010). These click trains are often referred to as feeding buzzes (Nurminen 2010) and have been used as an indicator of feeding activity (e.g. Weel 2016). These buzzes have been seen to continue beyond the first contact with the fish, often extending after the fish has been caught (De Ruiter et al. 2009).

The minimum or maximum ICI per train is the shortest or respectively longest recorded period between two successive clicks within a train (Carlström 2005). Click sequences with a minimum ICI below 10 ms have been used as an indicator for foraging activity for porpoise (Carlström 2005, Todd et al. 2009, Verfuß et al. 2009, Linnenschmidt et al. 2013, Nuuttila et al. 2013). Pirotta et al. (2014) used C-POD data to calculate the inter-click intervals (ICIs). Each ICI was classified as either a regular ICI (regular clicking for navigation and prey searching), a buzz ICI (buzzes associated with attempted prey captures or social communication), or an inter-train ICI (pauses between click trains). They found changes in buzz occurrence related to seismic activity. Schaffeld et al. (2016) found that foraging sequences of harbour porpoises can show extreme variations in ICI before a sudden decrease to below 10 ms. They analysed the data by using those sequences that showed a sudden decrease in ICI, of at least 5 clicks with an ICI <10 ms and with clicks at an ICI level between 40 and 70 ms before the decrease. Their results indicate that the most stereotypical part of foraging sequences is the sudden decrease in ICIs, and that using this value instead of the ICIs below 10ms is providing a conservative, but likely more accurate, indicator than only using the ICI.

At sea, a correlation between buzz activity and feeding success should not be assumed *a priori* without experimental evidence, since a higher buzz rate could just mean that more effort is put into capturing the same amount of prey (Todd et al. 2009). A proxy of potential feeding activity could be inferred, however, by investigating the relative incidence of rising click rates, emitted during range locking echolocation behaviour, and the accompanying decrease of ICI (Verfuss et al. 2002, Carlström 2005, Johnson et al. 2006, Todd et al. 2009, Leeney et al. 2011).

For this study, we used the feeding-buzz ratio (FBR) as an indicator of likely porpoise feeding activity (Todd et al. 2009, Leeney et al. 2011). The term feeding-buzz ratio was borrowed from bat literature (e.g. Vaughan et al. 1996, Turner 2002). Using the feeding-buzz ratio will help obtain a relatively continuous value of activity. In their study on porpoises, Todd et al. (2009) generated these ratios by dividing the number of trains with a minimum ICI (MICI) of <10 ms by those with MICIs of >10 ms for each diel phase. A similar approach was used by Leeney et al. (2011) in their study on Heaviside's dolphins (*Cephalorhynchus heavisidii*), but instead of minimum ICI, they used the mean ICI. This method allows for a ratio of fast, possibly feeding associated, click trains, to all other trains (Todd et al. 2009). A value greater than one would indicate that a greater proportion of porpoise click trains have ICIs <10 ms, indicative of potential feeding, and *vice versa* (Todd et al. 2009). A value of one would mean a near 50/50 share of clicks more or less than 10 ms. A higher ratio suggests more time spent producing buzz trains, and therefore possible feeding behaviour (Leeney et al. 2011). They base their description of a minimum ICI per train on Carlström (2005) and Philpott et al. (2007), and use 10 ms as a proxy indication of porpoise feeding activity (Todd et al. 2009).

One unresolved issue is that when animals move their heads side to side while searching for prey, click trains are recorded only partially. In addition to this, the actual number of click trains is influenced by the algorithm in the CPOD.exe program, which splits trains more often when the ICI is long. An assessment to what degree the number of trains created is consistent under different scenarios would therefore be very helpful for future analyses.

For our analyses, we followed Carlström (2005) and used the minimum ICI for the analyses. Whilst Carlström (2005) used the older model T-PODs, this approach was deemed useful to describe potential feeding activity for the newer C-PODs as well. To increase the chance of obtaining actual feeding click trains and in lieu of more recent studies (e.g. Koschinski et al. 2008, Verfuss et al. 2009, Nurminen 2010), an MICI of 3 ms was used in Weel (2016), instead of 10 ms. Buzz ratios were recorded on nearly all days, except for 21-31 October 2009 and 1-12 November 2010. More details on the performance of the feeding-buzz ratio in comparison to the visual detection of feeding buzzes can be found in Weel (2016).

Fish monitoring

The Demersal Fish Survey (DFS), an annual beam trawl survey, run by Wageningen Marine Research, is carried out in coastal waters from the southern border of the Netherlands to Esbjerg, Denmark (down to 25 m depth) (van Beek et al. 1989, Tulp et al. 2017). The survey also covers the Wadden Sea and the outer part of the Ems-Dollard estuary, and occurs during the period September-October (van Beek et al. 1989). The survey is stratified by regions, demarcated according to tidal basins or other geographic features (Boddeke et al. 1972).

Within the Wadden Sea and Ems estuary, sampling was carried out with a 3 m beam trawl (Tulp et al. 2017). The beam trawls were equipped with one tickler chain, a bobbin rope, and a fine-meshed cod-end (20 mm). Both gears were rigged in the same way; only the size of the beams varied. Fishing was limited to the tidal channels and gullies deeper than 2 m because of the draught of the research vessel. The combination of low fishing speed (2-3 knots) and finer mesh size results in the selection of smaller fish species and younger year classes (Tulp et al. 2017).

To study the possible links between porpoise and fish presence, data on the abundance of five potential fish prey species (smelt (*Osmerus eperlanus*), gobies, flounder (*Platichthys flesus*), herring and whiting) were used from the DFS. The study area was divided into four sub-areas and the average density of the five potential fish prey species was calculated for each area. As shown in figure 1, the C-PODs positioned in the Wadden Sea (GSP 01, 02, 03 and 05) were designated to area I; those near the outer part of the Ems (GSP 04, 06 and 07) to area II; those midway the Ems (GSP 08 and 09) to area III and POD GSP 10, positioned near Dollard, to area IV. For comparison with the fish data, the C-PODs were analysed for the period of 1-23 September 2010 for each of the sub-areas.

Data analysis

The C-POD data were analysed with the software from the manufacturer (CPOD.exe version V2.044, Chelonia Ltd). The default settings were used, for instance 'all cetacean species', unmodified 'train values', and 'click filters' (for more details see Brasseur et al. 2010, 2011). Only 'Hi' and 'Mod' trains were analysed, which is the designation CPOD.exe uses for trains most likely to have been produced by the target species. All automatic detections, and how their click train type is classified, were manually checked. Manual analysis also permitted exclusion of multiple false detections caused by noise, which are relatively easy to recognise by their broad frequency coverage, lack of coherence in temporal scale, pulse bandwidth, number of cycles and envelope (Castellote et al. 2015). Checking for false detections was only done for the one-year overview analysis and was not quantified.

Average counts of feeding buzzes as defined for this study were obtained for each day of every month and location where possible (similar to the study of Nurminen 2010). Next, the click activity data were aggregated into daily values of minutes in which porpoise clicks were detected. The parameter used was detection positive 10 minutes per day (DP10M/day), as the number of detections was usually low, and this measure minimises potential differences in sensitivity between C-PODs (Haelters et al. 2011). In addition, for this study, detection positive hours (DPH) were summed per day to obtain DPH/day, and further aggregated to DPH/month. The DPH value provides a proxy for porpoise occurrence. As mentioned above, min ICIs values were extracted from the data for the feeding-buzz ratio determination. More details on the data collection methodology can be found in Brasseur et al. 2010.

For the C-POD location GSP 03 (see figure 1), data have been logged for several years (Brasseur et al. 2010, 2011, Lucke et al. 2011). We chose GSP 03, as this location provided more than one continuous year of complete data. The dataset comprised 389 days of continuous recordings from 20 October 2009 to 12 November 2010.

Results

Seasonal and spatial pattern

The C-POD location GSP 03 showed that FBR varies greatly over time, with the highest feeding buzz ratio found in April 2010 and the lowest in June 2010 (figure 2). Porpoise occurrence (expressed as DPH per month) seems to show a more regular pattern with the high-

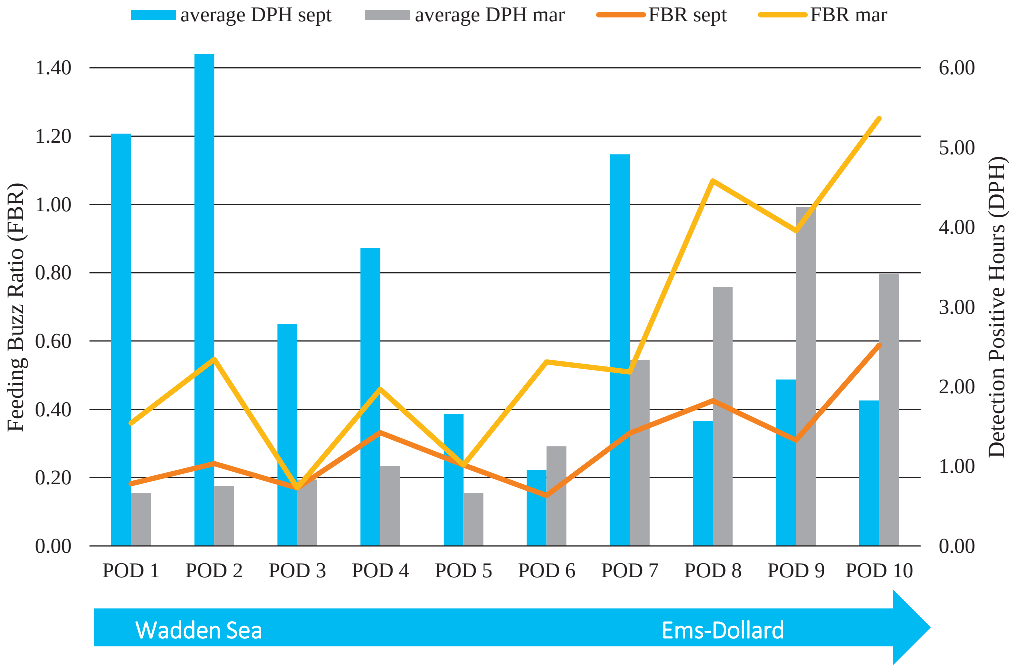

Figure 3. Feeding buzz ratio (FBR) determined for all C-PODs during 1-21 September (orange line) and 17-28 March (yellow line) in 2010 and detection positive hours (DPH) determined for all C-PODs during 1-21 September (blue bar) and 17-28 March 2010 (grey bar).

est click activity recorded from November to April, a strong decrease in May, and a gradual increase again in the late summer. In some months both FBR and DPH are high, which is to be expected as more animals clicking should lead to more feeding buzzes occurring. However, this is not always the case as some months show a reverse pattern. For example, in January 2010, porpoise occurrence is low while the FBR is high, while in August 2010, feeding buzz-ratio is low and DPH values are high.

DPH and feeding buzz-ratios showed no clear linear relationship and no significant correlation (Pearson's correlation coefficient -0.392, *P*-value 0.166; Spearman correlation coefficient -0.213, *P*-value 0.463).

The highest FBR is seen in POD stations 8, 9 and 10 in March 2010, and the highest FBR for POD 10 in September (figure 3). This suggests feeding activity was highest in March near POD stations 8, 9 and 10, and highest in September around POD 10. POD 3 and 5 showed low FBRs in March. FBR increased from outside the estuary upstream both in March and in September. DPH for both periods is also shown, the highest found during September for POD 1, the lowest found in March for POD 5. There is a generally lower number of DPH during March for most PODs, except at the inner estuary for PODs 8, 9 and 10.

The pattern of average DPH and FBR differed between March and September 2010. In March, both DPH and FBR increase from the Wadden Sea into the Ems-Dollard estuary. By contrast, in September the occurrence of porpoises is lower than in March for the first five POD stations, but higher for the last three. The FBR still increases with distance from the Wadden Sea.

The relationship between average DPH and FBR (figure 4) in March 2010 showed a significant positive correlation (Pearson's correlation coefficient 0.840, *P*-value 0.002; Spear-

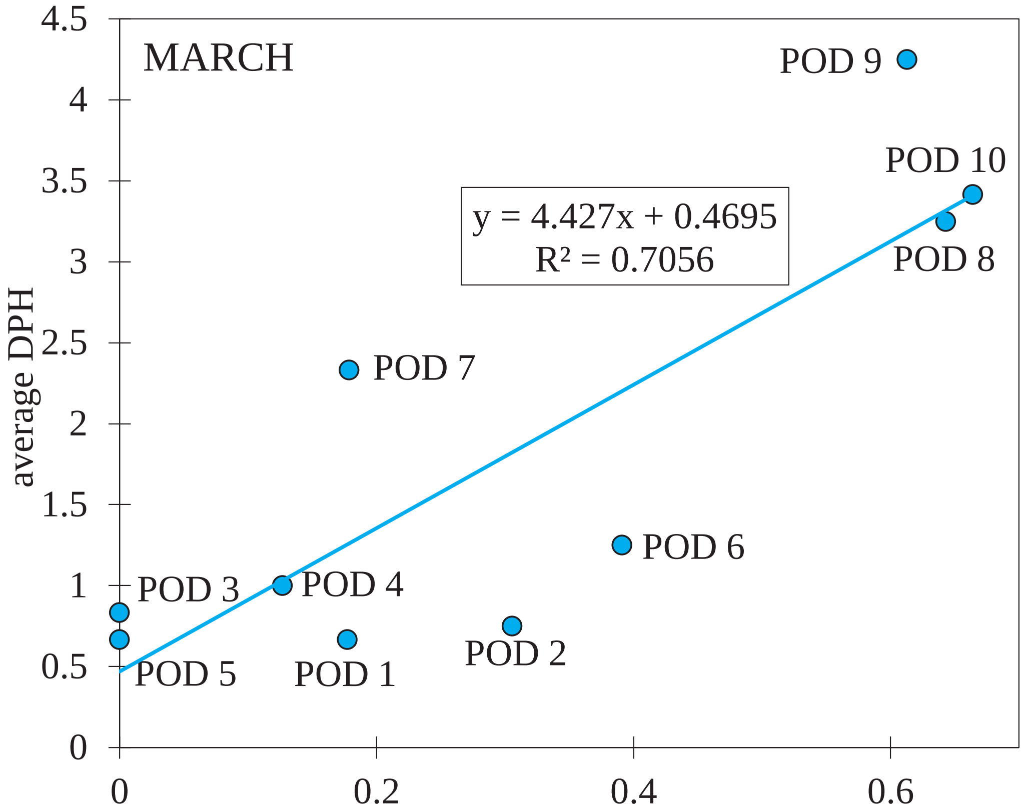

Figure 4. Scatter plot showing average detection positive hours (DPH) and feeding buzz ratio (FBR) per C-POD station (POD 1 to POD 10) for March 2010.

man correlation coefficient 0.777, *P*-value 0.012) whereas average DPH and FBR in September 2010 showed no significant correlation (Pearson's correlation coefficient – 0.212, *P*-value 0.557; Spearman correlation coefficient – 0.006, *P*-value 1).

Relation to fish occurrence

To investigate the relation between harbour porpoise and fish occurrence in the Ems we analysed a sub-sample of the C-POD dataset for the period from 1-23 September 2010. The fish sampling took place in September and October at the sampling stations shown in figure 1. To compare fish density with acoustic activity, the study area was sectioned into four areas (figure 1). The selection of the C-POD data time period was driven by the availability of complete data sets from all stations which allowed a direct comparison of the results.

Figure 5 shows the average fish density (per species) for all stations per area, in relation to the average DPH and FBR recorded on the C-PODs per area. The results show that acoustic activity of porpoises halved from area I towards area IV. At the same time, the feeding buzz ratio approximately triples from area I to area IV.

The occurrence of the five fish taxa in the Ems differs between the sample areas. Both smelt and flounder density increase upstream, while gobies, whiting and herring decrease (figure 5).

The data indicate that an overall increase in

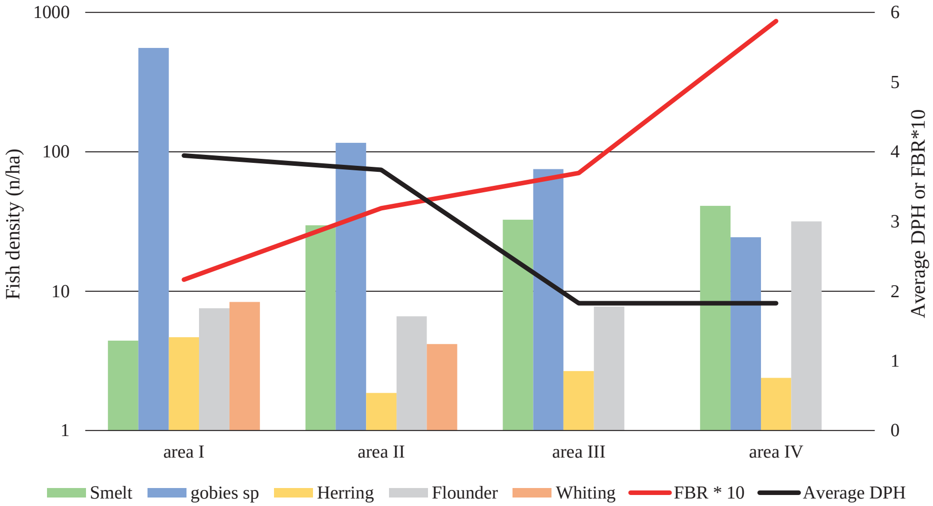

Figure 5. Average fish density for five taxa for all stations per area (expressed as n/ha on a logarithmic scale) and average DPH per area (black line) and FBR (red line, shown as FBR*10) for the period 1-23 September 2010.

fish abundance is not necessarily an indicator of an increase in foraging behaviour by harbour porpoises. Only for smelt and flounder is there an increase in fish abundance and FBR. For the other species, gobies, whiting and herring, this pattern is reversed (figure 5).

Discussion

Harbour porpoise distribution in the North Sea has shifted over the last two decades from the northern and central North Sea to the central and southern North Sea (Hammond et al. 2002, 2013, 2017). This is most likely the reason for the increase in porpoise occurrence in Dutch North Sea waters since the late 1990s (Camphuysen 2004). There are indications that the driving factors for this change could be linked to a change in prey availability (Camphuysen 2004, MacLeod et al. 2007), although the evidence is mostly circumstantial. Harbour porpoise occurrence in the Dutch sector of the North Sea shows a strong seasonal pattern, with highest densities in the early spring and lowest numbers in the summer (Geelhoed et al. 2013), although with an increase in summer densities this seasonal difference has been less distinct in the last few years (Geelhoed & Scheidat 2018).

There has been a number of studies showing that click frequency, and in particular the metrics of detection positive hours, can be used as a reliable proxy for the density of porpoises (e.g. Williamson et al. 2016, Anonymous 2016). Based on this premise, the C-POD monitoring study in the Ems shows that although there are seasonal changes with lowest density of porpoises in the winter (Brasseur et al. 2010), porpoises occur in the estuary year-round. The seasonal comparison specifically for station GSP03 showed that the lowest numbers of porpoises occurred in May and June. The comparison of all C-POD sampling stations between March and September shows a more complex pattern, indicating that in September porpoises are present throughout the estuary, with more animals occurring downstream, whilst in March this pattern notably changes, with more activity upstream. Interestingly, the feeding buzz ratio in both cases is showing a clear increase from the outer C-POD stations to the inner C-POD stations, indicating a relatively high occurrence of foraging behaviour in that area for both these months.

Harbour porpoises have a large body surface to volume ratio, and they require relatively large amounts of food (Kastelein 1998, Leopold 2015). Recent work using high-resolution sound and movement tags on porpoises have shown porpoises may hunt up to 550 small fish prey per hour with a >90% capture success rate (Wisniewska et al. 2016). Prey with high energy density, if available, is generally preferred (Leopold 2015). Harbour porpoises have been found to take small schooling fish with a high lipid content (Jansen et al. 2013, Leopold 2015). For example, animals feeding in the Western Scheldt showed the highest average energy density of prey of all sampled Dutch porpoises due to the smelt being eaten here (Leopold 2015). However, the costs of the hunt and the skills needed to catch certain prey probably also determine which prey is taken. Leaner prey species, such as gobies, dominate the prey of young porpoises (Leopold 2015). Specific needs, as well as foraging skills, probably vary amongst individual porpoises and with age, body condition, as well as reproductive status (Leopold 2015). Environmental factors (such as season, tidal state, sea temperature, time of day) further impact porpoises as well as their prey, thus driving the observed pattern. The local variation in fish occurrence adds to the complexity of the situation.

Our study indicates that porpoises in the inner waters of the Ems show a higher feeding buzz ratio in comparison to the area closer to the Wadden Sea. As the Ems estuary waters are turbid, with an increase from the outer to the inner estuary, one could hypothesise that this might have an impact on the echolocation of porpoises and affect the results for FBR as well. Several studies have shown that porpoises tend to use stable mean inter click intervals when navigating, as well as during the search and approach phases for prey (e.g. Teilmann et al. 2002, de Ruiter et al. 2009). These ICIs are all at least an order of magnitude larger than those for feeding buzzes (de Ruiter et al. 2009). Thus, one would expect that if porpoises need to intensify their echolocation to find prey or to navigate, that they would increase the overall click frequency. In contrast, our results point to an increase in FBR, which means a higher occurrence of feeding buzzes with very short ICIs of 3 ms or lower.

One hypothesis that could explain the apparent increase of feeding buzzes in the inner Ems estuary is that porpoises encounter prey here, such as the European smelt. Smelt is an anadromous fish that occurs in the estuary and migrates upstream from February to May. Its abundance has increased over the last decades in the Eastern Wadden Sea as well as in the Ems Dollard estuary (Tulp et al. 2017). Smelt swim upstream to spawn in February-March when the water temperature reaches 5°C (de Groot 2002). As the exact start of the smelt migration is dependent on water temperature, it is likely that there is an inter-annual variance in the onset of migration for smelt. At spawning, smelt form aggregations that may provide good feeding opportunities for porpoises. During our study, the time period in which our data on the overlap of fish occurrence and porpoise acoustic behaviour is fairly short. Also, the sample stations for fish and porpoises are not exactly in the same locations, and by pooling the data into larger areas, potential small-scale variation between stations is not considered. To appropriately determine how fish, and in particular smelt occurrence influences the behaviour of porpoise in the Ems estuary, a designated multi-year study of fish and porpoise occurrence, as well as feeding behaviour, would be needed.

A study on porpoises in the river Weser (Wenger & Koschinski 2012) confirmed that porpoises move up into the river and that this is a comparatively recent phenomenon. Porpoises have also increased in the Elbe River in Germany (Wenger & Koschinski 2012, Wenger et al. 2016) and in the Western Scheldt in the Netherlands (Leopold 2015). For all three cases, the observed occurrence was linked to the presence of anadromous fish.

The fact that porpoises are (re-)entering our estuaries and rivers can be considered good news. It is most likely an indicator of an abundance of prey that is highly sought-after due to their high energy content. However, when porpoises enter the Ems estuary, they are also entering an area that is intensively used by humans. Therefore, by following their prey, they are risking negative effects from anthropogenic activities. Even though contamination of the Ems has decreased, concentrations of polychlorinated biphenyls (PCBs) and dichlorodiphenyltrichloroethanes (DDTs) measured in organisms are still considerable high (Bos et al. 2012). The large number of vessels potentially causing risk of ship strike, construction works and other noise sources, most likely lead to an increase in stress for porpoises. However, the benefit of having high quality prey may outweigh the potential negative effects of anthropogenic activities.

Using C-POD data to analyse porpoise behaviour has some caveats, since the data lack full spectrum acoustical information, and the C-POD might not be in the path of the narrow echolocation beam of a foraging animal (Linnenschmidt et al. 2013). For benthic prey, porpoises will direct their search effort, and thus their buzzes, towards the bottom. For pelagic prey, which also tends to be more mobile, buzzes will occur in the water column. Sostres Alonso and Nuuttila (2014) discuss that changing foraging strategies could explain differences in click detection between different deployment depths of C-PODs.

We have described a number of studies that have attempted to improve the analyses of C-POD data to quantify when porpoises are catching prey (Pirotta et al. 2014, Schaffeld et al. 2016, Nuuttila et al. 2018). A thorough comparison to see which of these approaches is best is still lacking. From detailed foraging data collected in captivity (Verfuss et al. 2002), it is clear that C-POD data provide a very limited sample of the actual acoustic behaviour of porpoises. Recent work, using detachable tags recording the acoustic activity of porpoises, has confirmed this by providing in-depth information on foraging behaviour and actual feeding events in the wild (Wisniewska et al. 2016). In future studies, it would be good to use these data sets to allow a better interpretation of C-POD data. An assessment of the most adequate approach, in combination with an automated analysis tool, would allow analyses of the large amount of data that has been collected in the past. This could lead to important insights in the foraging behaviour of porpoises.

Our study explored porpoises in the Ems Dollard estuary, and offers the hypothesis that there is a link between increased feeding behaviour and the seasonal occurrence of prey. To fully test this hypothesis, designated studies would be needed that focus on both porpoise and fish at the same spatial and temporal scale, and that would consider both physical and biological factors that could affect data collection for the two taxa. Future work to obtain an improved understanding on this phenomenon – and how it links to environmental parameters, the presence of certain fish species, and its variation over time – is especially important to ensure adequate conservation action for the Ems harbour porpoise.

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Samenvatting

Foerageergedrag van bruinvissen (*Phocoena phocoena*) in het Eems-estuarium

Om het voorkomen en de verspreiding van foerageergedrag van bruinvissen (*Phocoena phocoena*) in het Eems-estuarium te bestuderen is gebruik gemaakt van Passieve Akoestische Monitoring (PAM). Het voorkomen werd uitgedrukt als 'detection positive hour' (DPH): een uur dat een bruinvis is gedetecteerd. De mate waarin naar verwachting foerageergedrag plaatsvond werd beschreven als 'feeding buzz ratio' (FBR). Hiermee werden drie analyses gedaan: 1. Een jaarrondanalyse van DPH en FBR voor een PAM-station vlakbij de Eemshaven; 2. Een analyse van DPH en FBR voor tien PAM-stations in het Eems-estuarium in maart en september 2010; 3. Een vergelijking van bruinvisactiviteit met visdichtheid in het gebied in september-oktober 2010. De jaarrondanalyse liet een seizoenspatroon in het voorkomen van bruinvissen zien, met over het algemeen lagere waarden in april-juli en hogere waarden in augustus-december. FBR en DPH per station verschilden tussen maart en september 2010. De maartgegevens tonen een landinwaartse toename van zowel DPH als FBR van de Waddenzee naar het estuarium. In september 2010 daalde DPH van buiten naar binnen in het Eems-estuarium, wat samenviel met een toename van het foerageergedrag. Visdichtheid werd bepaald voor vijf potentiele prooisoorten (spiering, wijting, grondel, bot en haring) op bemonsteringsstations in

vier gebieden in het estuarium. Bot en spiering namen toe van de Noordzeekant naar de binnenwateren van het estuarium. Smelt is een anadrome vis die bekend is als prooisoort voor bruinvissen. Deze studie suggereert dat bruinvissen het gehele jaar in het gebied voorkomen, en dat foerageergedrag jaarrond plaatsvindt, maar dat de aanwezigheid van een geprefereerde prooi de reden kan zijn dat bruinvissen op bepaalde tijden ver het Eems-estuarium in zwemmen. In de Eems vinden veel menselijke activiteiten plaats, waarvan sommige, zoals bouwwerkzaamheden en intensieve scheepvaart, mogelijk schadelijke gevolgen kunnen hebben voor de aanwezige bruinvissen. Aangezien deze studie slechts een korte periode beslaat, moeten de resultaten als voorlopig worden beschouwd. Toekomstige studies naar de relatie tussen het voorkomen van prooivissen en bruinvissen in dit gebied kunnen leiden tot een beter begrip van deze relatie en kunnen daarom van groot belang zijn voor beschermings- en beheersmaatregelen.

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Spatiotemporal trends in white-beaked dolphin strandings along the North Sea coast from 1991–2017

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Abstract: The white-beaked dolphin (*Lagenorhynchus albirostris*) is an endemic species in the North Sea with an estimated population of around 36,000 individuals. Recently, concerns have been raised among conservationists regarding increasing water temperatures as a result of climate change, which could result in a decline in population numbers in certain areas of the white-beaked dolphin's range. Here we use stranding frequencies of white-beaked dolphins as an indicator of distribution and investigate whether there have been spatiotemporal patterns and changes in stranding frequencies in the south western North Sea in the last 27 years (1991-2017). A total of 407 strandings was recorded and the distribution of stranded animals throughout this period revealed a higher density of animals in the southern countries in earlier years, with slightly increased densities in the north western area more recently. This could be a first indication of a change in habitat use and population distribution from southern to northern regions. A potential explanation for the observed shift is climate change and its effect on prey distribution and availability. This study highlights the potential of using stranding records as a way to collect high resolution spatiotemporal data, making this a valuable addition to surveys of live animals assessing species distribution and abundance. Additional research into metrics such as causes of mortality, life history and diet parameters (all of which are currently largely unknown for this species) would provide a welcome contribution to assess more detailed measures of the status of the population.

Keywords: *Lagenorhynchus albirostris*, cetaceans, mortality, spatiotemporal analysis, distribution, conservation, North Sea.

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Introduction

The white-beaked dolphin (*Lagenorhynchus albirostris*) is a species endemic to cold temperate to subpolar waters across the North Atlantic and adjacent waters including the North Sea. In the North Sea, white-beaked dolphins are prevalent in the northern part, and sightings have also been common as far south as the eastern English Channel. Strandings have occurred along the southern North Sea coasts for decades, indicating that this is also part of their distributional range (Reeves et al. 1999, Evans et al. 2003, Reid et al. 2003, Camphuysen & Peet 2006, Canning et al. 2008, Hammond et al. 2012, Galatius & Kinze 2016). Large-scale abundance surveys resulted in estimates of around 22,600 (CV=0.23) individuals in 1994 and around 37,700 (CV=0.36) in 2005. Similar numbers have been reported more recently, with 36,300 (CV=0.29) in 2016 (Hammond et al. 2017). This suggests that there has not been a significant increase or decrease in total population size since 1994, and therefore the white-beaked population in the North Sea can be considered stable (Paxton et al. 2016, Hammond et al. 2017).

A stable population is defined by having age-specific fertility and mortality rates that remain more or less constant over time (Lotka 1968). Little is known about the reproductive behavior of white-beaked dolphins, but calving is believed to occur in summer months from May to September (Camphuysen & Peet 2006, Weir et al. 2007, Evans & Smeenk 2008, Galatius et al. 2013). A number of potential threats have been identified that could affect the species' conservation status (Hammond et al 2012), including direct anthropogenic pressures such as bycatch in fishing gear across the whole area of distribution (e.g. Couperus 1997). The reported removal rates are low, but data on potential effects on the conservation status of the population remain scarce. Furthermore, similar to other toothed whales from the North Atlantic Ocean and North Sea, relatively high levels of organochlorines as well as heavy metals have been measured in tissues from white-beaked dolphins stranded in other areas (Muir et al. 1988). No more recent studies and data on contaminant burden of white-beaked dolphins stranded along the North Sea are available. It is known that in terrestrial wildlife these pollutants can have profoundly deleterious effects on the health of individuals, including immunosuppression and reproductive impairment (e.g. Aulerich et al. 1977, Kannan et al. 2000, Jepson et al. 2016). In marine mammals, a high contaminant burden and its effect on the endocrine systems has been demonstrated experimentally in seals (e.g. Reijnders 1986, Brouwer et al. 1989), and was more recently also suggested to affect the health and reproduction success of common dolphin (*Delphinus delphis*) and harbour porpoise (*Phocoena phocoena*) (Pierce et al. 2008, Murphy et al. 2015, Jepson et al. 2016). Finally, infectious diseases detected in stranded white-beaked dolphins along the North Sea include infection with the epizootic morbillivirus (e.g. Visser et al. 1993, van Elk et al. 2014).

Several authors highlight the potential impact of increasing water temperature as a result of climate change on marine mammals and their prey (e.g. MacLeod 2009, Simmonds & Eliott 2009, Evans et al. 2010, Evans & Bjørge 2013). For cold-water species like the white-beaked dolphin, increasing water temperature may lead to reduced suitable areas for foraging and habitat loss, following changes in prey distribution (MacLeod et al. 2005, Evans & Bjørge 2013). MacLeod et al. (2005) presented a decline in the relative frequencies of strandings and sightings of white-beaked dolphins in north-west Scotland and suggested that climate change could have been the cause of this decline. If water temperatures continue to increase this could have serious implications for the white-beaked dolphin population of the North Sea (MacLeod et al. 2005, Simmonds & Eliott 2009) and it can be expected that white-beaked dolphin sightings and strandings in the southern regions of the North Sea will become rarer.

Here, we analyse stranding frequencies of white-beaked dolphins on the coastlines of Belgium, the Netherlands, Schleswig-Holstein (Germany), and the east coast of the United Kingdom, investigating spatiotemporal patterns and changes in occurrence over the past 27 years (1991-2017).

Methods

Data collection

Stranding records across the southwestern North Sea area are collected and maintained at a national level by individual stranding networks. For this study, the stranding databases of Belgium, Schleswig-Holstein (Germany), the Netherlands, and the United Kingdom (UK) were combined. Data held by the following institutions were collated: Royal Belgian Institute of Natural Sciences (Belgium); the Institute for Terrestrial and Aquatic Wildlife Research, University of Veterinary Medicine Hannover (Schleswig-Holstein, Germany); Naturalis Biodiversity Center, Leiden (the Netherlands); Cetacean Strandings Investigation Programme (CSIP; United Kingdom). For the UK, only cases with a stranding location along the east coast (North Sea coastline) were included, starting at Romney Marsh (Kent) in the south of England, to Skerray (Sutherland) on the north coast of Scotland, and including the Orkney Islands. Shetland was not included.

To ensure equal temporal coverage across all areas, stranding records of white-beaked dolphins were selected from the first full year of the most recently initiated stranding network, until the last full year of data collection. This resulted in data on stranding frequencies from the last 27 years (period of 01-01-1991 to 31-12-2017). Partial remains (e.g. loose bones or incomplete carcasses) were excluded from the analysis. Records used for analysis included information on: stranding date, location, and the number of animals involved in the stranding event. No attempt was made to analyse (changes in) causes of death or the age/sex structure of the stranded individuals within this study.

Data analysis

Stranding frequencies of white-beaked dolphins were investigated both spatially and temporally. Data exploration was applied following Zuur et al. (2010) prior to analysis. All analyses were performed using R version 3.3.3 (R Core Team 2017).

The selected North Sea coastline was split into three geographical regions with Scotland representing the north; England the central; and Belgium, the Netherlands, and Germany collectively representing the southern North Sea area. Maps were created using the ggplot2 (Wickham 2009) and ggmap (Kahle & Wickham 2013) libraries available in R. To better visualise point density, kernel density estimation was performed using the stat_density_2d function integrated within ggmap. This estimates the underlying probability density function of a stranding at a particular location and visualises potential shifts in distribution over the study period. To facilitate data interpretation, the study period was divided in three equal periods of 9 years each, being 1991-1999; 2000-2008; and 2009-2017.

To assess whether there are any indications for regional within-year variation in white-beaked dolphin strandings, a kernel density plot was created estimating the probability density function of a stranding in a particular month for each region individually.

Changes in stranding frequencies over time were then further investigated. A generalised additive mixed model (GAMM) was used to model annual stranding frequencies as a function of time and the geographic regions as described above. Models were fitted using a log -link function with a Poisson error distribution, using the nlme (Pinheiro et al. 2017) and mgcv (Wood 2006) package available in R. The integrated smoothness estimation available within the mgcv package was utilised to find the optimal level of smoothness. Model selection was carried out by comparing different forms of inclusion of spatial and temporal variables (year and geographic region as described above, and assessing potential interactions between these), following a backward stepwise selection process. Autocorrelation was expected given the time series, and this was assessed following each model fit. The most appropriate model was selected by examination of normalized model residuals and evaluation of the approximate Akaike Information Criterion (AIC) where a value difference >2 was judged to be an improved model. The residual scaled deviance to the residual degrees of freedom-ratio (rdev/rdf-ratio) was calculated to examine possible overdispersion in the model. Finally model validation was applied on the optimal model to verify underlying model assumptions and evaluate model fit.

Results

Between 1991 and 2017, a total of 407 white-beaked dolphin strandings was recorded comprising 15 animals from Belgium, 25 from Schleswig-Holstein, 109 from the Netherlands and 258 from the United Kingdom (with 103 from England and 155 from Scotland). The distribution of stranded animals throughout the time period is shown in figure 1. There was a higher density of stranded animals in the southern areas in the 1990s compared to the period after 2009, with stranding numbers being more concentrated around the northern area in more recent years.

Both the northern North Sea and the southern North Sea have a relatively equal distribution of strandings throughout the year with no obvious seasonality to stranding occurance, while the majority of the reported strandings in the central North Sea occur in June and July (figure 2).

When considering all regions an overall

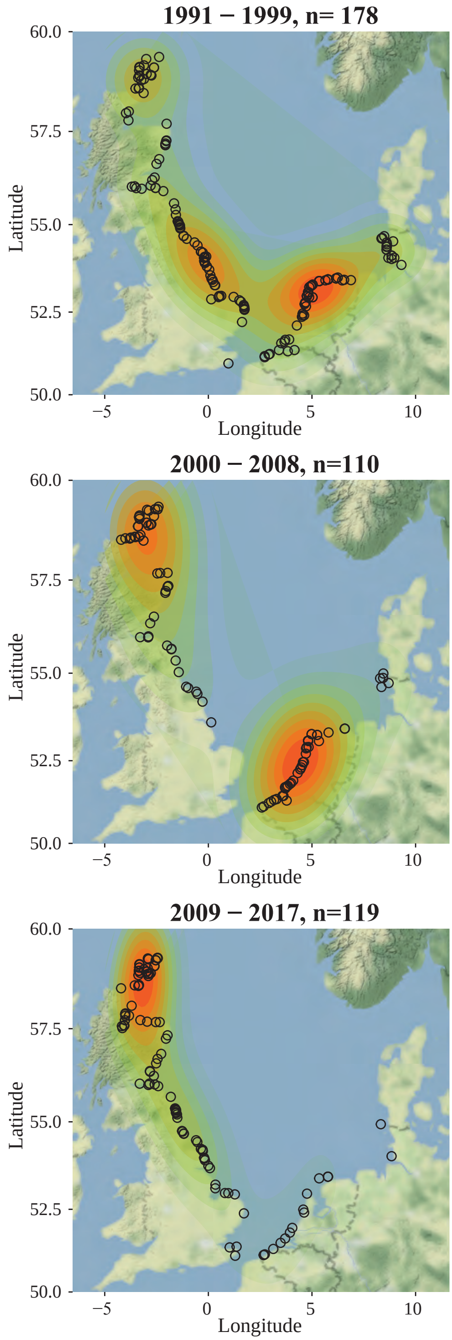

Figure 1: Study area showing the density of white-beaked dolphin strandings over three time periods (1991-1999; 2000-2008; 2009-2017) for the United Kingdom, Belgium, the Netherlands and Schleswig-Holstein, Germany.

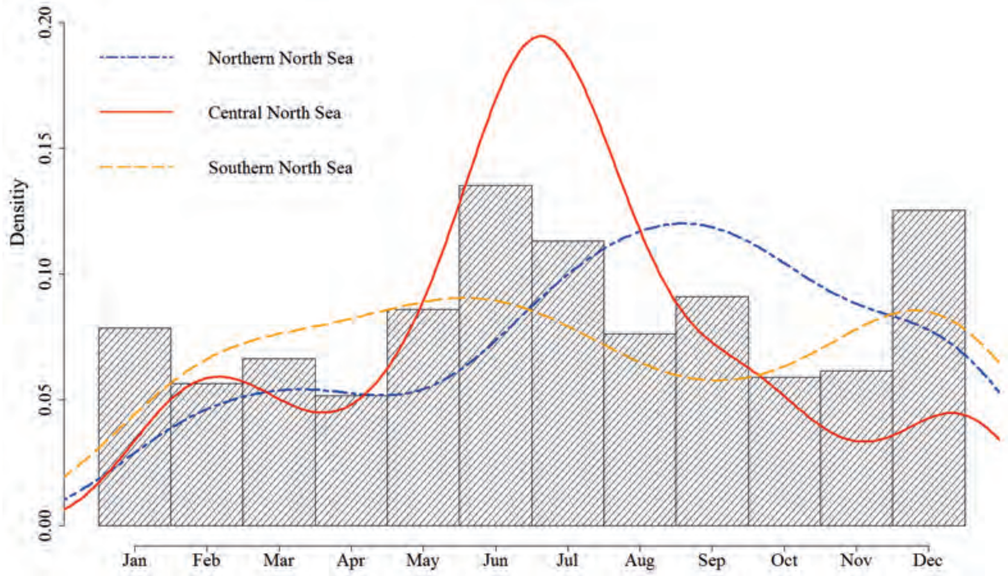

Figure 2: Density distribution estimation of white-beaked dolphin strandings per month using data from the entire study period 1992-2017. The coloured lines show kernel density estimates for the northern North Sea (blue dash and dotted line), the central North Sea (red solid line), and the southern North Sea (orange long dashed line) respectively.

Table 1. Results of the final Generalised Additive Mixed Model for the number of strandings with a separate smoother (circular regression spline) for year per region. Table values show the estimated degrees of freedom of each smoother (edf), and results from an F test of the significance of the smoothing effect.

	Smooth terms		
	edf	*F*	*P*
Northern North Sea	1.717	2.829	0.04
Central North Sea	4.626	8.798	<0.001
Southern North Sea	2.709	12.732	<0.001

decrease in stranding numbers is observed in the first five years of the study period, after which frequencies are relatively constant (figure 3A). Modelling stranding numbers throughout the study period, individual smoothers (cubic regression spline) describing the effect of year for each region individually, including an AR1 correlation structure (time lag of one year) accounting for autocorrelation throughout the study period, were finally incorporated into the final model. Each smoother was significant at the 0.05 level (table 1), and the model described above was preferred over a model with a single smoother for year (table 2), providing evidence for different non-linear trends over time for the northern North Sea, central North Sea, and southern North Sea coastlines respectively. The autocorrelation parameter, describing the autocorrelation left between the residuals separated by one year, was estimated to be 0.14. Normalised residuals were further assessed through (partial) autocorrelation plots and these results all indicated there was no strong evidence of autocorrelation left in the residuals. The rdev/rdf ratio was calculated at 0.345, meaning the values of the response variable were less dispersed than expected for a Poisson distribution. Underdispersion can lead to unnecessarily conservative parameter estimates which, given the model output, was not considered a problem for the interpretation of results presented here. The r^2 value, which is an adjusted value indicating the approximate variance explained by the model, was calcu-

Table 2. A selection of the model structures tested and their respective degrees of freedom (DF), Aikaike Information Criterion (AIC) estimate, and indication whether there were still patterns present in the model residuals. All are GAMM models with annual number of strandings as the response variable. All models were fitted using a log-link function with a Poisson error distribution, using the nlme and mgcv package available in R.

Model structure	DF	AIC	Correlation/patterns present in residuals?
s (year) + Region	6	442.2526	Yes
s (year by region)	8	176.4462	Yes
s (year by region) + Region	9	167.8253	Yes
s (year by region) + Region + AR1 correlation structure	10	167.2261	No

lated at 0.413.

White-beaked dolphin stranding numbers on the northern North Sea coastline have been stable throughout the 27 years, with the model suggesting a marginal increase in annual numbers over the study period (figure 3B). For the central North Sea coastline, a pattern can be described of declining numbers from the beginning of the study period until around 2000 followed by a slight increase (figure 3C). Finally, for the southern North Sea coastline, a declining trend can be described during most of the time series, with annual numbers decreasing slowly between 1995 and 2010 (figure 3D). These findings all correspond to the pattern seen in figure 1 and suggest that the overall decline in stranding numbers on the selected coastlines is mainly a result of decreasing numbers in the southern area.

Discussion

This study utilised white-beaked dolphin strandings data to investigate spatial and temporal occurrence patterns in the last 27 years. Results demonstrate that the number of stranded white-beaked dolphins has recently declined along the southeastern North Sea coastline compared to the first ten years of the study period, while numbers in the more northerly regions have been largely stable or even slightly increased. This suggests a potential change in distribution, with fewer animals being present in the more southern regions and the large majority of the population of white-beaked dolphins likely residing mainly in the northern regions of the North Sea; a shift previously predicted by others (MacLeod et al. 2005, Simmonds & Eliott 2009).

Monitoring marine mammal populations through live survey methods is often logistically challenging, due to the temporal heterogeneity of the marine environment and the range and mobility of cetacean species. Despite the number of biases, data on stranded animals when interpreted appropriately can yield valuable information which can be used in addition to live animal abundance surveys for population monitoring purposes (e.g. ten Doeschate et al. 2017). Strandings are recorded opportunistically, and reporting effort has likely not been constant throughout the time period used here, but improved over time with increasing public awareness, improved technology which facilitates submission of stranding reports, and interest in marine animal conservation. While it is difficult to characterise the potential effect of this on the observed stranding frequencies, there is no indication that the increase in reporting effort has been different between the individual regions and it was therefore assumed that variation in effort was equal across areas, hence data from different regions were considered comparable. Notably however, with increased public awareness one would expect an increase in strandings reported if other conditions remain the same. Yet the combined data series shows an overall decrease in stranding numbers at the beginning of the

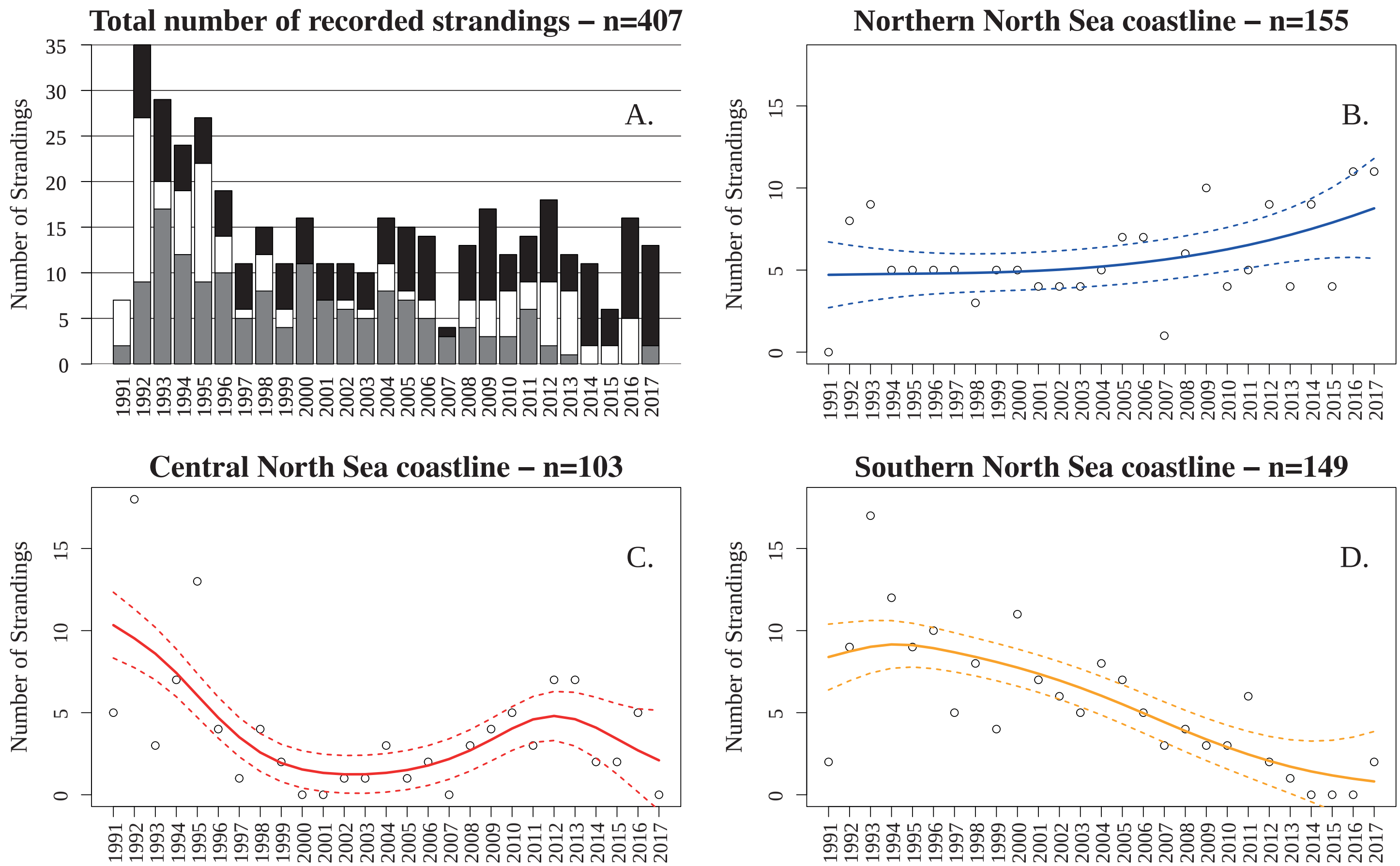

Figure 3. A: Total number of recorded strandings in the entire North Sea area partitioned by region being the northern (black), central (white) and southwestern (grey) North Sea coastline. B: Number of strandings and predicted values of model output for the northern North Sea coastline, with dotted lines representing 95% confidence intervals. C: Number of strandings and predicted values of model output for the central North Sea coastline, with dotted lines represent 95% confidence intervals. D: Number of strandings and predicted values of model output for the southern North Sea coastline, with dotted lines representing 95% confidence intervals.

time series, which suggests that the observed decrease in stranding frequencies may well be larger than can be demonstrated through the data presented here.

Large-scale decadal population survey results of SCANS revealed no significant change in abundance of white-beaked dolphins between 1994-2016; yet the results found here suggest a possible shift in population distribution during the period 1991 - 2017. Whilst these large scale abundance estimates are needed in order to assess population status and changes within this over time, smaller-scale distributional changes can have significant management consequences, especially when allocating marine protected areas or mitigating local threats. While extensively examining seasonality was beyond the aim and scope of this study, our data did suggest there may be within-year variability in distribution of white-beaked dolphins in the North Sea area, which would be useful information to consider when interpreting the more temporally limited large scale abundance survey outcomes.

The observed trends as presented in this study may have been driven by yet unknown underlying factors. Nevertheless the potential explanations for the observed change in distribution are largely anthropogenic in origin, for example climate change and its effect on habitat suitability and prey distribution and availability, as well as potentially increasing marine industry activities in certain regions. Coastal development, habitat degradation, and chemical or noise pollution all can result in ecosystem changes which influence population numbers and species composition in an area (Aguirre & Tabor 2004, Moore 2008, Wassmann et al. 2011). Marine mammals, like the white-beaked dolphin, can be used as sentinels for monitoring of marine ecosystems, as they are relatively long-lived, highly mobile species which feed at or near the top of the food chain (Aguirre & Tabor 2004, Moore 2008, Bossart 2011). Using apex predators as indicators however requires knowledge on abundance and distribution, including the establishment of reproduction and mortality parameters; most of which is currently unknown for this species.

This study focused on the analyses of stranding numbers and changes through time and between locations, but did not involve an assessment of causes of strandings and biological characteristics of stranded animals. These additional data would be required in order to assess more detailed metrics of population status, such as causes of mortality, life history and diet parameters. The regional Agreement on the Conservation of Small Cetaceans in the Baltic, North East Atlantic, Irish and North Seas (ASCOBANS) aims to achieve and maintain a favourable conservation status for small cetaceans. White-beaked dolphins are listed as native in the ASCOBANS agreement area. The data on population size and trends is however assessed as poor, and whilst the species is considered as 'least concern' on the IUCN red list, it seems undeniable that there is a deficiency in data and knowledge (Galatius & Kinze 2016). With limited information available on population biology, abundance trends, and threats and pressures affecting this species, the population of white-beaked dolphins warrants more intensive research in order to better assess its current status. Strandings provide a unique sample and data of the population that is difficult to obtain by most other means of surveillance, and can be collected continuously achieving a high spatial and temporal resolution. This study highlights the potential for using stranding records for spatiotemporal analysis assessing species distribution, providing a valuable addition to surveys of live animals particularly in a region like the North Sea with well-established systematically operating stranding networks.

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Samenvatting

Trends in ruimte en tijd in strandingen van de witsnuitdolfijn langs de Noordzeekust van 1991–2017

Hoewel de witsnuitdolfijn (*Lagenorhynchus albirostris*) gezien wordt als een inheemse soort in de Noordzee, suggereren recente studies dat de populatiegrootte in dit gebied afneemt als gevolg van een toenemende watertemperatuur door klimaatveranderingen. Dit kan resulteren in een daling van de aantallen witsnuitdolfijnen in bepaalde delen van het verspreidingsgebied. Wij hebben de aantallen gestrande witsnuitdolfijnen in de Noordzee geanalyseerd om veranderingen in de laatste 27 jaar (1991-2017) in tijd en ruimte te onderzoeken. Tussen 1991 en 2017 werden in totaal 407 strandingen van deze soort geregistreerd. De verspreiding van de gestrande dieren gedurende de onderzoeksperiode bracht een hogere dichtheid in de zuidelijke landen in eerdere jaren aan het licht, met een licht toenemende dichtheid in het noordelijke deel in recentere jaren. Dit kan een eerste indicatie zijn van een verschuiving van de populatie van zuidelijke naar meer noordelijke delen van het studiegebied en een daarmee samenhangende verandering van habitatgebruik. Mogelijke verklaringen hiervoor zijn klimaatveranderingen en de effecten hiervan op de verspreiding en beschikbaarheid van prooisoorten. Deze studie benadrukt de potentie van het gebruik van strandingsgegevens als een manier om gegevens in ruimte en tijd te verzamelen die met andere surveillancemiddelen nauwelijks kunnen worden verkregen. Dit maakt dat dergelijke analyses een waardevolle aanvulling kunnen vormen op studies die zich richten op de verspreiding en het voorkomen van soorten. Aanvullend onderzoek naar onder andere sterfte, reproductie- en dieetparameters is echter vereist om de populatiestatus van de witsnuitdolfijn meer gedetailleerd te kunnen beoordelen; hierover is nog weinig bekend.

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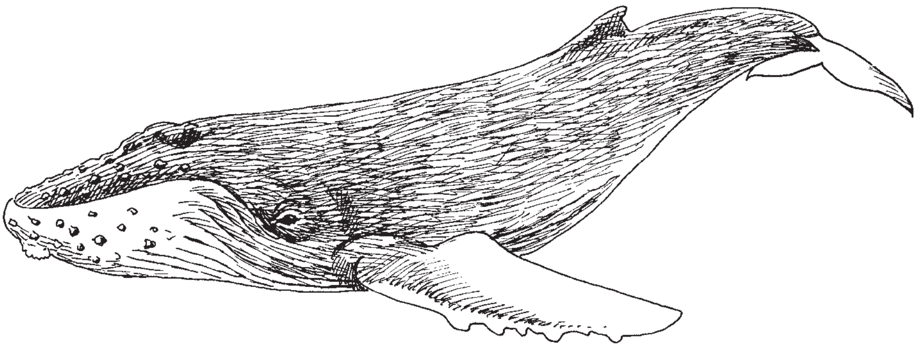

From nought to 100 in no time: how humpback whales (*Megaptera novaeangliae*) came into the southern North Sea

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Abstract: The humpback whale (*Megaptera novaeangliae*) has a cosmopolitan distribution: it occurs in all oceans and in many seas. Remarkably, the species was missing from the southern North Sea until recently. Even strandings of dead animals have always been very rare but from the 1990s onward this started to change. A trickle of dead humpback whales was the first sign that things were about to change, followed by sightings of live whales from 2001 on. Many of the first whales to arrive in the southern North Sea did not survive, and stranded, but this too has changed. Today, humpback whales visit the region every year in small numbers and both adults and juveniles are involved. The whales rarely fluke in the shallow coastal waters where they are mostly seen but a few well-marked individuals have been seen in different years and some stayed up to several months in the area. It remains unclear what might have triggered this range extension. Numbers of humpback whales in the Atlantic are increasing after the cessation of whaling, but numbers are still short of the pre-whaling population size (when the species was absent from the southern North Sea). Some forage fish species, like herring (*Clupea harengus*) are also on the increase, but stocks are still depleted compared to the past. Most likely, therefore, something has changed in the whales themselves, causing them to be more inquisitive and to explore new waters. Once they have arrived in the southern North Sea, their behaviour shows that they can find sufficient food here.

Keywords: humpback whale, *Megaptera novaeangliae*, North Sea, distribution, range extension, forage fish, explorative behaviour.

Introduction

The humpback whale (*Megaptera novaeangliae*) is a migratory baleen whale, found in all oceans and in many marginal seas (Bettridge et al. 2015). Like all large whales, humpback whale numbers have been severely depleted by commercial whaling, but populations of the species have been recovering since the end of whaling and its global conservation status is now considered "Least Concern" (Reilly et al. 2008).

The southern North Sea, taken here as south of 56°N, down to the line Calais-Dover, ca. 50°52'N, has long been an anomaly in the worldwide distribution of the humpback whale. The species probably never was part of the regular southern North Sea fauna. While there are extensive records of strandings of large whales, most notably of sperm

Figure 1. The first recent case of a humpback whale in the southern North Sea: Wilhelmshaven, Germany, 15 April 1991. Its skeleton is kept at the Natural Museum in Oldenburg. *Photo courtesy: Ursula Siebert.*

whales (*Physeter macrocephalus*) (Sliggers & Wertheim 1992, Smeenk 1997, Pierce et al. 2007, Smeenk & Evans, this volume), historic records of humpback whales, dead or alive, are very scarce in these parts. Only four historic strandings of dead animals are known: near Blankenberge, Belgium, 1751; Vogelsand, Elbe estuary, Germany, November 1824; near Berwick upon Tweed, Scotland, September 1829; and near Newcastle-upon-Tyne, September 1839 (van Deinse 1918, Camphuysen & Peet 2006, Haelters et al. 2006). A slightly greater number of historic strandings is known from further north, from NE Scotland, Norway, northern Denmark, and the Baltic (eleven cases, 1545-1918; van Deinse 1918, Camphuysen & Peet 2006). These northern strandings, including the 1829 and 1839 cases just south of 56°N in SE Scotland and NE England may have been related to the then regular presence of the species in the northern North Sea. Here, the species was hunted from shore stations in Shetland between 1903-14 (49 animals taken) (Thompson 1928). This practice probably led to local near-extinction and when whaling was resumed after World War I, only two more were killed, between 1920-1927 (Thompson 1928). Since then, the species became a rarity in Shetland waters, but returned in small numbers in summer in the 1990's (Evans et al. 1996, Evans 2006). If we consider that the two historic strandings in NE Scotland are an extension of a northerly occurrence rather than indicative of occurrence in the southern North Sea, only two historic records remain for this region: the Blankenberge (1751) and Vogelsand (1824) whales.

The status of the humpback whale in the southern North Sea has rapidly changed from “vagrant” to “annual visitor” in recent years. In this contribution, we aim to summarise the recent situation and to consider possible explanations for its new status.

Recent finds of dead humpbacks

The first two observations of humpback

Figure 2. Humpback whale, entangled in rope and (orca) rake-marked. Stranded fresh, 22 June 2004, Vlieland. the Netherlands *Photos: Dirk Bruin and Carl Zuhorn (detail of rake marks).*

whales in the southern North Sea in recent times were of two floating carcasses in German waters, in the early 1990s. The first was seen on 15 April 1991, floating near Wilhemshaven (Meyer 1994) (figure 1). The second was observed (but not recovered) on 12 October 1994, 50 km west of Helgoland; both were emaciated juvenile females (Lick et al. 1995, Camphuysen & Peet 2006). The whale found in 1994 was necropsied at sea and its (incomplete) skeleton preserved in the Marine Museum of Stralsund (Lick et al. 1995). Possibly related to the latter case was the “catch” of a rather fresh scapula of a juvenile humpback whale at the Cleaver Bank (55°40’N, 3°50’E) by the Dutch beam trawler UK 43 in February 1995 (Kompanje 1996). Six years passed without further finds, but from 2003 to 2013, twelve strandings and floaters were found in the southern North Sea, including the first case (Nieuwe Waterweg; port entry to Rotterdam, and four subsequent cases for the Netherlands; Camphuysen 2007) and the first case for Belgium (Nieuwpoort, 5 March 2006; Verbelen & Haelters 2011). A rather curious case concerns a freshly dead humpback whale, entangled in rope and (orca) rake-marked, found freshly dead on Vlieland, the Netherlands, 22 June 2004 (figure 2). The carcass was buried on the beach, but exhumed again when it was realised how rare this find was; its skeleton is now on display at museum Ecomare, Texel, the Netherlands. In addition, a single humpback whale vertebra of unknown origin was found on March 2012 in the Dutch Wadden Sea (collection Ecomare, Texel). Strandings varied from bare bones and long-dead animals to strandings of animals that were seen alive close by, just days before. All cases in these years concerned juveniles. In contrast to recent sightings of humpback whales around Shetland (May through Sep-

Figure 3. The first stranded humpback whale on the UK side of the southern North Sea in recent times. Pegwell Bay, Kent, England, 21 March 2001. This animal stranded alive, and was euthanised soon afterwards. *Photo and ©: CSIP-ZSL; http://ukstrandings.org/how-to-identify-a-stranding/*.

tember; Evans 1996, 2006, Evans et al. 2003), these strandings in the southern North Sea occurred in all seasons.

Live strandings of animals that died at the location of stranding

The first animal ever seen alive in the southern North Sea was an emaciated, 10.66 m long whale that stranded alive in Pegwell Bay, Kent, UK, 21 March **2001** (figure 3) (further details on this and all other cases are in the Appendix). This animal was only found after it had stranded; there were no previous live sightings at sea. A second animal got itself caught in the Humber Estuary between the river bank and jetties at the entrance to King George Dock, Hull, 22 September **2006**. This animal, a 9 m long immature female, died as well, despite rescue attempts by British Divers Marine Life Rescue (BDMLR). Another sad case concerns a whale seen alive on 10 September **2009**, just off Gravesend in the River Thames, England. The animal was found dead on 12 September 2009, still in the River Thames, near the Queen Elizabeth II Bridge. The animal was necropsied and found to be a starved immature male, 9.5 m long (Deaville & Jepson 2011; UK Cetacean Strandings Investigation Programme). A fourth live stranding occurred in the Netherlands (another first!) on 12 December **2012** at the offshore sandflat Razende Bol, Texel (52˚59'N, 4˚42'E) (figure 4). This whale, a 10.34 m long immature female that got named "Johanna", died four days later, despite several attempts to rescue her. Her remains are kept at Naturalis, the Netherlands.

Live sightings at sea

The vast majority of cases involve live sightings at sea, both nearshore and offshore. The Netherlands had the first live sightings at sea, of a mother/calf pair swimming just off the beach near Scheveningen, on 18 December **2003** (figure 5). Unfortunately, the calf washed up dead at Katwijk two days later, entangled in local fishing gear (Camphuysen 2007). After the calf had died, the larger whale remained in the area and was occasionally seen until 25 January **2004** (Camphuysen 2007). A photograph of this animal, taken on 16 December 2003 (figure 6), could be matched to photographs of the same animal, nine years later, off the Dutch coast (figures 10 and 11): the first whale known to return to roughly the same area within the southern North Sea. Another adult, supposedly another animal, was seen on 21 January 2014 from the offshore platform Papa 18, only 10 nautical miles (18.5 km) west of Scheveningen. It may indeed have been another adult, as two "equally large adults" were seen in the area four days later.

Across the North Sea, in UK waters, a live whale was seen at sea five miles off Hartle-

Figure 4. Humpback whale "Johanna" live-stranded, Razende Bol, off Texel, the Netherlands, 12 December 2012. *Photo: Susanne Kühn, Wageningen Marine Research*.

Figure 5. Mother-calf pair off Scheveningen, the Netherlands, 18 December 2003. *Photo: A. Verbaan, KNRM.*

pool, England, 7 September **2006**. Presumably the same animal was seen slightly further south, off Whitby, a month later. Like the first case of a live whale in the Netherlands, this ended badly, with a dead, quite rotten whale (Decomposition Code, DCC 3-4) found ashore on 19 October (UK Cetacean Strandings Investigation Programme).

The first truly offshore sighting was made by de Boer et al. (2010) in the Tail End (NE part) of the Dogger Bank, 3 May **2007**, from a distance too great for photography. This may well have been an animal in transit, as an (immature) humpback arrived in the Marsdiep tidal inlet, between Den Helder and Texel, the Netherlands, on 10 May, where it was extensively

Figure 6. The mother of the calf, that would die later, off Scheveningen, the Netherlands, 16 December 2003. *Photo: A. Verbaan, KNRM*.

watched and photographed while swimming and feeding (Camphuysen 2007). The animal was well-marked on its dorsal and head and was subsequently re-sighted off Toe Head (near Cork), Ireland on 28 September 2007. It returned to Dutch waters (IJmuiden) where it stayed from 16-21 November 2007 (Strietman 2008, www.waarneming.nl) and may have swam back south, as a humpback with a white-rimmed dorsal was filmed off Boulogne sur Mer (18 February) and Wimereux (22 February), in the Manche (Channel) area of NW France (Strietman 2018 and https://www.youtube.com/watch?gl=UG&hl=en-GB&v=3dD74bSZ-6g). A further sighting of this animal, confirmed by fluke photographs, came more than four years later (17 November 2012), from nearshore waters off Tromsø, Norway (Broms 2013).

From 3 December 2008 to 7 February 2009, several sightings of a single humpback whale, swimming and feeding in coastal waters between IJmuiden and Texel (the Netherlands) were reported to www.waarneming.nl. It is unclear if more than one animal was involved but several photographs taken show that these records do not relate to the animal that was previously seen off Texel, Southern Ireland, IJmuiden, and Norway (dorsal not white-rimmed). The animal was first seen and photographed from a distance on 3 December **2008** (Tamara van Polanen Potel, Wageningen Marine Research), from a ship working near the two offshore wind farms west of Egmond aan Zee. Subsequently, it was photographed by a helicopter crew (Bristow Helicopter Group) on 27 December, off Texel, re-sighted here from the beach (Texel) on 3 January 2009 (Thijs den Otter), and slightly further south in the Marsdiep tidal inlet on 7 January (by the crew of the Texel ferry). Presumably the same animal was briefly followed by warden vessel MV *Phoca*, watched feeding, and photographed off Texel on 9 January (Strietman 2009; figure 7), and was last seen on 7 February 2009, again from a Bristow helicopter, slightly further offshore off Texel, at 53˚10.6’E, 4˚47.6’E. This animal may have succumbed too, as a whale was reportedly seen alive near Omonville-la-Rogue, Normandy, France on 14 February, but found dead here in fishing gear a day later.

Also in **2009**, another small humpback whale was spotted off the Farne Islands,

Figure 7. Three images of the same, feeding, humpback whale off Texel, the Netherlands, 9 January 2009. Note the northern gannets (*Morus bassanus)* in attendance. *Photos: Bram Fey.*

Figure 8. Humpback whale off the Farne Islands, 18 September 2009. *Photo: Julie Forrest*.

Figure 9. Variation in dorsal shapes in humpback whales photographed off Whitby, UK. Left: 4 September 2010. Right: 20 October 2012. *Photos: Robin Petch, Sea Watch Foundation*.

Northumberland, UK (55˚39'N, 1˚36'W), from 7 until 20 September (Daniel 2009; figure 8). Like the whale seen earlier near Texel, this animal was followed by a flock of northern gannets (*Morus bassanus*), and photographed. About two months later, a much larger animal was reported by sea anglers near Whitby, North Yorkshire, UK. The Whitby area would evolve as a hotspot for humpback whale sightings in the following years (Parkin & Parkin 2010).

A small (juvenile) whale was filmed off Whitby, tail-slapping on 11 September **2010**, from the Whitby Coastal Cruises vessel *Specksioneer* (http://www.youtube.com/watch?v=IG7RY7gd5s4). A presumed second animal was intermittently reported between Whitby and Whitburn Coastal Park, some 70 km NW of Whitby, from 2 September 2010 until New Year's Day (Robin Petch, Sea Watch Foundation; figure 9).

The next animal was seen in Dutch waters, but only once, on 31 January **2011**, by the crew of the MS *Frans Naerebout* (Rijkswaterstaat), ca 10 km NW of Westkapelle, Walcheren. Even though the animal was heading NE, i.e. deeper into Dutch waters, it was not seen again (www.waarneming.nl). However, probably the same animal had been seen earlier, in the English Channel (NW France), already from 15 December 2010 onward (Jan Haelters, personal communication). It was photographed by Sylvain Pezeril, of OCEAMM (Observatoire pour la Conservation et l'Etude des Animaux et Milieux Marins) on 11 January 2011 off Sangatte, near Calais, and filmed off Boulogne-sur-Mer (just south of Calais), on 19 January, by fisheries biologists from IFREMER, on board RV *Thalassa* (http://www.zeezoogdieren.org/wordpress/?p=5209#more-5209). The next day, the animal was seen breaching close to the Belgian border (Zuydcoote), and again a day later off Hardelot Plage (21 January), feeding in the company of some harbour porpoises (*Phocoena phocoena*), and further south, ca 2 km off Wimereux (France, 50˚46'N) on 24 January 2001 (http://www.zeezoogdieren.org/wordpress/?p=5248#more-5248). If indeed these sightings were of the same animal as seen off Walcheren, Netherlands on 31 January, it was swimming up and down the coast, from NW France to SW Netherlands, rather than passing by. During this chain of events, the animal produced the first (recent) record for Belgium, on 19 January 2011 (http://www.marinemammals.be/observations/view/5716).

The next humpback whale that turned up in Dutch waters was an immature with a dorsal shaped differently from previous whales seen (http://waarneming.nl/waarneming/view/53659129). This animal was filmed on 19 April 2011 in Dutch waters, some 25 km off Katwijk by Ed Barneveld on board the coastguard vessel Zeearend, (http://www.youtube.com/watch?v=AzYRQSoYn9o), and seen on the same day in Belgium (http://www.marinemammals.be/observations/view/5910). Like the previous case, this whale probably swam up and down the coast for some time. Immature humpbacks were reported subsequently, from 15 May to 16 June 2011 near Den Helder and off the Dutch Wadden Islands, from Terschelling to Schiermonnikoog. The distance between Terschelling, where it was last seen off the Wadden Isles on 15 June and Den Helder, where it turned up on 16 June, is ca 60 km via the shortest route. The time between these two sightings was 19 hours and 45 minutes, so a swimming speed of 3 km/h would have sufficed to cover the distance. Subsequent records, of humpback whales seen in the Belgian sector of the North Sea (2 July, by Johan Tas) and in the English Channel, between Brighton and the French Coast (5 July) may refer to the same animal leaving the North Sea.

From Whitburn, Durham, England, seawatchers reported a fluking humpback whale on 6 August 2011 (M. Newsome, P. Hindess and D. Gilmore, www.trektellen.com), and again a humpback two days later, without further details. On 30 September 2011 and again on 1 and 5 October a humpback whale was reported from the Thornton Bank, 13.5 nautical miles (25 km) off Zeebrugge, Belgium (Verbelen & Haelters 2011).

The first live sighting of a humpback whale in the German sector of the North Sea was made from the air, during a harbour porpoise line transect survey, on 26 May **2012** (Anita Gilles, personal communication). Four days later, yachtsman Paul Brinkhof and family spotted a whale, between the Dutch Wadden isles Texel and Vlieland. Estimated length was circa 9 m, it was later identified as a humpback whale. A similarly small animal (estimated 8-9 m) was spotted by the crew of harbour patrol vessel *RPA15*, on 14 August 2012, at the entrance to the port of Rotterdam (Maasmond). The animal was filmed breaching and was ushered out of harm's way (Westlanders.nu 2012, http://www.portofrotterdam.com/nl/actueel/pers-en-nieuwsberichten/Pages/walvis-dartelt-in-havenmond.aspx).

Almost concurrently with the whale sighted off Rotterdam, another (?) young humpback whale came up to two 10 m long angler's boats and rubbed itself alongside them, in an area of sea known as 9-mile ground off Whitby, UK (54°36'N, 0°27'W), on 7 August 2012. The animal was filmed during the encounter (http://www.seawatchfoundation.org.uk/?p=2179) and, probably the same whale, was seen again on 17 August, a little further north off Skinningrove (54°35'N, 0°54'W) (http://www.sea-

Figure 10. Humpback whale off Callantsoog, the Netherlands, 20 December 2012, feeding along 10 m isobath on large schools of sprat. *Photo: Hans Verdaat, Wageningen Marine Research*.

Figure 11. The same humpback whale as shown in figures 10 and 6 (compare dorsals), off Callantsoog, the Netherlands, 20 January 2013. *Photo: Steve Geelhoed*.

watchfoundation.org.uk/?p=2660).

Two months later, on 18 October 2012, Robin Petch of Sea Watch, on board MV *Specksioneer* observed two humpback whales off Whitby: a juvenile and a larger individual. Subsequently, a single humpback whale was seen here on 20 and 21 October 2012 (http://www.seawatchfoundation.org.uk/?p=2949 and http://www.dolphinspotter.co.uk/). On that same day, 21 October 2012, another lone humpback whale was reported some 100 nautical miles up the coast, at the north-western limit of our study area, at Belhaven Beach, Dunbar, East Lothian, Scotland (56°0'N,

Figure 12. The same whale as in figures 10 and 11, now seen in close proximity of Offshore Wind farm Egmond aan Zee (OWEZ), 12 January 2013. Note flock of gulls in attendance. *Photo: Roelof de Beer (www.walvisstrandingen.nl).*

Figure 13. Emaciated humpback whale, spotted during an aerial survey circa 11 km off Middelkerke, Belgium, 3 September 2013. *Photos: Jan Haelters/RBINS.*

2°31'W), by Graeme Ferris (http://seawatch-foundation.org.uk/legacy_tools/region.php?output_region=4). The largest group to date, three humpback whales, was reported

Figure 14. Sequence of a breaching humpback whale photographed from the ferry from Newport, UK, to IJmuiden, the Netherlands, 15 July 2013 (http://orcaweb.worldpress.com).

on 13 December **2012**, off Hartlepool, Durham (54°41'N, 1°13'W), heading north (http://www.seawatchfoundation.org.uk/?p=3192).

Along the eastern seaboard of the southern North Sea, seawatcher Rob Berkelder spotted two whales, swimming south past The Hague, the Netherlands (52˚05'N, 4˚01'E), in high winds on 29 November 2012. Blows were clearly visible; one animal was appreciably larger than the other. The whales were tentatively identified as humpbacks. On 2 December, these whales were seen by many observers, between the towns of Castricum (52˚33'N) and Bergen aan Zee (52˚39'N) and were now positively identified, photographed, and filmed (from a distance: www.waarneming.nl). The animals were constantly accompanied by flocks of gulls, mostly kittiwakes (*Rissa tridactyla*) and sometimes by flocks of auks. The two whales were seen together again, NW off Egmond aan Zee (52˚38'N) by seawatchers on 4 December, but disappeared thereafter.

A 10.34 m long juvenile animal live-stranded on 12 December 2012 at the Razende Bol, Texel (figure 4). Possibly this was one of the two animals (i.e. the smaller one of these two) sighted two weeks earlier off the Dutch mainland coast. This possibility is supported by a sighting of a larger, solitary whale, feeding off Callantsoog (52˚35'N, 4˚35'E) on 20 December 2012. Photographs taken at close range (figure 10) while the animal was apparently feeding, showed it to be the same individual as the adult female (with calf) seen nine years earlier off Scheveningen (figure 6). On the vessel's echo-sounder, large fish schools were continuously in view and sampling proved these fish to be sprat (*Sprattus sprattus*) (Leopold et al. 2013).

As close-up photographs of the other animal seen here earlier are lacking, we cannot ascertain whether this could be the other animal sighted here. However, a life guard boat sent to the scene an hour later reported two animals together, a larger and a smaller one. As the animal that was sighted first was clearly alone, three different humpback whales may have been involved: a single adult and a mother-calf pair. All whales disappeared from sight the same day, but one re-appeared briefly on 4 January **2013** (12:18h Hondsbossche Zeewering: 52˚44'N; 15:30h Castricum: 52˚33'N) only to disappear again. At least one humpback was seen by many observers off the same stretch of coastline, from 9-18 January 2013, but two animals were seen together here on 9, 10, 12 and 13 January (www.trektellen.nl). Several photographs have been taken, but always of just one animal, which on several images clearly was the same individual already seen on 20 December 2012 (figures 10-12).

No photographs could be obtained from the pair reported earlier in these parts, so the identity of the larger one remains unclear. The whole area was surveyed by plane on 12 January 2013. The observers claim that with certainty only a single humpback was present in the area between IJmuiden (52˚28'N) and the

Figure 15. The Eastern Scheldt whale, followed from a distance by a Dutch government patrol vessel, 16 February 2015. *Photo: Liliane Solé*.

Hondsbossche Zeewering (52°44'N) which was photographed from the plane (www.trektellen.nl). However, two animals, a larger one accompanying a smaller individual, were reported in the middle of the area surveyed, off Bergen aan Zee (52°37'N), only two hours later (www.trektellen.nl).

Another case for Belgium was found during an aerial survey, circa 6 nautical miles (11 km) off Middelkerke, 3 September 2013 (figure 13). The animal was alive but appeared emaciated, even though many schools of pelagic fish were spotted from the plane, presumably herring (*Clupea harengus*) or sprat (Verbelen & Haelters 2013).

Passengers on the Newcastle ferry were given a show by a breaching humpback whale on 15 July 2013, some 50 km out of port (figure 14). Probably the same whale was seen twice, nearly three weeks later (3 August): off Whitburn, Sunderland, and at Cresswell, Northumberland (Sea Watch database).

Further south along the UK East coast, a humpback whale was seen on at least 13 occasions, between Happisburgh, Norfolk and Minsmere, Suffolk, from 13 September to 19 November 2013. Further offshore, a humpback whale produced only a single sighting on 9 April **2014**. The animal was seen 80 nautical miles (ca. 150 km) out of the Humber estuary, from a DFDS ferry service from Immingham (near Hull) to Cuxhaven in Germany, by volunteer researcher Carol Farmer-Wright, for conservation charity MARINElife. Several unconfirmed sightings followed in 2014 and early 2015 (see Appendix), but an unmistakeable humpback whale entered the semi-enclosed estuary Eastern Scheldt, on 14 February **2015**. The animal entered this water body by swimming through one of the openings in the barrier dam, made a tour through the estuary (figure 15) and swam out again two days later.

Two or three more humpback whales were sighted in 2015: the first one was seen off the Norfolk (UK) coast, 17-23 November, and overlapping with this time span, during which the whale was not reported each day, e.g., not from 10-13 November, a single humpback whale sighting was made near IJmuiden, Netherlands, some 200 km to the east. Subsequently, a humpback was spotted near the mouth of the River Scheldt (NL) on 2 December and an unidentified whale was

Figure 16. Humpback whale breaching off Castricum, the Netherlands, 26 January 2017. *Photo: Hans Verdaat, Wageningen Marine Research*.

reported from Terschelling on 29 December. Early in **2016**, the trickle of humpback whale sightings continued along the eastern North Sea seaboard. A humpback whale was briefly filmed near the entrance to the port of Rotterdam om New Year's Day; on 16 January one was reported breaching, in the company of a flock of gulls, off Camperduin (NL). All these records could in fact relate to the same whale. However, on 28 January, two humpback whales were seen together, just 200 m from the coast at Raversijde Duinenkerkje in the Belgium sector of the North Sea (Jan Haelters, personal communication). All went quiet again until a humpback whale turned up in the Sloehaven, Vlissingen, in the Western Scheldt on 22 October 2016.

On 16 January **2017**, a humpback whale was seen close to the Dutch mainland coast, off Noordwijk (www.waarneming.nl). What first seemed to be just another isolated sighting, turned out to be the start of a long series of observations in Dutch waters. Presumably the same animal was found back on 20 January and seen on almost each subsequent day until 4 February (excepting 23-25 January) (figure 16). The animal was sometimes joined by a second whale, as on several occasions two whales were seen together. They travelled up and down the coast between the towns of Castricum and Bergen, and were often seen being followed by flocks of gulls and apparently feeding. After the last sighting on 4 February the animal(s) disappeared but one turned up later in the naval port of Den Helder where it stayed from 27 February to 3 March (www.waarneming.nl).

Two more humpback whales were seen in Dutch waters in 2017: one from 10-22 July off Scheveningen and one on 7 October close to the Maasvlakte 2 (Rotterdam). All whales seen in 2017 attracted crowds of observers that came to witness the spectacle, unheard of just 15 years before. The final observation to date is of a humpback whale seen offshore in the UK sector of the North Sea, from the ferry Stena Hollandica by the Rugvin Foundation on 14 April **2018** (https://observation.org/waarneming/view/154742031#).

Feeding and diet

Not much is known about the food taken by humpback whales in the southern North

Figure 17. Small sprats were caught in the wake of a feeding humpback whale, off Texel, the Netherlands, 9 January 2009. *Photo: Bram Fey*.

Sea. In other parts of the Atlantic, humpback whales are known to feed mostly on crustaceans and small schooling pelagic fishes, like capelin *Mallotus villosus*, herring and sandeels (Ammodytidae) (Mitchell 1973, Whitehead & Carscadden 1985, Payne et al. 1986, Christensen et al. 1992, Friedlaender et al. 2009), and humpbacks have been observed feeding on shoals of sprat (confirmed by sampling) off the west coast of Scotland (P.G.H. Evans, personal observations). Observations of apparently feeding humpback whales in the southern North Sea are in line with this. Whales were on occasions followed by flocks of gulls that seemed to profit from the whale's feeding behaviour. Verbelen & Haelters (2013) observed many fish schools, thought to be herring or sprat, near the whale seen in Belgian waters in September 2013. This whale, however, appeared to be starving. The whale that was followed by MV *Phoca* off Texel on 9 January 2009 was feeding and surrounded by northern gannets (Strietman 2009). A small trawl was lowered in the wake of the whale, and small sprats and brown shrimps *Crangon crangon* were caught, suggesting that the whale was feeding on these (figure 17).

Necropsies of stranded humpback whales in the North Sea either did not include a thorough examination of stomach and gut contents, or came up empty (Lick et al. 1995). Only in the gut of "Johanna", the whale that stranded on 12 December 2012 at the offshore sandflat Razende Bol, Texel and that died here four days later, we found a few remains of sprats (vertebrae, pro-otic bullae and a few very worn sagittal otoliths). A diet of sprat would be consistent with observations of several humpback whales feeding of the Dutch mainland coast, around the 10 m isobaths, where large concentrations of sprat were found in winter (Leopold et al. 2013).

Discussion

The status of the humpback whale in the southern North Sea has changed 'overnight' from a very rare vagrant to a yearly visitor. Whales have been mainly spotted near the coast, both along the eastern and western seaboard of the southern North Sea, but there are also several offshore sightings, in waters with fewer observers. Clearly, the whales must come from somewhere outside the North Sea, and travelling whales may thus be encountered anywhere in the study area (figure 18). Some 45 cases, often of lone whales but occasionally of small groups of whales could be tentatively identified (see Appendix) in the present century (figure 19). At first, mostly dead whales were found floating at sea or washing ashore, or live whales that died soon after they were first seen. From 2007 onward, however, most whales seen were alive, and seemed to be doing well: some were observed feeding and some became long-stayers.

In the light of the absence of the species for centuries, it is unlikely that something, relevant to the whales, has changed suddenly and dramatically in the southern North Sea in the last 20 years or so. Fish stocks have fluctuated greatly, but most have been relatively sta-

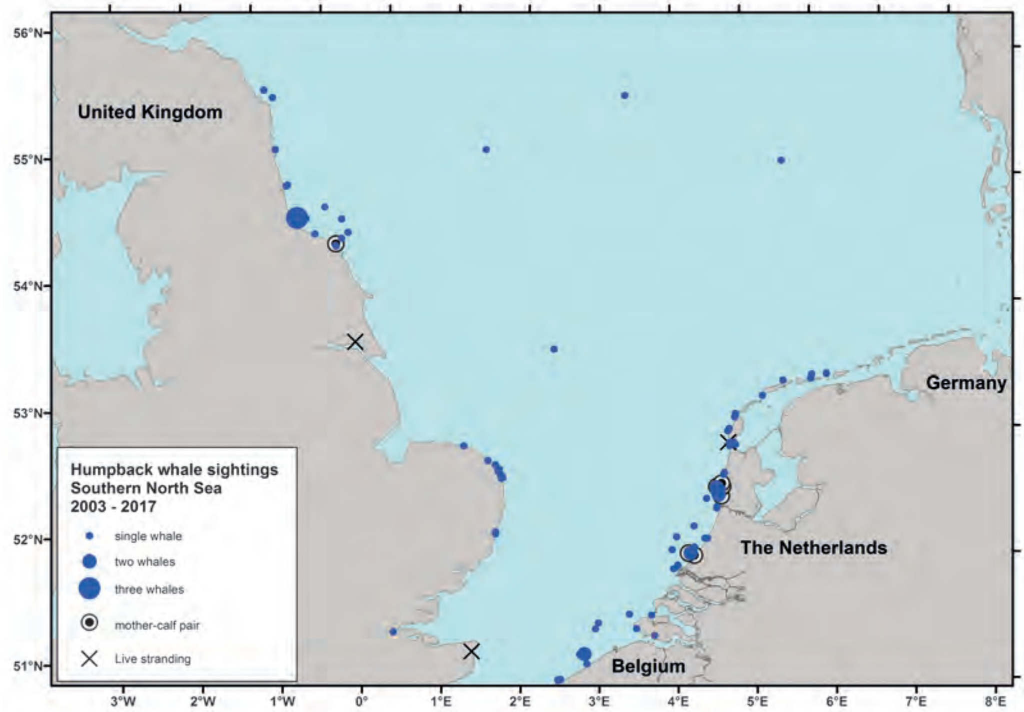

Figure 18. Distribution of sightings of live humpback whales in the southern North Sea, 2003-2017.

ble over the past 20 years. Even though some stocks have been increasing, e.g., herring, this increase was modest compared to earlier changes (ICES 2017) and stocks were probably much larger centuries ago (when humpback whales were absent from the southern North Sea). Rather, therefore, relevant changes must have occurred elsewhere, or in the whales themselves. Numbers of humpback whales worldwide are rapidly increasing, with annual growth rates >10% reported from waters between Iceland and Greenland (Wedekin et al. 2017). Whale numbers are still lower than in the pre-whaling era (when humpback whales were absent from the southern North Sea), so the recent population increase alone cannot explain why these whales now venture deeply into the North Sea. Something in the behaviour of (some of) the whales must have changed as well. Today, the whales may be more inclined to test new waters, and once they have entered the southern North Sea, they can find good feeding opportunities and some animals became long-stayers. As many whales that come into the North Sea are immatures, new individuals are probably coming into the North Sea each year, which raises the question how whales "know" that good feeding grounds lie ahead if they turn into the North Sea on migration. Some individuals evidently have come back multiple times (Strietman 2008, 2009; this paper) but as humpback whales do not tend to travel in groups and most animals seen were single individuals, most probably found their way there by themselves. Communication and cultural transmission of new information are known in humpback whales (Allen et al. 2013). It is tempting to speculate that whales somehow "tell" each other that swimming into the North Sea would be a good idea. In any case, (some) humpback whales have dis-

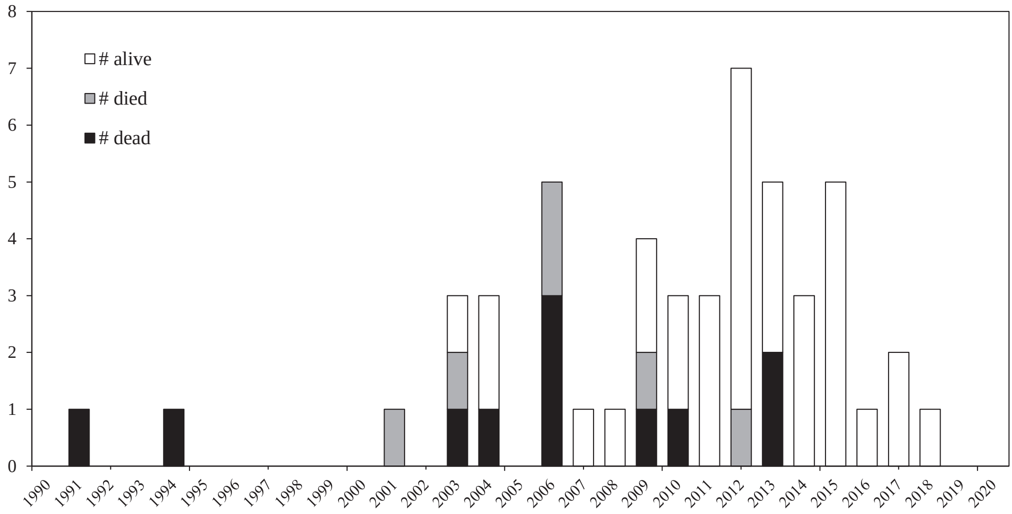

Figure 19. Numbers of cases tentatively identified per year. Strings of observations of presumably the same animal(s) are assigned to the same case, and to the year in which they were first seen. Groups of more than one whale are also considered one case. See Appendix for further details.

covered the southern North Sea as a new, suitable habitat, and numbers of these massive visitors have been increasing steeply, since the first were found (dead) in the 1990s.

It is worth noting that humpback sightings have also increased markedly elsewhere around the British Isles in the last twenty years. This may be the result of a steady recovery of the North Atlantic population following cessation of whaling (Clapham & Evans 2008). Both sprat and herring are abundant again in the southern North Sea, after a supposed increase in the region since the 1990s (Heessen et al. 2015, ICES 2017) and humpback whales need not starve here.

As humpback whales are seen in the southern North Sea in all months of the year, the sudden occurrence of humpback whales does not seem to be simply related to migration, with some animals entering the North Sea either willingly or by accident. The fact that more animals are present in the northern North Sea may have led to more individuals ranging further south. However, whereas humpback numbers have been decimated by past whaling, and are recovering, numbers are still much lower than in pre-whaling times, when the species was never seen in the southern North Sea. Therefore, a recovery of whale numbers cannot entirely explain the increase in the North Sea: it is not so much a come-back as a new phenomenon, which is not entirely understood at present.

Whatever the reasons for the regular presence of humpbacks now in the North Sea, mortality in the region appears to be disturbingly high. One clear anthropogenic cause is that of entanglement in creel lines and other fishing gear (Camphuysen 2007, Ryan et al. 2016), presenting serious concern for the conservation of what must still be a rather small population.

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Samenvatting

Hoe de bultrug plotseling verscheen in de zuidelijke Noordzee

De bultrug is een walvis die wereldwijd voorkomt. De soort is in alle oceanen te vinden, maar is in zijn verspreiding niet beperkt tot diepere wateren en komt ook voor in de meeste randzeeën. De zuidelijke Noordzee, tussen Het Kanaal en de Doggersbank, vormde tot voor kort de uitzondering op de regel. Van voorbije eeuwen zijn slechts vier strandingen van dode bultruggen bekend, dit in tegenstelling tot de geschiedenis van tal van andere soorten grote walvissen in de zuidelijke Noordzee. Aan deze opvallende absentie van de bultrug is echter een einde gekomen. Achteraf gezien is de ommekeer begin jaren negentig ingezet, met het aandrijven van enkele dode dieren, eerst in Duitsland (1991 en 1994), daarna in Nederland (2003, bij de Nieuwe Waterweg) en in België (2006, bij Nieuwpoort). Ondertussen werden ook de eerste levende exemplaren gezien. De eerste in de monding van de Thames, Engeland, in 2001, maar dit dier strandde en moest worden geëuthanaseerd. Een bultrug die (vers) dood op Vlieland aanspoelde in 2004, met een touw om zijn lichaam, heeft vermoedelijk ook op eigen kracht de zuidelijke Noordzee weten te bereiken. Scheveningen had de primeur van de eerste levende bultruggen die niet meteen strandden: een moeder met een kalf. Het kalf spoelde echter na een paar dagen dood op het strand aan. Foto's van het moederdier toonden aan dat deze walvis negen jaar later weer terugkeerde voor de Nederlandse kust: een andere primeur. Vanaf 2006 worden bultruggen jaarlijks waargenomen in de zuidelijke Noordzee. De meeste dieren worden dicht onder de kust gezien in Nederland (waar zich veel waarnemers op het strand bevinden en waar enkele dieren weken tot maanden verbleven) en in Engeland, bij Whitby, waar walvistochtjes worden georganiseerd. In België zijn de waarnemingen nog relatief schaars en in Duitsland is nog slechts een enkele bultrug levend gezien. Een verklaring voor het feit dat bultruggen, na eeuwenlange afwezigheid, opeens jaarlijks opduiken in de zuidelijke Noordzee is moeilijk te geven. Er zijn voortdurend veranderingen in hydrografie of in de visstand van de Noordzee, maar die zijn de afgelopen 30 jaar, in vergelijking met wat zich eeuwenlang aan veranderingen heeft voorgedaan, niet zo groot geweest dat ze deze omslag kunnen verklaren. Het aantal bultruggen neemt wereldwijd weer toe, na een lange periode van walvisvaart met het ineenstorten van populaties walvissen als gevolg. Het aantal bultruggen is echter nog niet op het niveau van vóór de walvisvaart en toen kwam de soort ook niet voor in de zuidelijke Noordzee. Er lijkt dus iets veranderd in de walvissen zelf. Wellicht zijn ze wat ondernemender geworden en meer geneigd tot het bezoeken van nieuwe gebieden. En eenmaal gearriveerd in de zuidelijke Noordzee, vinden bultruggen hier voldoende te eten, wat het soms lange verblijf van sommige individuen hier kan verklaren.

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Appendix. List of all sightings presented in this paper, with further details. Strings of sightings, of presumably the same animal(s), have been given the same case number, with an increasing decimal for each subsequent sighting. Sightings outside the study area are marked in red. m-c = mother-calf. See http://www.zoogdierwinkel.nl/lutra for an extended version, with more details, of this list.

Day	Month	Year	Status	Type	Group composition	North	East	Country	Location	Case
30	11	1751	Dead	Floater	single	51.333	3.117	Belgium	Blankenberge	historic-1
	11	1824	Dead	Stranding	single	54.000	8.546	Germany	Vogelsand, Elbe mouth	historic-2
	9	1829	Dead	Stranding	single	55.763	-1.989	UK	Berwick upon Tweed	historic-3
	9	1839	Dead	Stranding	single	55.000	-1.413	UK	Newcastle	historic-4
15	7	1991	Dead	Floater	single	53.833	8.250	Germany	Jadebusen near Wilhelmshaven	Semi-recent 1
12	10	1994	Dead	Floater	single	54.183	7.117	Germany	50 km west of Helgoland	Semi-recent 2
	2	1995	Dead	Sunk: bone	single	53.667	3.833	Netherlands	Klaverbank	Semi-recent 2.1
21	3	2001	Died	Live stranding	single	51.311	1.377	UK	Pegwell in Sandwich Bay, Kent (Thames mouth)	Recent 1
29	9	2003	Dead	Floater	single	52.020	3.950	Netherlands	Nieuwe Waterweg	Recent 2
18	12	2003	Alive	Live m-c pair	m-c pair	52.100	4.150	Netherlands	Scheveningen	Recent 3
20	12	2003	Dead	Stranding	single	52.216	4.402	Netherlands	Katwijk aan zee	Recent 3.1
21	1	2004	Alive	Live nearshore	single	52.216	4.402	Netherlands	13:00: 4 nm off Scheveningen	Recent 3.2
25	1	2004	Alive	single mother	single	52.217	4.367	Netherlands	at least up to Katwijk	Recent 3.3
21	1	2004	Alive	Live offshore	single	52.128	3.939	Netherlands	off the Hague	Recent 4
25	1	2004	Alive	Live nearshore	two adults	52.100	4.179	Netherlands	off the Hague	Recent 4.1
22	6	2004	Dead	Stranding	single	53.243	4.906	Netherlands	Vliehors, Vlieland	Recent 5
5	3	2006	Dead	Stranding	single	51.155	2.726	Belgium	Nieuwpoort	Recent 6
13	6	2006	Dead	Stranding	single	52.186	1.408	UK	Kingsdown beach near Deal in Kent	Recent 7
12	9	2006	Dead	Stranding	single	51.465	0.258	UK	near Dartford Bridge, Thames	Recent 8
22	9	2006	Died	Live stranding	single	53.741	-0.279	UK	King George Dock (Hull)	Recent 9
7	9	2006	Alive	Live nearshore	single	54.700	-1.033	UK	five miles east of Hartlepool	Recent 10
	10	2006	Alive	Live nearshore	single	54.500	-0.608	UK	off Whitby	Recent 10.1
19	10	2006	Dead	Stranding	single	54.532	-0.747	UK	Runswick Bay, North Yorkshire	Recent 10.2
3	5	2007	Alive	Live offshore	single	55.749	3.356	Netherlands	North of Tail End, Dogger Bank	Recent 11.0?
10-13	5	2007	Alive	Live nearshore	single	52.975	4.750	Netherlands	Marsdiep (Texel-den Helder)	Recent 11.1
28	9	2007	Alive	Live nearshore	single	51.475	-9.233	Ireland	off Toe Head, near Cork	Recent 11.2
15-21	11	2007	Alive	Live nearshore	single	52.465	4.532	Netherlands	IJmuiden	Recent 11.3
18	2	2008	Alive	Live nearshore	single	50.750	1.583	France	Boulogne sur mer	Recent 11.4
22	2	2008	Alive	Live nearshore	single	50.775	1.550	France	Manche, off Wimereux	Recent 11.5
17	11	2012	Alive	Live nearshore	single	69.875	18.233	Norway	off Tromso	Recent 11.6
3	12	2008	Alive	Live, offshore	single	52.533	4.400	Netherlands	Between IJmuiden and OWEZ	Recent 12
3	1	2009	Alive	Live, nearshore	single	53.068	4.696	Netherlands	off Texel	Recent 12.1
7	1	2009	Alive	Live, nearshore	single	52.976	4.766	Netherlands	Marsdiep	Recent 12.2
9	1	2009	Alive	Live, nearshore	single	53.087	4.717	Netherlands	west of Texel	Recent 12.3
7	2	2009	Alive	Live, offshore	single	53.177	4.793	Netherlands	west of Texel, last sighting	Recent 12.4
15	2	2009	Dead	Bycatch	single	49.706	-1.829	France	off Omonville-la-Rogue, Normandy	Recent 12.5

8	10	2009	Dead	Stranding	single	53.430	5.629	Netherlands	Ameland, Hollum	Recent 13
10	9	2009	Alive	Live nearshore	single	51.446	0.371	UK	off Gravesend (Thames)	Recent 14
12	9	2009	Dead	Stranding	single	51.463	0.258	UK	Queen Elizabeth II Bridge, River Thames	Recent 14.1
7	9	2009	Alive	Live nearshore	single	55.700	-1.733	UK	off Lindisfarne, Northumberland	Recent 15
13&20	9	2009	Alive	Live nearshore	single	55.646	-1.604	UK	Longstone Island, Farne Islands, Northhumberland	Recent 15.1
	11?	2009	Alive	Live nearshore	single	54.500	-0.608	UK	near Whitby, Yorkshire	Recent 16
15	8	2010	Dead	Floater	single	50.206	-5.431	UK	Just off the beach at The Towans, Hayle, Cornwall	Recent 17
18	8	2010	Dead	Stranding	single	52.206	4.392	Netherlands	Katwijk	Recent 17.1
2-11	9	2010	Alive	Live nearshore	single	54.500	-0.608	UK	near Whitby, Yorkshire	Recent 18.1
20	9	2010	Alive	Live nearshore	single	54.492	-0.600	UK	near Whitby, Yorkshire, very closely inshore	Recent 18.2
mid	10	2010	Alive	Live nearshore	single	54.558	-0.533	UK	near Whitby, Yorkshire, 5 miles offshore	Recent 18.3
late	12	2011	Alive	Live nearshore	single	54.958	-1.317	UK	moving north, past Whitburn Coastal Park (70 km NW of Whitby)	Recent 18.4
1	1	2011	Alive	Live nearshore	single	54.958	-1.317	UK	passing Whitburn Coastal Park (ca 70 km NW of Whitby)	Recent 18.5
19	12	2010	Alive	Live nearshore	single	51.092	2.475	France	off Zuydcoote	Recent 19
20	12	2010	Alive	Live nearshore	single	51.096	2.508	France	off Bray Dunes	Recent 19.1
30	12	2010	Alive	Live nearshore	single	50.979	1.833	France	Pas-de-Calais	Recent 19.2
11	1	2011	Alive	Live nearshore	single	50.967	1.750	France	Sangatte	Recent 19.3
19	1	2011	Alive	Live nearshore	single	51.123	2.458	France	off Zuydcoote	Recent 19.4
19	1	2011	Alive	Live nearshore	single	50.733	1.550	France	Boulogne	Recent 19.5
21	1	2011	Alive	Live nearshore	single	50.634	1.568	France	off Hardelot plage	Recent 19.6
24	1	2011	Alive	Live nearshore	single	50.770	1.590	France	off Wimereux	Recent 19.7
31	1	2011	Alive	Live nearshore	single	51.617	3.383	Netherlands	10 km off Walcheren, Zeeland	Recent 19.8
19	4	2011	Alive	Live nearshore	single	52.230	4.000	Netherlands	20 km off Den Haag; different animal	Recent 20
14	5	2011	Alive	Live nearshore	single	53.504	6.083	Netherlands	Ameland Westgat	Recent 20.1
15	5	2011	Alive	Live nearshore	single	53.498	6.030	Netherlands	just seaward of ebb-tidal delta Ameland-Schiermonnikoog	Recent 20.3
1	6	2011	Alive	Live nearshore	single	52.963	4.729	Netherlands	den Helder	Recent 20.5
2	6	2011	Alive	Live nearshore	single	52.950	4.717	Netherlands	den Helder	Recent 20.6
2	6	2011	Alive	Live nearshore	single	52.974	4.717	Netherlands	Den Helder - Breewijd	Recent 20.7
7	6	2011	Alive	Live nearshore	single	53.496	5.833	Netherlands	Ameland	Recent 20.8
9	6	2011	Alive	Live nearshore	single	53.468	5.819	Netherlands	Ameland paal 16	Recent 20.9
15	6	2011	Alive	Live nearshore	single	53.344	5.167	Netherlands	Terschelling, westpunt	Recent 20.10
16	6	2011	Alive	Live nearshore	single	52.972	4.778	Netherlands	den Helder	Recent 20.11
2	7	2011	Alive	Live nearshore	single	51.221	2.842	Belgium	1 NM off Raversijde	Recent 20.12
5	7	2011	Alive	Live offshore	single	50.417	0.500	UK	English Channel, between Brighton and the French Coast	Recent 20.13
6	8	2011	Alive	Live offshore	single	54.950	-1.333	UK	Whitburn, Durham	Recent 21
8	8	2011	Alive	Live offshore	single	54.950	-1.333	UK	Whitburn, Durham	Recent 21.1
30	9	2011	Alive	Live offshore	single	51.547	2.987	Belgium	Thorntonbank. 25 km off Zeebrugge	Recent 22
1	10	2011	Alive	Live offshore	single	51.547	2.987	Belgium	Thorntonbank. 25 km off Zeebrugge	Recent 22.1
5	10	2011	Alive	Live offshore	single	51.547	2.987	Belgium	Thorntonbank. 25 km off Zeebrugge	Recent 22.2
23	3	2012	Dead	single vertebra	single			Netherlands	Wadden Sea, NE of Texel	
26	5	2012	Alive	Live offshore	single	55.207	5.530	Germany	German sector of the North Sea	Recent 23
30	5	2012	Alive	Live nearshore	single	53.204	4.801	Netherlands	off the Eierlandse Gronden, NW Texel	Recent 23.1

7	8	2012	Alive	Live offshore	single	54.608	-0.450	UK	9 mile ground, off Whitby	Recent 24
17	8	2012	Alive	Live offshore	single	54.583	-0.900	UK	Skinningrove	Recent 24.1
14	8	2012	Alive	Live nearshore	single	52.001	4.012	Netherlands	Maasmond, off Hook of Holland	Recent 25
18-21	10	2012	Alive	Live m-c pair	m-c pair	54.513	-0.608	UK	north of Whitby, Yorkshire: seven sightings of (max) two whales	Recent 26
13	12	2012	Alive	Live nearshore	gr. of three	54.700	-1.158	UK	Hartlepool	Recent 26.1
16	12	2012	Alive	Live nearshore	m-c pair +1	56.546	-2.567	UK	Arbroath	Recent 26.2
29	11	2012	Alive	Live m-c pair	m-c pair	52.083	4.225	Netherlands	off the Hague, moving south	Recent 27
2	12	2012	Alive	Live m-c pair	m-c pair	52.551	4.589	Netherlands	off Castricum, Noord-Holland (southernmost position that day)	Recent 27.1
2	12	2012	Alive	Live m-c pair	m-c pair	52.652	4.598	Netherlands	off Bergen, Noord-Holland (northernmost position that day)	Recent 27.2
4	12	2012	Alive	Live m-c pair	m-c pair	52.628	4.609	Netherlands	off Egmond, Noord-Holland	Recent 27.3
20	12	2012	Alive	Live nearshore	single	52.583	4.500	Netherlands	mother and calf seen near single, lone, large animal	Recent 27.4
9-10	1	2013	Alive	Live nearshore	m-c pair	52.623	4.605	Netherlands	mother and calf seen from land, off Egmond	Recent 27.5
12	1	2013	Alive	Live nearshore	m-c pair	52.614	4.588	Netherlands	mother and calf seen from land, off Egmond	Recent 27.6
13	1	2013	Alive	Live nearshore	m-c pair	52.627	4.534	Netherlands	mother and calf seen from land, off Egmond (last sighting of 2 animals)	Recent 27.7
12	12	2012	Died	Live stranding	single	52.979	4.700	Netherlands	Razende Bol, SW Texel	Recent 28
20	12	2012	Alive	Live nearshore	single	52.588	4.543	Netherlands	Full-sized animal, off Callantsoog feeding in band of sprat	Recent 29
20	12	2012	Alive	Live nearshore	single	52.557	4.593	Netherlands	one animal,off Castricum, southernmost position that day	Recent 29.1
4	1	2013	Alive	Live nearshore	single	52.735	4.638	Netherlands	one animal, northernmost position that day: HBZ	Recent 29.2
11-18	1	2013	Alive	Live nearshore	single	52.605	4.611	Netherlands	one animal, numerous sightings, southernmost position (Castricum)	Recent 29.3
12	1	2013	Alive	Live nearshore	single	52.615	4.589	Netherlands	aerial survey (Pim Wolf & Sander Lilipaly), slightly further offshore	Recent 29.4
24	3	2013	Dead	Stranding	single	51.467	0.767	UK	Thames mouth, at Sheerness	Recent 30
20	5	2013	Dead	Stranding	single	53.617	-0.083	UK	Mud flats beside Sunk Island village, Kingston upon Hull, Yorkshire	Recent 31
15	7	2013	Alive	Live offshore	single	54.800	-0.783	UK	Newcastle ferry	Recent 32
3	8	2013	Alive	Live nearshore	single	54.950	-1.333	UK	Whitburn, Sunderland	Recent 32.1
3	8	2013	Alive	Live nearshore	single	55.233	-1.517	UK	Cresswell, Northumberland	Recent 32.2
4	9	2013	Alive	Live offshore	single	51.297	2.747	Belgium	11 km off Middelkerke	Recent 33
13	9	2013	Alive	Live nearshore	single	52.267	1.650	UK	Dunwich, Suffolk	Recent 34
29	10	2013	Alive	Live nearshore	single	52.833	1.533	UK	Happisburgh, Norfolk	Recent 34.1
29	10	2013	Alive	Live nearshore	single	52.700	1.733	UK	Hemsby, Norfolk	Recent 34.2
30	10	2013	Alive	Live nearshore	single	52.717	1.717	UK	Winterton-Sea Palling	Recent 34.3
30	10	2013	Alive	Live nearshore	single	52.767	1.683	UK	Horsey, Norfolk	Recent 34.4
31	10	2013	Alive	Live nearshore	single	52.800	1.633	UK	Sea Palling, Norfolk	Recent 34.5
4	11	2013	Alive	Live nearshore	single	52.250	1.650	UK	Minsmere, Suffolk	Recent 34.6
9	11	2013	Alive	Live nearshore	single	52.800	1.633	UK	Sea Palling, Norfolk	Recent 34.7
10	11	2013	Alive	Live nearshore	single	52.800	1.633	UK	Sea Palling, Norfolk	Recent 34.8
13	11	2013	Alive	Live nearshore	single	52.800	1.633	UK	Sea Palling, Norfolk	Recent 34.9
14	11	2013	Alive	Live nearshore	single	52.800	1.633	UK	Sea Palling, Norfolk	Recent 34.10
15	11	2013	Alive	Live nearshore	single	52.833	1.533	UK	Happisburgh, Norfolk	Recent 34.11
17	11	2013	Alive	Live nearshore	single	52.800	1.633	UK	Sea Palling, Norfolk	Recent 34.12
9	4	2014	Alive	Live offshore	single	53.725	2.392	UK	80 miles out of the Humber esturary, en route to Cuxhaven	Recent 35

31	5	2014	Alive	Live offshore	single	54.712	-0.544	UK	Central North Sea	Recent 36
25	12	2014	Alive	Live nearshore	single	52.723	4.627	Netherlands	Camperduin	Recent 37
1	6	2015	Alive	Live offshore	single	55.307	1.420	Netherlands	Doggerbank	Recent 38
14-16	2	2015	Alive	Live nearshore	single	51.608	3.668	Netherlands	Eastern Scheldt, via barrier dam, in and out again	Recent 39
7	11	2015	Alive	Live nearshore	single	52.947	1.212	UK	Sheringham, Norfolk	Recent 40.1
9	11	2015	Alive	Live nearshore	single	52.696	1.714	UK	Hemsby, Norfolk	Recent 40.2
14	11	2015	Alive	Live nearshore	single	52.751	1.667	UK	Horsey, Norfolk	Recent 40.3
18-23	11	2015	Alive	Live nearshore	single	52.715	1.704	UK	Winterton, Norfolk	Recent 40.4
12	11	2015	Alive	Live nearshore	single	52.455	4.527	Netherlands	IJmuiden	Recent 41
2	12	2015	Alive	Live nearshore	single	51.501	3.474	Netherlands	Western Scheldt	Recent 42
29	12	2015	Alive	Live nearshore	single	53.459	5.447	Netherlands	Terschelling, North-East	Recent 42.1
1	1	2016	Alive	Live nearshore	single	52.006	4.010	Netherlands	Maasmond	Recent 42.2
16	1	2016	Alive	Live nearshore	single	52.723	4.627	Netherlands	Camperduin	Recent 42.3
28	1	2016	Alive	Live nearshore	pair	51.300	2.808	Belgium	Oostendebank	Recent 42.4
22	10	2016	Alive	Live nearshore	single	51.445	3.705	Netherlands	Sloehaven	Recent 43
16	1	2017	Alive	Live nearshore	single	52.315	4.229	Netherlands	off Noordwijk	Recent 44
20	1	2017	Alive	Live nearshore	two	52.621	4.534	Netherlands	Egmond aan Zee	Recent 44.1
4	2	2017	Alive	Live nearshore	two	52.561	4.559	Netherlands	Egmond aan Zee	Recent 44.2
27	2	2017	Alive	Live nearshore	single	52.959	4.791	Netherlands	Den Helder	Recent 44.3
3	3	2017	Alive	Live nearshore	single	52.959	4.791	Netherlands	Den Helder	Recent 44.4
10-22	7	2017	Alive	Live nearshore	single	52.147	4.227	Netherlands	Scheveningen	Recent 44
7	10	2017	Alive	Live nearshore	single	51.976	3.956	Netherlands	Maasvlakte 2	Recent 45
14	4	2018	Alive	Live offshore	single	52.023	2.097	UK	55 km SE of Lowestoft	Recent 46

A case for *Tursiops tursio* (Gunnerus, 1768)

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Abstract: Since about 1903 *Tursiops truncatus* (Montagu, 1821) has gradually replaced *Tursiops tursio* (Fabricius, 1780) as the scientific name for the bottlenose dolphin. In 1903, American cetologist Frederick W. True (1858-1914) had rejected Danish scholar Otto Fabricius' (1744-1822) specific name tursio on grounds of: 1. dubious features given in the original description and 2. the mere fact that bottlenose dolphins never had been documented from Greenlandic waters. However, Fabricius' name is a homonym and junior synonym of *Delphinus tursio* Gunnerus, 1768. The Norwegian scholar Johann Ernst Gunnerus (1718-1773) had proposed this scientific name to differentiate between the "stourvagn", the orca of the old Norse people, and the "lillevagn", the other and smaller orca of the northern seas. Gunnerus' brief description and his reference to the "Orca" skull depicted in the 1741 work of German scholar Jacob Theodor Klein (1685-1759) immediately determine *Delphinus tursio* Gunnerus, 1768 to *Tursiops truncatus* (Montagu, 1821). To balance between the principles of priority and stability of the International Code of Zoological Nomenclature, I propose to resurrect *Tursiops tursio* as the scientific name of the bottlenose dolphin granting original authorship to Gunnerus (1768) and designate Puck Bay, Poland as the type locality for the species. Further, I propose to preserve *Orcinus orca* (Linnæus, 1758) for the killer whale.

Keywords: nomenclature, *Tursiops tursio*, resurrection.

Introduction

The origin of zoological nomenclature has been set to the 10th edition of Carl Linnæus' *Systema naturae* published by the year 1758. Serving to provide clarity and stability of scientific names, the International Code of Zoological Nomenclature, however, only dates back to 1895. This code recognises the first and oldest available scientific i.e. Latin name published and disseminated by Linnæus himself in 1758 and subsequently by him or others.

Concerning the cetaceans, Linnæus had to draw from the knowledge of other scientists namely the works of Per Artedi (1705-1735) and Jacob Theodor Klein (1685-1759). Within the genus *Delphinus* Linnæus, following Artedi's (1738) and Klein's (1741) division, listed three species: *Delphinus phocæna* L. 1758 = the *Phocæna* of Klein; *Delphinus delphis* L., 1758 = the *Delphinus* of Klein and *Delphinus orca* L. = the *Orca* of Klein – often also referred to as "Orca Kleinii" and obviously identical with the extant bottlenose dolphin. Linnæus, however, used *Delphinus orca* for a smaller dolphin like species – as he already in 1748 had included a woodcut based on Klein's 1741 orca table for the 6th edition of his Systema Naturae (Linnæus 1748: table IV no 1; figure 1).

The three Linnean dolphin species were based on rather poor and somewhat ambiguous descriptions and therefore these species subsequently have been confused with one another on several occasions over time. Early depictions of the exterior features and habitus of the various species were rather crude – except for the well-known harbour porpoise. Klein's (1741) engraving of his *Orca* rather resembles a bottlenose dolphin than a com-

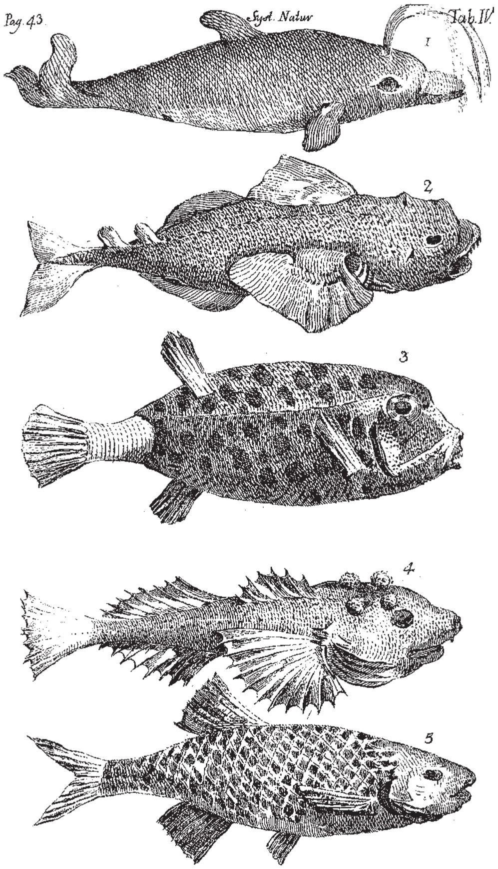

Figure 1. Tabel IV of Linnæus (1748) showing a copy of Klein's Orca as no 1.

mon dolphin (figure 2). In contrast, depictions of the crania match the precision of modern standards allowing an unequivocal species assignment. Klein's depiction of an *Orca* skull hence exhibits the diagnostic features of a bottlenose dolphin (shape and size of the rostrum, tooth count, shape and size of the face and vertex etc.) (figure 3).

Gunnerus (1768) was the first to point out the existence of two *Orca* species: a larger and a smaller one and he is, therefore, in nomenclatorial terms considered first reviser. His treatise deals mostly with the orca of the ancient Norse people the *stourvaugn* - which he found to differ significantly from the *Delphinus orca* of Linnæus 1758 – the *lillevaugn*. In order to differentiate between the two species he reserved *Delphinus orca* for the larger Norse species and proposed the name *Delphinus tursio* for the smaller Linnean species. On page 111 he gave the following description of the species:

Foruden de Gamles rette Orca ere der adskillige andre, som have faaet selvsamme Navn. Hid regner jeg Orca Kleinii de pisc Miss II § XXVII sqq p. 22 sqq; thi denne er, saavidt jeg af Beskrivelsen og den Tab. 1 n. 1 hos føiede Tegning paa Hovedet med Tænderne i samt Fig. 1-4, som afbilde nogle særskilte Tænder, kan skiønne, meget forskiellig fra vores Stour-Vagn, og kalder den derfor, til Forskiel Delphinus Tursio dentibus subteretibus, apice planiusculo og er det nok den samme som Schoenewelde i hans Ichthyolgie p.53 handler om under det Navn: Orca, paa Tydsk :Grosser Braunfisch, og paa Dansk: Øresvin eller Springer.

[Besides the elders rightful Orca there are several others that have received the same name. Here to I count Orca Kleinii de pisc Miss II § XXVII sqq p. 22 sqq, for it is, as far as I can judge based on the description and the attached Tab. 1 n.1 of the head with teeth in place as well as Fig. 1-4 which depict single teeth, very different from our Stour-Vagn, and I therefore name it Delphinus Tursio dentibus subteretibus, apice planiusculo and it is likely the same which Schoenevelde treats in his Ichthyologie p. 53 under the Name: Orca, in German Grosser Braunfisch, and in Danish: Øresvin or Springer.]
[*dentibus subteretibus* = slightly tapered teeth; *apice planisculo* = flattened beak]

Klein (1741) reported the dolphin to have been captured in Puck Bay near Gdansk ("*In sinu Pucensi prope usque Gdani est capta*"). The skull of the animal was prepared for the town hall library of Gdansk and overseen by Christopher Gottwald. According to Bock (1784) the 11 foot animal had been captured in the early 1700s. Therefore, the referred town hall keeper was Johann Christopher Gottwald (1670-1713) (Pekacka-Falkowska 2017). The skull of the specimen is not known

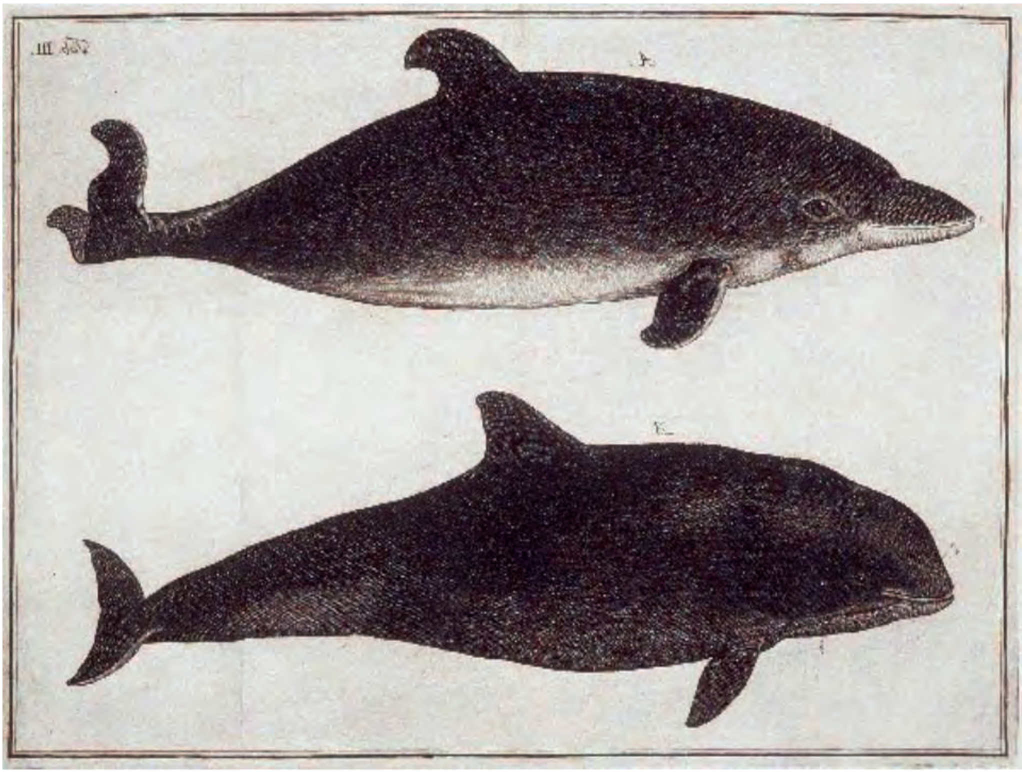

Figure 2. The Orca Kleinii (top) depicted together with the *Phocæna* of Klein (bottom) (1741).

still to exist.

Müller (1776) adopted the Gunnerus orca duality, but listed *Delphinus orca* twice: as no 56 for the smaller species and no 57 for the larger. Fabricius (1780), however, applied Gunnerus' name *Delphinus tursio* – with reference to Gunnerus' treatise but without quoting Gunnerus by name. As a consequence, for many years, the scientific name of the bottlenose dolphin almost undisputedly was *Delphinus tursio* but erroneously with credit to Fabricius' 1780 work on Greenlandic animals and not correctly to Gunnerus. Therefore, as a side effect, the species was believed to dwell in Artic waters and to be a rarity in European waters.

Hunter (1787), when depicting a bottlenose dolphin from the Scottish North Sea coast also used the scientific name *Delphinus delphis* for this bottlenose with reference to Linnæus. Along the French coasts bottlenose dolphins were well known by their vernacular names *souffleur* and *grand marsouin,* but scientifically they were wrongly assigned to *Delphinus delphis,* despite of the many obvious diagnostic features separating common and bottlenose dolphins. Bonnaterre (1789) copied both Hunter's figure, re-naming the dolphin *Delphinus tursio* – the northern dolphin species of Fabricius (1780), and Klein's Orca of 1741 for which he used the name *Delphinus delphis.* Lacépède (1804) proposed to rename the bottlenose dolphin *Delphinus nersernack* as a new name for *Delphinus tursio,* hereby acknowledging the Greenlandic name given by Fabricius, but also quoting Müller (1776) and thereby indirectly Gunnerus. *Delphinus nersernack* antedates *Delphinus truncatus* of Montagu (1821), but has been suppressed by the ICZN based on the proposal of Hershkovitz (1961, 1966).

Billberg (1828), in turn, gave credit to Fab-

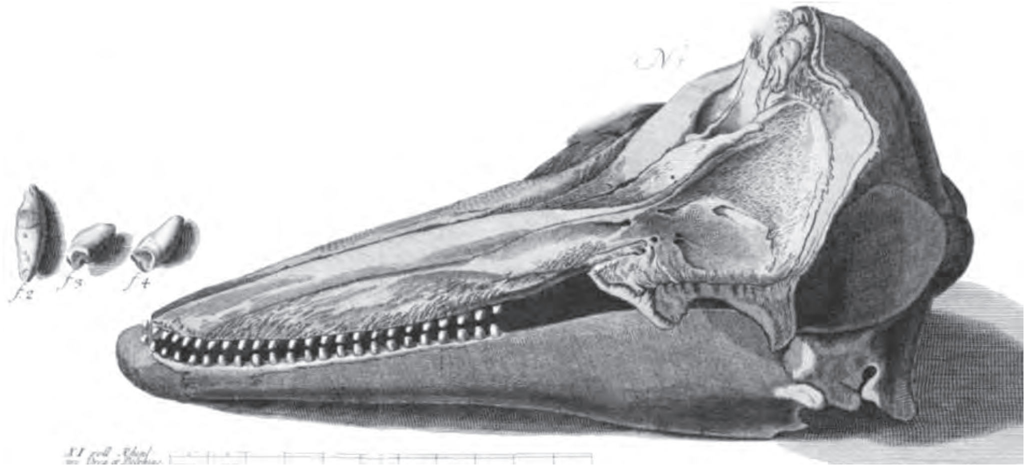

Figure 3. *Tursiops* skull depicted on Tab 1 N 1 in Klein (1741).

ricius by renaming the species *Delphinus fabricii*, a name which has fallen into oblivion. The name *Delphinus tursio* and subsequently *Tursiops tursio* for many years remained unchallenged the scientific name of the bottlenose dolphin, especially on the European continent.

Montagu (1821) described a dolphin taken in 1814 from the British west coast. Due to the very prominent and truncated tooth wear of the type specimen he baptised the species *truncatus*. In the British literature Montagu's species was believed to be a junior synonym of Fabricius' species or maybe a closely allied species of it. As late as 1889 American cetologist Frederick W. True as well held this position in his review of the Delphinidae.

In the second half of the 19th century, doubts had been raised whether Fabricius really had described a bottlenose dolphin or rather - with reference to the Greenlandic name given in his treatise - a pilot whale. Reinhardt (1857) synonymised *Delphinus tursio* Fabricius, 1780 with *Delphinus globiceps* (= *Globicephala melas* (Traill, 1809)) and only listed the white-beaked and the white-sided dolphin among the marine mammals of Greenland. Brown (1868) likewise considered the Fabricius' species a pilot whale as subsequently did Winge (1902) and eventually True (1903).

While True (1903) put emphasis on the descriptive parts in Fabricius (1780) that indeed cannot refer to a bottlenose dolphin he seems to have neglected the other part that provided much more dolphin-like features:

Cauda minus attenuata, quam in reliquis. Pinna dorsalis ut Balaena rostratae. Totus nigricans, abdomine parum albicante. Pulli etiam pallidiores. Reliqua ut in Phocaena.

[The tail less attenuated than in other cetaceans. Dorsal fin like in the piked whale. The whole body dusky in coloration, belly though a little whitish. Juveniles in general paler. Other features as in the porpoise.]

The dorsal fin shape rather points to a white-beaked dolphin while the coloration could easily match both a pilot whale and a white-beaked dolphin since either of the two species may be termed "porpoise-like".

However, Fabricius did quote the work of Gunnerus (1768) – although only by reference and not by name. Gunnerus is to be considered the first user of this scientific name placing Fabricius' homonym into junior-synonymy. He used the name to tell apart a smaller dolphin species, i.e. *Delphinus tursio*, from the ordinary killer whale (*Delphinus orca*). Gunnerus' rather precise Latin description of the teeth (dentibus subteretibus = slightly tapered teeth) and beak (apice planisculo = flattened beak) seemingly has been overlooked by the scientific community - presumably not due to lacking language skills, but rather restrains in circulation to a wider scientific community. The original account was published in Danish, but two years later also a German translation was provided (Gunnerus 1770).

White-beaked dolphins remained until their formal description a "hidden species" under a wider bottlenose dolphin umbrella. The two species also subsequently frequently were confused with one another and often remained undifferentiated in decades after with several incorrect determinations, especially on the European mainland. To unravel all these cases, however, is not the purpose of the present paper, but for the nomenclatorial refinement it is mandatory to accept and fix a proper name for the bottlenose dolphin in *sensu stricto.*

Given the fact that no bottlenose dolphin ever has been documented from Greenland, the true identity of *Delphinus tursio* Fabricius, 1780 indeed may lay among the rarer Greenlandic delphinid species which besides the pilot whale could also have been the white-beaked dolphin. In contrast, *Delphinus tursio* of Gunnerus is based on unequivocal evidence of the genus *Tursiops*.

Conclusion

Gunnerus (1768) referred his *Delphinus tursio* to the work of Klein (1741). Here in Klein's table 1 beyond any doubt a *Tursiops* skull is depicted (figure 3). Since Gunnerus' scientific name is accompanied by a proper description and further supported by an unambiguous illustration in Klein's work his name is available and prompts the following nomenclatorial changes:

The *Delphinus orca* described by Linnæus is not the killer whale in the present sense, but possibly a bottlenose dolphin or conglomerate of several dolphin species. Instead, the killer whale (*Orcinus orca* (L, 1758)) fits Linnæus' description of *Physeter microps*, the "small eyed sperm whale" for which the presence of a tall dorsal fin ('pinna altissima') is given as the key feature. Therefore, the bottlenose dolphin most stringently should be known as "*Tursiops orca* (Linnæus, 1758)" and the killer whale as "*Orcinus microps* (Linnæus, 1758)", but since this would unnecessarily shatter the present nomenclature, I propose Gunnerus be acknowledged as the first reviser and accept his differentiation: the killer whale would still be *Orcinus orca* (Linnæus, 1758 in sensu Gunnerus 1768) and the bottlenose dolphin would again be *Tursiops tursio*, not of Fabricius (1780) but of Gunnerus (1768):

Tursiops tursio (Gunnerus, 1768)
Delphinus orca Linnæus 1758 sensu originale
Delphinus orca no 57 Müller 1776
Delphinus tursio Fabricius 1780
Delphinus tursio Bonnaterre 1789
Delphinus nersanack Lacépède 1804
Delphinus truncatus Montagu 1821
Delphinus fabricii Billberg 1828
The type locality: Puck Bay near Gdansk (Poland, Baltic Sea).
Type specimen: Depiction of the Orca skull no 1 on Table I in Klein (1741) (Fig 3). An 11 foot animal captured in the early 1700s at the type locality.
A summary table is provided of the changes and proposed changes over time (table 1).

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Table 1. Summary of changes and proposed changes.

Norse people	Klein 1741	Linnæus 1758	Gunnerus 1768	Müller 1776	Fabricius 1780	Hunter 1787	Lacépède 1804	Montagu 1821	Gervais 1855	True 1889	True 1903	Proposed / current
"illevagn"	*Orca* [from Gdansk] ["*Orca Kleinii*" of authors]	*Delphinus orca* n sp	*Delphinus tursio* n sp	*Delphinus orca no 56*	*Delphinus tursio*	*Delphinus delphis*	*Delphinus nersernack* n sp	*Delphinus truncatus* n sp	*Tursiops* n gen	*Tursiops tursio* (Fabricius, 1780)	*Tursiops truncatus* (Montagu, 1821)	*Tursiops tursio* (Gunnerus, 1768)
"stourvagn"		*Physeter microps* n sp	*Delphinus orca*	*Delphinus orca* no 57	*Delphinus orca*							*Orcinus orca* (Linnæus, 1758) (sensu Gunnerus 1768)

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Samenvatting

Een pleidooi voor *Tursiops tursio* (Gunnerus, 1768)

Sinds ongeveer 1903 heeft *Tursiops truncatus* (Montagu, 1821) geleidelijk aan *Tursiops tursio* (Fabricius, 1780) vervangen als de wetenschappelijke naam voor de tuimelaar. In 1903 had de Amerikaanse walvisdeskundige Frederick W. True (1858-1914) de naam *tursio*, gegeven door de Deense wetenschapper Otto Fabricius (1744-1822), verworpen op grond van 1. twijfelachtige kenmerken in de oorspronkelijke beschrijving; en 2. het feit dat tuimelaars nooit gedocumenteerd waren in Groenlandse wateren. De naam gegeven door Fabricius is echter een homoniem en jonger synoniem van *Delphinus tursio* Gunnerus, 1768. De Noorse wetenschapper Johann Ernst Gunnerus (1718-1773) had deze wetenschappelijke naam voorgesteld om onderscheid te maken tussen de 'stourvagn', de naam die het oude Noorse volk gaf aan de orka, en de 'lillevagn', de naam gegeven aan de andere, kleinere 'orka' van de noordelijke zeeën. De beknopte beschrijving van de soort door Gunnerus, samen met zijn verwijzing naar een afbeelding, uit 1741, van een 'orka'-schedel in een werk van de Duitse wetenschapper Jacob Theodor Klein (1685-1759), tonen echter onmiskenbaar aan dat *Delphinus tursio* Gunnerus, 1768 dezelfde soort betreft als *Tursiops truncatus* (Montagu, 1821). Om een evenwicht te vinden tussen de principes van prioriteit en stabiliteit van de *International Code of Zoological Nomenclature*, stel ik voor om *Tursiops tursio* opnieuw in te stellen als de wetenschappelijke naam van de tuimelaar, waardoor origineel auteurschap verleend wordt aan Gunnerus (1768), en om Puck Bay, Polen, aan te duiden als type-localiteit voor de soort. Verder stel ik voor om de wetenschappelijke naam *Orcinus orca* (Linnaeus, 1758) te behouden voor de orka.

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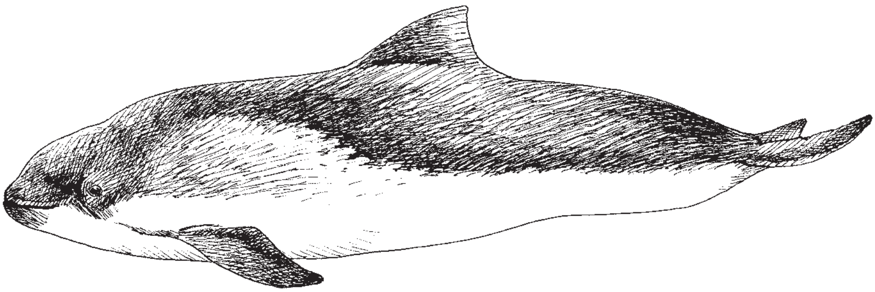

A chronological review of the nomenclature of *Delphinus rostratus* Shaw, 1801 and *Delphinus bredanensis* (Lesson, 1828)

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Abstract: A chronological review is provided, elucidating the intertwined nomenclature of *Delphinus rostratus* Shaw 1801 and *Delphinus bredanensis* Lesson, 1828. Based on this review, *Delphinus rostratus* Shaw, 1801 is considered to be a senior synonym of Ina geoffrensis, and not a junior synonym of *Delphinus gangeticus* Lebeck, 1801. F. Cuvier in 1836 had found that the name *Delphinus rostratus* Cuvier was available for the rough-toothed dolphin, erroneously crediting his brother G. Cuvier 1812 and not Shaw 1801. The correct name of the rough-toothed dolphin is *Steno bredanensis* (Lesson, 1828). The type locality of the rough-toothed dolphin is the mouth of the river Scheldt. If Shaw´s type specimen of *Delphinus rostratus* cannot be located and re-examined, it may be best to consider the name as "nomen dubium" because the description is insufficient for identification or else to ask the International Commission on Zoological Nomenclature to suppress the name.

Editor's Note

Upon his death, the cetological community, in Chris Smeenk, lost one of the greatest experts in cetacean nomenclature. Among Chris Smeenk's unfinished manuscripts there is a contribution modestly entitled "Steno bredanensis *(Lesson, 1828) – a few notes on nomenclature" and even marked with a note "[not for publication]". We have had the privilege to read and comment on this very detailed and important piece of work and repeatedly urged Chris to publish his findings and eventually received his promise that he would proceed. We therefore feel content to share these findings under a new and more appropriate title - since the paper not only provides new important insights into cetacean nomenclature but also chronologically and profoundly unravels the intertwined and complicated history of the rough-toothed dolphin and one of its alleged synonyms,* Delphinus rostratus *Shaw, 1801.*

Introduction

The review given beneath commences with the work of Shaw (1801) and takes the reader on a chronological journey to the present. For each work, detailed information is given as well as the consequences for nomenclature that are implied. Several quotations are given from historical documents in their original language. The editors have tried their best to translate these into modern English so that the reader can more easily follow the points being made although we recognise that we cannot know exactly what the original author was meaning to convey. The English translations are given as footnotes.

Chronological review

Shaw (1801: 514)

Shaw (1801: 514) published the name *Delphinus Rostratus*, with a very brief description:

"Narrow-snouted dolphin.
Delphinus Rostratus[1]. *D. rostro attenuato.*
Dolphin with greatly attenuated snout.
Known only from the head, or bones of the jaws. Supposed to inhabit the Indian seas. The jaws are extremely narrow in proportion to their length, which is about two feet: the teeth are small, not numerous, distant, and shaped somewhat like the molares of quadrupeds".

This species has until now been assumed to be the Ganges dolphin, which in the same year had been described as *Delphinus gangeticus* by Lebeck (1801) and Roxburgh (1801), with Lebeck taking priority; see Kinze (2000) who, however, does not discuss the name given by Shaw. Whatever the specific identity of this animal, the name *Delphinus rostratus* Shaw, 1801 is not available for other species placed in the genus *Delphinus*. [Note: *Delphinus rostratus* Shaw, 1801 is a junior synonym of *Delphinus gangeticus* and therefore not available; in nomenclatorial terms it is preoccupied.]

It seems highly unlikely that Shaw's brief description does indeed represent the Ganges dolphin. That species has very sharp and pointed teeth, totally different from Shaw's description. The teeth of Shaw's *Delphinus rostratus* appear to agree with those of the Amazon dolphin or boto, which have a unique structure, are differentiated, often obtuse, and the inner ones are often broadened and indeed could be described as being somewhat reminiscent of molars. In the following text, I have for practical reasons adhered to the common opinion that *Delphinus rostratus* Shaw, 1801 is a synonym of *Delphinus gangeticus* Lebeck, 1801, since re-identification of Shaw's type specimen as an Amazon dolphin would have consequences for the name of that species, which would then become *Inia rostrata* (Shaw, 1801). This is undesirable for reasons of stability. If the specimen cannot be relocated and re-examined, it would be best to either to ask the International Commission on Zoological Nomenclature to suppress the name *Delphinus rostratus* Shaw, 1801, or if the specimen cannot be relocated and re-examined[2], to consider this "nomen dubium" in the absence of a more detailed original description.

Georges Cuvier (1812: 9-10)

Georges Cuvier (1812: 9-10), in a paper largely dealing with a group of stranded pilot whales *Globicephala melas* near Paimpol in France, describes (1) two series of undocumented skulls in the Paris Museum, (2) a mounted skin with a very bulbous forehead received from Portugal, and (3) the drawing of a head of an animal from Canada.

The Paris skulls (1) clearly belong to different species:
"Or, le Muséum possède plusieurs têtes de deux vrais dauphins à museau grèle, différentes de celles du *delphis* et du *tursio*.
Les uns ont les mêmes dents grèles et pointues que les delphis, mais seulement au nombre de 35 partout, en totalité 140. Leur museau est déprimé comme celui du delphis, mais un peu plus court à proportion. Nous n'avons aucune notion de l'animal entier.
Les autres n'ont que 26 dents partout, 104 en totalité, fortes, coniques, tronquées au bout

[1] The use of capital letters here and in subsequent quotations follows the source text

[2] Editors' note: George Kearsley Shaw was assistant keeper (1791-1806) and, subsequently, keeper (from 1806) of the British Museum Natural History Department until his death in 1813. He inherited the founding collection of specimens donated by Sir Hans Sloane. This included many in poor condition that were later destroyed. It is possible that the skull he refers to here was one of those and did not make it across London from the old Bloomsbury site to its present location in South Kensington since there is no record of it in the current archives.

comme celles du tursio; leur museau plus long encore que celui du delphis, en diffère en ce qu'il n'est pas déprimé, mais au contraire comprimé latéralement." [3]

Both series of skulls are left unnamed.

Of the mounted skin (2), Cuvier writes:
"L'animal entier a été tout récemment rapporté de Portugal par M. Geoffroy. Il a le front beaucoup plus bombé que le delphis, et ceux qui l'ont empaillé l'ont peint d'un gris de perle en dessus et de blanchâtre au-dessous, ce qu'ils ont probablement imité d'après ses couleurs naturelles." [4]

Cuvier does not associate this skin with any of the above skulls. The history and provenance of this specimen has been unravelled and documented by Van Bree & Robineau (1973). It had come from the Amazon in Brazil[5] and, moreover, at the time, its skull was still in situ in the skin, so for that reason alone an association with any of the above skulls can be ruled out.

Cuvier finally suggests that the drawing of the head of an animal from Canada (3) may be of the same species as the Portuguese (Brazilian) skin: "En parcourant les naturalistes nous n'avons guère trouvé qu'une figure de tête donnée par Duhamel (*Pêches*, II^e^. partie, section X, pl. X, fig. 4), sous le nom de *marsouin blanc*, qui paroisse s'en rapprocher un peu. L'auteur dit que le dessin lui en avoit été envoyé de Canada. Il semble aussi que c'est l'espèce légèrement indiquée par *Shaw* (*General. Zool.*, tome II, part. 2, p. 514), sous le nom de *delphinus rostratus*." [6]

So, under the name *Delphinus rostratus* Shaw, 1801, Cuvier here combines – in a very tentative way – the skin of a species with a very bulbous forehead received from Portugal (later proved to have originated from Brazil) with the drawing of the head of an enigmatic animal published by Duhamel and said to have come from Canada [Note: and obviously referring to the beluga whale *Delphinapterus leucas*], and Shaw's specimen supposed to be from the Indian seas. Cuvier does not include the undocumented Paris skulls, which he leaves unnamed[7].

[3] English translation: "But the Museum has several heads of two narrow-snouted dolphins, different from those of delphis and tursio. Some have the same spindly and pointed teeth as the delphis, but only 35 each side of each jaw, 140 in all. Their beak is depressed like that of the delphis, but a little shorter in proportion. We have no notion of the whole animal. The others have only 26 teeth each side of each jaw, 104 in all, strong, conical, truncated at the end like those of the tursio; their beak even longer than that of the delphis, differs in that it is not depressed, but on the contrary compressed laterally."

[4] English translation: "The entire animal was recently brought back from Portugal by Mr. Geoffroy. It has a much more swollen forehead than delphis, and those who have prepared the specimen have painted it pearl grey above and whitish below, which they probably have imitated from its natural colours."

[5] It was thus an Amazon river dolphin (*Inia geoffrensis*).

[6] English translation: "In browsing naturalists' reports we have occasionally found a figure of a head given by Duhamel (Fisheries, Part II, Section X, Plate X, Fig. 4), under the name of white porpoise, which appeared to be slightly similar to it [i.e. the Portuguese (Brazilian) skin]. The author states that the drawing had been sent to him from Canada. It also seems that it is the species suggested by Shaw (General Zool., Volume II, part 2, p 514), under the name of *Delphinus rostratus*."

[7] In a paragraph also referring to *D. delphis*, he says: "cet autre dauphin dont nous avons parlé ci-dessus à 140 dents ou environ, que nous appellerons provisoirement *D. dubius*", i.e. in relation to the dolphin with around 140 teeth, he proposed to call it *D. dubius*. WoRMS (www.marinespecies.org) lists this species

Georges Cuvier (1817: 278)

G. Cuvier (1817: 278), in his Règne animal, now clearly regards the skin in Paris and the Canadian animal as conspecific with Delphinus rostratus Shaw, 1801:

"*Le Dauphin à bec mince*. (*Delph. rostratus*. Shaw)
A tête plus bombée et à bec plus comprimé, plus grêle, avec seulement vingt-une ou vingt-trois dents coniques de chaque côté et à chaque mâchoire; ses teintes sont plus pâles, ce qui lui a valu le nom de *dauphin blanc*. On le dit des mers d'Amérique (2)." The footnote reads: "(2) On n'a encore gravé que sa tête et grossièrement. Duhamel, Pêches part. II, sect. X, pl. x, f. 4." [8]

So, in *Delphinus rostratus* Shaw, 1801, Cuvier now positively includes the Paris skin obtained through Portugal, the Canadian animal of which he had seen a drawing of the head, and Shaw's specimen. Again, he does not mention the undocumented Paris skulls.

Desmarest (1817: 151-163)

Desmarest (1817: 151-163), in his encyclopedic review of dolphins, describes as his "*Première Espèce*" (p. 151-152) the "*Dauphin de Geoffroy, *Delphinus Geoffrensis*, Blainville; *Dauphin à bec mince*, Cuv.
Cette espèce est établie sur un individu de la collection du Muséum d'Histoire naturelle de Paris, rapporté du Portugal par M. le professeur Geoffroy Saint-Hilaire. Son corps est allongé, presque cylindrique; sont front est beaucoup plus bombé que celui du dauphin ordinaire (*Delphinus delphis*); son museau est long, mince, étroit, analogue à celui du crocodile gavial; ses mâchoires, émoussées à l'extrémité, sont sensiblement égales en longueur, fort étroites, à bords parallèles, armées de chaque côté de vingt-six grosses dents coniques, également distantes, et s'engrenant lorsque la gueule est fermée; les antérieures sont un peu plus petites que les autres, et en général un peu émoussées à la pointe; toutes sont coniques, obtuses, avec une sorte de collet inférieurement, et en outre leur surface est rugueuse, ce qui offre un rapprochement avec le dauphin à bec mince, *Delphinus rostratus*, Cuv. Dans cette espèce, les yeux sont placés un peu au-dessus de la ligne de la commissure des lèvres; les nageoires pectorales sont grandes et attachées très-bas. Il n'y a pas de nageoire dorsale proprement dite, mais une sorte de pli longitudinal de la peau sur la partie postérieure du dos. L'évent a ses cornes tournées en arrière." [9, 10]

as "nomen nudum", i.e. an unavailable or invalidly published name, although ITIS (www.itis.gov) lists it as "nomen dubium"and associates it with the valid name *Stenella attenuata* (Gray, 1846). Cuvier´s intent in naming the species "dubius" remains unclear.

[8] English translation: "The narrow-snouted dolphin. (Delph rostratus, Shaw) With a more swollen head, a more bulging and slender beak, with only twenty-one or twenty-three conical teeth on each side and in each jaw; its shades are paler, which earned it the name of white dolphin. It is said to belong to the seas of America (2). "The footnote reads:" (2) So far, we have only and roughly engraved its head. Duhamel, Fisheries part. II, sect. X, pl. x, f. 4".

[9] The asterisk * used here and in other quotes below, relates to a statement made in the text "Nous devons avertir que les espèces dont l'existence est bien constatée, seront désignées par une astérisque.", i.e. we must warn that species whose existence is well established, will be designated by an asterisk.

[10] English translation: "Geoffroy's dolphin, Delphinus Geoffrensis, Blainville; slender-beaked dolphin, Cuv. This species is based on an individual from the collection of the Museum of Natural History of Paris, brought back from Portugal by Professor Geoffroy Saint-Hilaire. Its body is elongated, almost cylindrical. The forehead is much more rounded than

This description clearly refers to a river dolphin. The cranial part of the skull is not described, as it was hidden in the mounted skin. Desmarest emphatically compares the rough surface of the teeth with that observed in *Delphinus rostratus*, his "tenth species" (see below). In the following paragraph, Desmarest emphasises that this species differs considerably from the Canadian animal which Cuvier had assumed was conspecific.

This is followed by a citation of a report communicated to Desmarest by de Blainville, who describes a dolphin observed on the coast of Brazil, which he regarded as conspecific with the previous species: "Il croit qu'il résulte de cette description, toute incomplète qu'elle est, une concordance assez marquée avec l'espèce rapportée par M. Geoffroy, du Portugal, et qui provenoit probablement aussi du Brésil." [11]

that of the ordinary dolphin (*Delphinus delphis*); its beak is long, thin, narrow, analogous to that of the fish-eating crocodile; its jaws, blunt at the extremity, are equal in length, very narrow, with parallel edges, armed on each side with twenty-six large conical teeth, equidistant, and meshing when the mouth is closed; the anterior ones are a little smaller than the others, and generally a little blunt at the tip; all are conical, obtuse, with a kind of lower collar, and in addition their surface is rough, which offers a similarity with the slender-beaked dolphin, *Delphinus rostratus*, Cuv. In this species, the eyes are placed a little above the line of the corner of the mouth, the pectoral fins are large and held very low. There is no dorsal fin proper, but a kind of longitudinal fold of the skin on the posterior part of the back. The blowhole has its horns turned back."

[11] "He believes that this description, incomplete as it is, is fairly consistent with the species reported by M. Geoffroy of Portugal, which probably also came from Brazil."

This assumption later turned out to be correct, see van Bree & Robineau (1973).

Desmarest attributes the name *Delphinus Geoffrensis* to de Blainville, who communicated this to him in writing, hence the name should be attributed to de Blainville in Desmarest, 1817. The Paris skin is thus the holotype of this species (*Inia geoffrensis*), as identified by van Bree & Robineau (1973). Its skull was later extracted and has been extensively described and figured by these authors. Although referring to the "dauphin à bec mince" of Cuvier (1817), Desmarest does not include Shaw's *Delphinus rostratus* in this species (see below) as Cuvier had done, and incorrectly and on page 160 confusingly attributes that name to Cuvier instead of Shaw.

As his "*Troisième Espèce*" (p. 153-154) Desmarest describes the "*Dauphin de Shaw (*Delphinus Shawensis*, Blainv.); *Delphinus rostratus*, Shaw. (*general zoology*, vol. II, part. II, pag. 514; *Slender beaked dolphin*.).
Cette espèce réunie par M. Cuvier avec celle qu'il appelle *dauphin à bec mince*, en diffère néanmoins beaucoup par l'extrème minceur de son bec, et doit en être séparée.
M. de Blainville, qui a observé une mâchoire d'un individu de cette espèce dans la collection du collège royal des chirurgiens, à Londres, en a fait une description fort détaillée, dont nous ne donnerons ici qu'un court extrait.
Au premier abord, on pourroit prendre ces mâchoires pour le museau du *gavial* ou du *crocodile tenuirostre*, tant elles sont grêles et allongées. Dans l'etendue de l'espace dentaire, les deux branches de la mâchoire inférieure sont absolument contiguës, les dents sont cependant un peu séparées en arrière, et elles se rapprochent d'autant plus qu'elles sont placées plus près du bout de la mâchoire, où enfin elles se touchent presque par leur base; ces dents sont plus ou moins déjetées en dehors, en général comprimées, fort larges, surtout celles du milieu; les postérieures sont

les plus longues; les antérieures sont presque carrées ou tétragones et extrêmement serrées à la base. Dans les grosses du milieu, la base est striée. La plupart de ces dents sont très-usées, etc. Leur nombre est de trente de chaque côté à la mâchoire inférieure et de vingt-huit à la supérieure. Cette mâchoire longue de deux pieds, est presque tout-à-fait droite, un peu plus élevée à sa base, et à peu près égale en hauteur dans toute son étendue, jusqu'à l'extrémité qui se recourbe brusquement en en[12] haut; sa largeur près de la tête est de deux pouces sept lignes et de sept lignes seulement vers son extrémité tronquée. La mâchoire inférieure est encore plus étroite que la supérieure.
Une portion de crâne jointe à cette partie, indique une forme de tête à peu près semblable à celle des autres dauphins. La peau conservée dans quelques parties est fort épaisse et recouverte d'un épiderme noir.
On ignore d'où provient cette singulière dépouille. Shaw, sur l'observation de ces mêmes mâchoires, soupçonne que le dauphin qu'il annonce plutôt qu'il ne décrit, sous le nom de *Delphinus rostratus*, vivoit dans la mer des Indes." [13]

So, this incomplete skull in London is the one described in 1801 by Shaw and thus the holotype of *Delphinus rostratus* Shaw, 1801. The description of the jaw, teeth and partial cranium does not agree with the Ganges dolphin, but very well fits an older specimen of the Amazon dolphin. If still preserved, it should be carefully studied and re-identified.

As his "*Dixième Espèce*" (p. 160-161) Desmarest gives: "*Dauphin à bec mince, *Delphinus rostratus*, Cuv., Rapport sur les cetacés échoués à Paimpol, en janvier 1812. *Ann. Mus.*, tom. XIX, pag. 9.
Cette espèce est celle des dauphins à museau grêle jusqu'alors inconnue, dont M. Cuvier dit, dans son rapport, 'qu'elle n'a que vingt-six dents partout, cent quatre en totalité, fortes, coniques, tronquées au bout comme les dents du souffleur (*delphinus tursio*, Bonnaterre);

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[12] There appears to be a typographical error in the original (1817) text here, and presumably should read 'brusquement et en haut'

[13] English translation: "Shaw's Dolphin (Delphinus Shawensis, Blainv.); Delphinus rostratus, Shaw. (General Zoology, Vol II, part II, page 514, Narrow beaked dolphin.). This species, reunited by M. Cuvier with the one he calls the narrow-beaked dolphin, nevertheless differs a great deal from the extreme thinness of its beak, and must be separated from it. M. de Blainville, who has observed a jaw of an individual of this kind in the collection of the Royal College of Surgeons in London, has given a very detailed description of it, of which we shall give only a short excerpt here. At first glance, one could take these jaws for the muzzle of the gavial or fish-eating crocodile, as they are slender and elongated. In the extent of the tooth space, the two branches of the lower jaw are absolutely contiguous, the teeth are, however, a little separated behind, and they come closer as they are placed towards the end of the jaw, where finally they touch almost by their base; these teeth are more or less bent outside, generally compressed, very wide, especially those in the middle; the posterior ones are the longest; the anterior ones are almost square or with four angles and extremely tight at the base. In the big teeth of the middle, the base is striated. Most of these teeth are very worn, etc. Their number is thirty on each side at the lower jaw and twenty-eight at the upper one. This jaw, two feet long, is almost entirely straight, a little higher at its base, and nearly equal in height in all its extent, to the extremity which curls abruptly upward; its width near the head is two inches seven lines, and only seven lines towards its truncated end. The lower jaw is even narrower than the upper one. A portion of the skull attached to this part indicates a head shape similar to that of other dolphins. The skin preserved in some parts is very thick and covered with a black epidermis. We do not know where this unique body comes from. Shaw, on the observation of these same jaws, suspects that the dolphin which he claims rather than describes, under the name of *Delphinus rostratus*, lived in the Indian seas."

qu'elle a le museau plus long encore que celui du *delphinus delphis* et en différant en ce qu'il n'est pas déprimé, mais, au contraire, comprimé latéralement.'
M. de Blainville a été à même d'observer un crâne de cette espèce dans le cabinet de M. Sowerby, à Londres; et ce crâne est, au nombre de dent près, en tout semblable aux cinq ou six qui existent dans la collection du Muséum d'Histoire naturelle de Paris, et qui ont servi à l'établissement de l'espèce par M. Cuvier."[14]

Desmarest continues by citing de Blainville's description of this London skull, noting some differences with the Paris specimens, and describing the teeth: "Les dents de la tête qui fait partie de la collection de M. de Sowerby, n'étoient qu'au nombre de vingt - deux de chaque côté des deux mâchoires, en tout quatre-vingt-huit, ce qui diffère de ce que l'on observe dans les têtes du Muséum de Paris, qui sont munies de cent quatre dents. Mais ce qui est commun à toutes, et ce qui fournit un excellent caractère dont la remarque est due à M. de Blainville, c'est que ces dents, toutes absolument de la même forme, coniques, un peu courbées en arrière ou plutôt en dedans, beaucoup plus grosses que celles du dauphin vulgaire et mousses à leur extrémité, ont une sorte de collet, et toute la partie saillante hors des gencives comme rugueuse ou plutôt guillochée.
On ignore dans quelles mers habite ce dauphin, mais il y a lieu de croire qu'on le trouve au moins quelquefois dans celles d'Europe, puisque le crâne que possède M. Sowerby étoit tout frais lorsque M. de Blainville en fit la description."[15]

Desmarest here describes a series of five or six skulls in Paris, obviously the same specimens mentioned in 1812 by Cuvier in the second paragraph of page 10 of his work, and regards a fresh skull in Sowerby's collection in London, reported by de Blainville, as belonging to the same species. The rough surface of the teeth is unmistakably described.

Desmarest's descriptions agree with the rough-toothed dolphin. Desmarest calls this species, at the time still only known from skulls, *Delphinus rostratus* Cuvier (as opposed to *Delphinus rostratus* Shaw), again erroneously referring to Cuvier's 1812 paper, though

[14] English translation: "Slender-beaked Dolphin Delphinus rostratus, Cuv., Report on cetaceans stranded in Paimpol, January 1812. Ann. Mus., Tom. XIX, pag. 9. This species is that of the hitherto unknown slender-mouthed dolphins, of which M. Cuvier says, in his report, that it has only twenty-six teeth everywhere, a hundred and four in all, strong, conical, truncated at the end like the teeth of the bottlenose dolphin (*Delphinus tursio*, Bonnaterre); that it has a beak still longer than that of *Delphinus delphis*, and differing in that it is not depressed, but, on the contrary, compressed laterally. M. de Blainville was able to observe a skull of this species in the cabinet of Mr. Sowerby, in London; and this skull is, in every respect including the number of teeth, similar to the five or six that exist in the collection of the Museum of Natural History of Paris, and which were used for the establishment of the species by M. Cuvier."

[15] English translation: "The teeth of the head, which is part of the collection of M. de Sowerby, were only twenty - two on each side of the two jaws, in all eighty - eight, which differs from what is observed in the heads in the Paris Museum, which are fitted with one hundred and four teeth. But what is common to all, and what provides an excellent feature, the relation of which is due to M. de Blainville, is that these teeth, all absolutely of the same form, conical, somewhat curved backwards, or rather inwards, much larger than those of the common dolphin, and blunt at their extremity, have a sort of collar, and all the part protruding from the gums as rough or rather braided. It is not known in what seas this dolphin inhabits, but there is reason to believe that one can find it at least sometimes in those of Europe, since the skull which Mr. Sowerby possesses was quite fresh when M. de Blainville made its description."

here Cuvier correctly mentions Shaw (1801) as the author and, moreover and importantly, does not include the Paris skulls in that species. Hence, the name *Delphinus rostratus* Cuvier is incorrectly used. Desmarest adds to the confusion by applying Cuvier's (1817) vernacular "dauphin à bec mince" to this species as well as to *Delphinus geoffrensis*.

So quite confusingly, Desmarest here describes three species which he associates in one way or another with Cuvier's (1817) "dauphin à bec mince". His "first species" is the Amazon river dolphin or boto *Delphinus geoffrensis*, which name he attributes to de Blainville. His "third species" has always been taken to represent the Ganges dolphin, but clearly is an Amazon dolphin, too. Desmarest calls it *Delphinus Shawensis* de Blainville or, correctly, *Delphinus rostratus* Shaw, which he states should be separated from Cuvier's "dauphin à bec mince". His "tenth species", described from undocumented skulls in Paris and London, can only be the rough-toothed dolphin, which he erroneously identifies with *Delphinus rostratus* Cuvier, 1812 (= Shaw, 1801).

Desmarest (1822: 512-515)

Desmarest (1822: 512-515), in the second volume of his Mammalogie, does not basically differ from his 1817 overview, albeit that he changes the name of the Brazilian dolphin to "*delphinus Geoffroyi*", and the Ganges dolphin to "*delphinus gangeticus*, Lebeck". Of the remaining species he writes (p. 515):
"764 [e]. Esp. Dauphin à bec mince, *delphinus rostratus*.
(Non figuré.) *Dauphin à bec mince, delphinus rostratus*, Cuv. Rapp. sur les cétacés échoués à Paimpol en 1812. Ann. du Mus. tom. 19. p. 9. – Desm. nouv. Dict. d'hist. natur. tom. 9. pag. 160."[16]

After a diagnosis ("Car. essent."), Desmarest gives a more extensive description of the skull: "Descript. Cette espèce, dont on ne connoît que la tête osseuse, diffère du dauphin ordinaire,… Les dents, au nombre de vingt-six dans une tête décrite par M. G. Cuvier, et de vingt-deux seulement dans une seconde observée par M. de Blainville, sont toutes absolument de la même forme, c'est-à-dire, coniques, un peu courbées en arrière ou plutôt en dedans, beaucoup plus grosses que celles du dauphin vulgaire et mousses à leur extrémité, pourvues d'une sorte de collet à leur base, et elles ont toutes, leur partie saillante comme rugueuse ou guillochée.
Habit. Inconnues.
Patrie. Ignorée. La grande fraîcheur d'une tête possédée par M. Sowerby, a donné lieu à M. de Blainville de conjecturer que cette espèce habitoit les mers d'Europe." [17]

So here again, Desmarest's concept of *Delphinus rostratus* is incorrectly attributed to Cuvier (1812) under the latter's 1817 vernacular "dauphin à bec mince", and applies to the same skulls in Paris and London, although he

[16] English translation: "764 e. Esp. Slender-beaked dolphin, Delphinus rostratus. (Not shown.) Slender-beaked dolphin Delphinus rostratus, Cuv. Rep. on cetaceans stranded at Paimpol in 1812. Ann. of Mus. tom. 19. p. 9. - Desm. nouv. Dict. of hist. natur. tom. 9. pag. 160."

[17] English translation: "Descript. This species, of which we know only the bony head, differs from the ordinary dolphin, ... The teeth, twenty-six in a head described by Mr. G. Cuvier, and only twenty-two in a second observed by M. de Blainville , are all absolutely of the same shape, that is to say, conical, somewhat curved backwards or rather inwards, much larger than those of the common dolphin and blunt at their extremity, provided with a sort of collar at their base, and they all have their prominent part as rough or braided. Habit. Unknown. Country. Ignored. The freshness of a head possessed by Mr. Sowerby, gave rise to M. de Blainville to speculate that this species inhabited the seas of Europe."

now seems to refer to only one of the skulls (with 26 teeth per jaw) in Paris described by Cuvier, and to the London skull (with 22 teeth per jaw) in Sowerby's collection, reported by de Blainville.

Georges Cuvier (1823: 278)

G. Cuvier (1823: 278), in his review of cetaceans, now renames the Paris skin from Portugal *Delphinus frontatus* and expresses a different opinion on the other material:
"Une espèce de dauphin moins connue que les précédens, à la chute de sa convexité frontale plus rapide, le bec plus prononcé et plus comprimé...
On a au Muséum un individu entier venu de Lisbonne et plusieurs têtes d'origine inconnue…Je nommerai maintenant cette espèce *frontatus*, pour éviter toute équivoque (1)." [18]

The footnote (1) says "C'est le dauphin que M. Desmarest (Mammalogie, p. 512) nomme *dauphin de Geoffroy*… J'avois aussi soupçonné que ce pouvoit être celui que Shaw (Gener. zool., vol. II, part III, p. 514) indique d'une manière fort abrégée sous le nom de *delphinus rostratus*, et qu'il croit de l'Inde; mais il se pourroit aussi que ce dernier fût un vieil individu de *gangeticus*: toutes ces indications incomplètes ne servent qu'a mettre les naturalistes à la torture".[19]

Although Cuvier now obviously regards the series of skulls in Paris which he had described in his second pararaph in 1812 as conspecific with the skin from Portugal, he does not associate any of those with that specimen; as emphasised above, that would have been impossible, as its skull was still in situ in the skin. He also doubts where to place *Delphinus rostratus* Shaw, 1801. On p. 296 he gives an extensive description of one of the Paris skulls, although not mentioning the characteristic structure of the teeth: "Le *frontatus* (pl. XXI, fig. 7 et 8) s'en distingue davantage. Il a le museau plus comprimé vers le bout, un peu plus enlargé vers son quart supérieur; le lobe du devant l'orbite plus marqué et séparé du museau par une plus grande échancrure; les os de nez plus larges, moins saillans et touchant aux intermaxillaires, la crête occipitale plus effacée; la tempe beaucoup plus grande, et l'occiput en conséquence plus étroit. Le vomer s'y montre en dessous comme dans les précédens." [20]

Pl. XXI figs 8 and 9 show a dolphin skull which agrees well with that of the rough-toothed dolphin, although here too, the structure of the teeth is not visible.

The name *Delphinus frontatus* G. Cuvier, 1823

[18] English translation: "A species of dolphin less known than the previous ones, with the downward slope of its frontal convexity steeper, the beak more pronounced and more compressed ... We have in the Museum a whole individual from Lisbon and several heads of unknown origin ... I will now name this species frontatus, to avoid any ambiguity (1)."

[19] English translation: "It is the dolphin that M. Desmarest (Mammalogie, p.512) calls Geoffroy's Dolphin ... I also suspected that it could be the one that Shaw (... p 514) very briefly indicates under the name of delphinus rostratus, and that he believes it came from India; but it could also be that the latter was an old individual of gangeticus: all these incomplete indications serve only to torture naturalists."

[20] English translation: "The frontatus (Plate XXI, Figs 7 and 8) differs further. It has a beak more compressed towards the end, a little more enlarged towards its upper quarter; the lobe in the front of the orbit more marked and separated from the beak by a larger indentation; the larger nasal bones, less prominent and touching the intermaxillaries, the occipital crest more erased; the temporal bones are larger, and the occipital bone accordingly narrower. The vomer is shown below as in the preceding ones. "

thus appears to be based on composite material: the Paris skin from Portugal *Delphinus geoffrensis* de Blainville in Desmarest, 1817 (with the suggestion that *Delphinus rostratus* Shaw, 1801 may be conspecific), and a series of undocumented skulls in the Paris Museum.

In this connection, Cuvier's complaint about the incomplete descriptions by other authors, which to him only seem fit to torture naturalists, is quite ironic, since he himself provided perhaps the most inaccurate and puzzling accounts of all.

However, Cuvier's addition on p. 400 of his work is most important; it is here cited in full: "Addition importante a cette septième partie. Nous avons décrit, p. 296 ci-dessus, et représenté pl. XXI, fig. 7 et 8, les têtes d'une espèce de dauphin, que nous avons rapportées par conjecture à une espèce du cabinet du roi, qui a les mêmes dents à peu de choses près, et que nous avons nommée, p. 278, à cause de son front bombé, *delphinus frontatus*.
M. *van Breda*, très-habile professeur d'histoire naturelle à Gand, et gendre de feu mon ami Adrien Camper, vient de me communiquer le dessin de la véritable espèce dont proviennent ces sortes de têtes, ce qui est d'autant plus certain qu'il est accompagné du dessin de la tête de l'individu même d'après lequel est fait. Il en résulte que ce dauphin n'a pas le front relevé, mais que le profil de son crâne se perd insensiblement dans celui de son museau.
Le dessin d'un animal très-semblable a été envoyé de Brest au Muséum; en sorte que je ne doute point que nous n'ayons dans ces dessins et dans ces têtes la preuve qu'il doit être ajouté une espèce à la liste des dauphins authentiquement connus, et une espèce à museau pointu, mais non distinguée du front par une brisure marquée de son profil.
Sa dorsale est élevée et en demi-croissant, à peu près sur le milieu de sa longueur; ses pectorales sont taillées en faux, sa caudale est en croissant et échancrée au milieu. L'individu observé par M. van Breda avoit huit pieds de longueur.
N.B. Le *delphinus frontatus*, p. 278, a la dorsale presque aussi basse que le dauphin du Gange. Fin du cinquième volume." [21]

The seventh part of this volume, containing this "addition importante", was printed in 1825. The drawings shown to him in that year by van Breda from Ghent in present-day Belgium, of a fresh dolphin and its skull (no locality given) immediately made Cuvier realise that the skulls that he had assumed "par conjecture" to belong with the Paris skin with bulbous forehead, agreed with the one in van Breda's drawing. However, the latter's figure

[21] "Important addition to this seventh part. We have described, p. 296 above, and represented pl. XXI, fig. 7 and 8, the heads of a species of dolphin, which we have reported by conjecture to be a species of the King's cabinet, which mostly has the same teeth, and which we have named, p. 278, because of its bulging forehead, delphinus frontatus. M. van Breda, a very skillful professor of natural history at Ghent, and son-in-law of my late friend Adrien Camper, has just communicated to me the drawing of the true species from which these types of heads come, which is all the more certain, accompanied as it is by the drawing of the head of the same individual. As a result, this dolphin does not have its forehead raised, but the profile of its skull is imperceptibly lost in that of its beak. The drawing of a very similar animal has been sent from Brest to the Museum; so that I have no doubt that we have in these drawings and in these heads the proof that a species must be added to the list of authentically known dolphins, and a species with a pointed beak, but not distinguished from the forehead by a marked break of its profile. Its dorsal fin is high and half-crescent shaped, about in the middle of its length; its pectoral fins are falciform, its tail is crescent-shaped and indented in the middle. The individual observed by Mr. van Breda was eight feet in length. *N.B.* The delphinus frontatus, p. 278, has the dorsal fin almost as low as the Ganges dolphin. End of the fifth volume. "

of the fresh animal showed a dolphin with a very flat forehead and a pronounced dorsal fin. By coincidence, Cuvier had also received a drawing of a similar animal from Brest in Brittanny. He recognised that here was a species new to science, of which until then he only had a series of undocumented skulls in the Paris Museum. He now restricted the name *Delphinus frontatus* to the mounted skin in view of its bulbous forehead, but did not yet name the newly recognised species, which clearly was a rough-toothed dolphin.

By this action, the name *Delphinus frontatus* G. Cuvier, 1823 has become an objective synonym of *Delphinus geoffrensis* de Blainville in Desmarest, 1817 (*Inia geoffrensis*), and is not available for other species placed in the genus *Delphinus*.

Lesson (1828: 206-207)

Lesson (1828: 206-207), in his volume on cetaceans, is the first to name this newly recognised species, which he arranged under de Blainville's "delphinorhynques", dolphins with a long and narrow beak. The paragraph on this species is cited here in full:

"Le delphinorhynque de Breda.
(*Delphinus bredanensis*. Cuv.)
En figurant le crâne de cette espèce, M. Cuvier l'avoit rapportée au delphinorhynque de Geoffroy ou *delphinus frontatus*[1]. Ce savant, ayant reçu de M. *Van Breda* de Gand un dessin de l'espèce véritable d'où provenoient les têtes qu'il avoit examinées, a été conduit à reconnoître l'existence d'un cétacé nouveau et authentique (*Oss. foss.*, t. V, p. 400). Depuis on a aussi envoyé de Brest un dessin de dauphin qui se rapporte encore à ce delphinorhynque." The footnote reads: "[1] *Delphinus frontatus*, G. Cuv., *Oss. foss.*, t. V, pl. XXI, fig. 7 et 8 (par erreur). Addit. importante, G. Cuv. t. V, p. 400."
He continues: "L'individu observé par M. van Breda avoit huit pieds de longueur; une dorsale élevée et en demi-croissant, à-peu-près sur le milieu de la hauteur; des pectorales taillées en faux; sa caudale façonnée en croissant et échancrée au milieu. Mais ce qui caractérise cette espèce est le profil du crâne qui se perd insensiblement dans celui du museau, tandis qu'on remarque le contraire dans celui qui précède.
Sa tête osseuse[1] se distingue en effet par un museau plus comprimé vers le bout, un peu plus élargi vers son quart supérieur; le lobe du devant de l'orbite plus marqué et séparé du museau par une plus grande échancrure; les os du nez sont plus larges, moins saillants et touchent aux intermaxillaires. La crête occipitale est le plus effacée; la région temporale beaucoup plus grande, et l'occiput en conséquence plus étroit." The footnote says: "[1] G. Cuvier, *Oss. foss.*, t. V, p. 296." [22]

[22] English translation: "The Breda Dolphin. (*Delphinus bredanensis*, Cuv.) In depicting the skull of this species, M. Cuvier had related it to the (small) dolphin of Geoffroy or delphinus frontatus. This scientist, having received from M. van Breda of Ghent a drawing of the true species from which the heads he had examined came from, had been led to recognise the existence of an authentic new cetacean (Oss. V, 400). Since then a drawing of a dolphin has also been sent from Brest, which still relates to this dolphin. "The footnote reads:" 1 Delphinus frontatus, G. Cuv., Oss. foss., t. V, pl. XXI, fig. 7 and 8 (by mistake). Addit. important, G. Cuv. t. V, p. 400. " He continues: "The individual observed by Mr. van Breda was eight feet in length; an elevated and half-crescent-shaped dorsal, at about the middle of the height; falciform pectorals; its tail is crescent-shaped and indented in the middle. But what characterises this species is the profile of the skull, which is imperceptibly lost in that of the snout, while we notice the opposite in that which precedes. Its bony head[1] is distinguished by a beak more compressed towards the end, a little more enlarged towards its upper quarter; the lobe in front of the orbit more marked and separated from the beak by a larger indentation; the nasal bones are wider, less prominent and in contact with the intermaxillaries. The occipital crest is the most

He concludes: "Ce delphinorhynque sur lequel nous ne possédons que les renseignements qu'on vient de lire, habite les mers d'Europe." [23]

Lesson kindly attributes the name *Delphinus bredanensis* to Cuvier who, however, had not named the species, or at least not published a name. In the index to this work (p. 440), Lesson listed the species as *Delphinorhynchus bredanensis*.

The locality of van Breda's specimen remained unknown to Lesson, but he does mention the animal from Brest. His description of the exterior of the dolphin and its skull is nearly literally copied from Cuvier (1823, 1825) with only slight changes, hence the peculiar structure of the teeth is not mentioned here either: Lesson had only second-hand information, which he "vient de lire". Nonetheless, Cuvier did not write nor provide the author with this text, such as de Blainville had to Desmarest (1817). The account on this species is by Lesson himself, though with due reference to and careful citation of Cuvier's (1823-1825) descriptions. Schevill's statement in Watkins et al. (1987: 78) that Cuvier "later" (meaning after 1823) "distinguished the species as *Delphinus bredanensis*" is incorrect; or at least, he did not publish that name.

Thus, the valid name of the rough-toothed dolphin is *Delphinus bredanensis* Lesson, 1828 (= *Steno bredanensis*), with Lesson as the author, not G. Cuvier, or G. Cuvier in Lesson, 1828 as it is given in most modern handbooks and other treatises: Rice (1998: 102), Reeves et al. (2002: 346), Mead & Brownell (2005: 734), Jefferson et al. (2008: 191), West et al. (2011: 177) and Wang et al. (2014: 512). The name has been correctly used by Maigret (1994: 269), Miyazaki & Perrin (1994: 1), Rudolph et al. (1997: 10), Robineau (2005: 345) and others. The animals collected by van Breda and recorded from Brest, as well as the undocumented skulls in Paris regarded as conspecific by Cuvier, are syntypes of *Delphinus bredanensis* Lesson, 1828.

Van Breda (1829)

Van Breda (1829) gives an extensive description of his specimen (in Dutch), accompanied by the drawings of the animal and its skull which he had shown to Cuvier. The picture of the animal is rather primitive, but the flat forehead and narrow beak are characteristic of the rough-toohed dolphin. He emphasises the differences of his dolphin from Cuvier's *Delphinus frontatus*, but does not clearly describe or picture the stucture of the teeth. He suggests adoption of the name *Delphinus Bredanensis* which he clearly attributes to Lesson, concluding with a brief diagnosis in Latin: "Delphinus Bredanensis, rostro valde acuto, fronte planâ, pinnis pectoralibus falcatis margine postero medio gibbo, caudali lunatâ emarginatâ".

Strangely, van Breda still does not disclose where and when he obtained this specimen. In fact, the skull, recognisable from van Breda's plate, that, following Schlegel (1862), was "[…] caught near the mouth of the river Scheldt", was recently rediscovered by Bekker et al. (2016; cf. Heerebout et al. 2014) as it is preserved in the University Museum of Ghent.

Fischer (1829: 505)

Fischer (1829: 505), in his Synopsis Mammalium, uses the name "*Delphinus Bredanen-*

erased; the temporal region much larger, and the occipital bone accordingly narrower. "The footnote says:" 1 G. Cuvier, Oss. foss., t. V, p. 296. «

[23] "This (small) dolphin, on which we have only the information we have just read, lives in the seas of Europe."

sis Cuv.", not attributing the name to Lesson. About the locality he adds: "*Ad oras Batavas. Van Breda.*" In those days, "Orae Batavae" applied to the coasts of the Netherlands and Flanders. Probaby, Fischer had assumed this provenance, since van Breda was then based in Ghent.

Georges Cuvier (1829: 288-289)

G. Cuvier (1829: 288-289), in the new edition of his Règne animal, very briefly mentions the following species:
On p. 288: "Notre *D. frontatus* n'a que vingt-une dents partout, plus grosses qu'au précédent, et le museau plus long et plus comprimée; on ne connaît pas son origine."
On p. 289: "Un autre, que nous voyons aussi quelquefois (*D. rostratus*, Cuv.), a le museau grêle, et extérieurement tout d'une venue avec la tête, et les dents au nombre de vingt-une surtout. Sa dorsale est de grandeur ordinaire (2)." [24]

The footnote (2) does not concern the rough-toothed dolphin, but adds another species to his list. He clearly describes the flat forehead.

He concludes with the Ganges dolphin: "On doit distinguer de ce première groupe le *Dauphin du Gange* (*D. gangeticus*, Roxburg [= Roxburgh]), dont l'évent est en ligne longitudinale, et qui a les mâchoires grêles, renflées au bout. Il remonte très loin dans le Gange: c'est probablement la *platanista* de Pline." [25]

An unnumbered footnote reads: "*N. B.* Le *D. rostratus* de Shaw n'est que le *gangeticus*." [26]

See Kinze (2000) for the publication dates of Lebeck and Roxburgh, who both described *Delphinus gangeticus* in 1801.

This account is utterly erroneous and confusing; Cuvier seems to have forgotten his observations made in 1825. Though referring the name *Delphinus rostratus* Shaw to the Ganges dolphin, he blatantly uses *Delphinus rostratus* Cuvier for the rough-toothed dolphin, as Desmarest (1817) had incorrectly done. He overlooks Lesson's (1828) name *Delphinus bredanensis* for the species that he had recognised as new in 1825, and which Lesson had attributed to him.

Frédéric Cuvier (1833: unpaginated; 1836: 156-158)

Frédéric Cuvier (1833: unpaginated; 1836: 156-158) published good descriptions, each accompanied by a lithographic plate (in 1833 hand-coloured, in 1836 reduced, in reverse and in black and white) of the animal from Brest, which indeed clearly is a rough-toothed dolphin. He also refers to the drawings that van Breda had shown to his brother Georges Cuvier. In 1833, he only uses a French vernacular "Dauphin à long bec", but in 1836 applies the name *D. Rostratus*, since his brother had

[24] English translation: "On p. 288: "Our D. frontatus has only twenty-one teeth everywhere, larger than in the previous one, and the beak longer and more compressed; we do not know where it comes from. "
On p. 289: "Another, which we sometimes also see (D. rostratus, Cuv.), has a slender beak, and externally in continuity with the head, and the teeth number twenty-one on each side of each jaw. Its dorsal fin is of ordinary size (2). "

[25] English translation: "We must distinguish from this first group the Ganges dolphin (*D. gangeticus*, Roxburg [= Roxburgh]), whose blowhole is in longitudinal line, and which has slender jaws, swollen at the end. It goes very far upstream in the Ganges: it is probably the platanista of Pliny."

[26] English translation: "N.B. Shaw's *D. rostratus* is only *gangeticus*."

taken van Breda's animal "… pour type d'une espèce nouvelle qu'il nomma *rostratus* (1)", [27] the footnote saying: "(1) Cette espèce entre pour beaucoup dans le dauphin à bec mince de mon frère. Règ. anim., édit. de 1817, p. 278." [28]

This is incorrect, as in 1817 G. Cuvier had emphasised the bulbous forehead of his "dauphin à bec mince" and in 1825 had recognised that the newly distinguished species was different from his *Delphinus frontatus*.

Although F. Cuvier acknowledges that the name *Delphinus rostratus* had been given to the Ganges dolphin by Shaw (1801), he writes, overlooking or ignoring Lesson (1828): "Le nom de *rostratus* est sans doute celui que ce dauphin conservera dans les catalogues méthodiques, quoiqu'il ait été donné par Schaw [= Shaw] à l'espèce du Gange; mais ce dauphin du Bengale a lui-même changé de nom et comme genre et comme espèce" [29], no doubt referring to the name *Platanista gangetica* (Lebeck or Roxburgh, 1801) although he does not specify, the generic name *Platanista* having been published in 1830.

Thus, F. Cuvier apparently found that the name *Delphinus rostratus* Cuvier had now become available for the rough-toothed dolphin.

Strangely, Robineau (2005: 351), in his review of the cetaceans of France, rejects the record from Brest, erroneously stating: "Cuvier fait référence à un dessin (non publié) reçu de Brest, ce qui paraît insuffisant". Obviously, he has overlooked the lithographs made after this drawing and published by F. Cuvier in 1833 and 1836, as well as the plate from a different source, published by Jardine in 1837 (see below).

Jardine (1837: 252)

Jardine (1837: 252), in his natural history of Cetacea, gives the species as:

"Delphinorhynchus of Breda.
Plate XXVII.
Delphinorhynchus Bredanensis, *Less.* – D. Rostratus, *Cuv.* – Delphinus à long bec, *Fr. Cuvier.*"

The genus *Delphinorhynchus* was used by Lesson (1828) in the index of his work (p. 440), not in the main text. Jardine's description is based on Lesson's account. Pl. 27 figures the animal washed ashore near Brest: "The specimen of which our Plate is a representation was stranded at Brest and there faithfully delineated." The hand-coloured lithograph clearly is of a rough-toothed dolphin, and is obviously based on another drawing than the one reproduced by F. Cuvier (1833, 1836). This plate too, has been overlooked by Robineau (2005).

Schlegel (1841: 27)

Schlegel (1841: 27), in his review of cetacean species, calls the rough-toothed dolphin *Delphinus planiceps*, which name he erroneously atributes to van Breda (1829): "Delphinus planiceps, Tab. IV, Fig. 8 (Zähne). Unter diesem Namen aufgeführt von van Breda, Verhand. Nederl. Instit. 1829, p. 235, Tab. 1 et 2. Cuvier, Oss. foss. V, Pl. 21, Fig. 7 et 8, p. 278 et p. 296 hat zuerst den Schädel dieser Art abge-

[27] English translation: "... for the type of a new species he named rostratus (1)",

[28] English translation: the footnote saying: "(1) This species is a big part of my brother's slender-beaked dolphin. Reg. anim., ed. from 1817, p. 278.»

[29] English translation: "The name of rostratus is undoubtedly the one that this dolphin will retain in the methodical catalogues, even though it was given by Schaw [= Shaw] to the species of the Ganges; but this Bengal dolphin itself has changed its name as a genus and as a species."

bildet, aber denselben fälschlich als zu seinem D. frontatus gehörend, beschrieben, welchen Jrrthum er jedoch schon in dem nämlichen Werke p. 400, berichtigte, und kurz darauf, Règne an. p. 289, den früher von Shaw für den gangetischen Delphin gebrauchten Namen D. rostratus, auf unser Thier anwendete. Letzteren behielt auch Fr. Cuvier bei, der in seinen Mammifères ein bei Brest gestrandetes Exemplar abbildete. Fischer aber, Synopsis p. 505, nannte diese Art: D. Bredanensis." [30]

Schlegel too, overlooks Lesson (1828). He refers to both animals that had been figured: "Die äussere Gestalt des Thieres ist nur nach den beiden, bei Brest und an den holländischen Küsten gestrandeten Individuen bekannt" [31], thus giving the Dutch coast as the locality of van Breda's animal.

In fact, Schlegel had copied the name *Delphinus planiceps* from a label of an undocumented skull in the Leiden Museum. He corrected this error in 1862 (p. 85 – see below). He does not mention the structure of the teeth, nor is this character visible in his plate IV fig. 8. Robineau (2005: 346) repeats Schlegel's erroneous attribution of the name *Delphinus planiceps* to van Breda.

The name *Delphinus planiceps* Schlegel, 1841 is thus an objective synonym of *Delphinus bredanensis* Lesson, 1828. Its syntypes are the animals collected by van Breda and near Brest.

Gray (1846: 43), in his review of cetaceous animals, places *Delphinus rostratus*, erroneously attributed to Cuvier (1812) in the new genus *Steno*.

Schlegel (1862: 84-86)

Schlegel (1862: 84-86), in his book on the mammals of the Netherlands (in Dutch), now opts for the name *Delphinus rostratus*, while in the same sentence recognising that Lesson had earlier named the species *Delphinorhynchus Bredanensis*, the name that Lesson had given in the index of his work. Again, Schlegel also mentons the animal from Brest.

Most importantly, he specifies that van Breda's dolphin had been obtained in or near the mouth of the river Scheldt, that is, in the border area between Dutch and Belgian waters. He must have received this information from van Breda himself, as the two colleagues were well acquainted and had jointly published a paper on a cetacean subject. After the Belgian uprising in 1830, van Breda had left Ghent for a professorship at Leiden and later moved to Haarlem, where he became the director of Teylers Museum. The animal obtained by van Breda (cf. Bekker et al. 2016) represents the northernmost record of the rough-toothed dolphin in European waters and the only documented specimen from the North Sea to date.

Later revisions

Later revisions concerning the name of the rough-toothed dolphin are not considered here, except for the following notes:

[30] English translation: "Delphinus planiceps, Tab. IV, Fig. 8 (Teeth). Under this name listed by van Breda, Verhandl. Nederl. Instit. 1829, p. 235, Tab. 1 et 2. Cuvier, Oss. foss. V, Pl. 21, Fig. 7 et 8, p. 278 et p. 296 first depicted the skull of this kind, but mistakenly described it as belonging to D. frontatus, an error which he had already corrected in the same work p. 400, corrected, and shortly thereafter, to Règne. p. 289, formerly used by Shaw for the gangetic dolphin name D. rostratus, applied to our animal. The latter name was also kept by Fr. Cuvier, who depicted a specimen stranded at Brest in his Mammifères. Fischer, however, Synopsis p. 505, called this species: D. Bredanensis."

[31] English translation: "The external form of the animal is known only from the two individuals stranded at Brest and on the Dutch coasts."

Hershkovitz (1966: 15) uses *Steno bredanensis* Lesson [= (Lesson, 1828)], wrongly mentioning *Delphinus rostratus* Cuvier (no year given) as type species, noting that the name *Delphinus rostratus* Desmarest, 1817 (which Desmarest attributed to Cuvier) was preoccupied by *Delphinus rostratus* Shaw, 1801. His overview is extremely confused and confusing, and contains numerous mistakes.

Schevill in Watkins et al. (1987: 78) uses *Steno bredanensis* (G. Cuvier in Lesson, 1828). He also mentions that Desmarest (1817) discussed the Paris skulls under the name *Delphinus rostratus* Cuvier, referring to Cuvier's 1812 paper, which is incorrect.

Maigret (1994: 269) correctly uses *Steno bredanensis* (Lesson, 1828).

Miyazaki & Perrin (1994: 1) correctly use *Steno bredanensis* (Lesson, 1828).

Rice (1998: 102) uses *Steno bredanensis* (G. Cuvier in Lesson, 1828) and states that the name *Steno rostratus* (G. Cuvier, 1817) had long been in use, but was preoccupied [by *Delphinus rostratus* Shaw, 1801)].

Mead & Brownell (2005: 734) use *Steno bredanensis* (G. Cuvier in Lesson, 1828) and erroneously attribute the name *Delphinus rostratus* to Desmarest (1817)[32].

Robineau (2005: 345-346) correctly uses *Steno bredanensis* (Lesson, 1828), but wrongly states that Cuvier (1812) included the Paris skulls in his *Delphinus rostratus*; he erroneously attributes the name *Delphinus planiceps* to van Breda (1829).

West et al. (2011: 177) use *Steno bredanensis* (Cuvier in Lesson, 1828) and again wrongly attribute the name *Delphinus rostratus* to Desmarest (1817).

[32] This error is perpetuated in online taxonomic resources such as WoRMS (www.marinespecies.org) and ITIS (www.itis.gov).

Conclusion

In conclusion, the correct name of the rough-toothed dolphin is *Steno bredanensis* (Lesson, 1828). The type locality of the rough-toothed dolphin is the mouth of the river Scheldt. *Delphinus rostratus* Shaw, 1801 is considered a senior synonym of *Ina geoffrensis*, not a junior synonym of *Delphinus gangeticus* Lebeck 1801.

Re-identification of Shaw's type specimen as an Amazon dolphin would have consequences for the name of that species, which would then become *Inia rostrata* (Shaw, 1801). This is undesirable for reasons of stability. If the specimen cannot be relocated and re-examined, as seems likely, it would be best to consider this "nomen dubium", because the description is insufficient for identification, or else to ask the International Commission on Zoological Nomenclature to suppress the name *Delphinus rostratus* Shaw, 1801.

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Samenvatting

Een chronologisch overzicht van de naamgeving van *Delphinus rostratus* Shaw, 1801 en *Delphinus bredanensis* (Lesson, 1828)

Om de sterk met elkaar verweven naamgevingen van *Delphinus rostratus* en *Delphinus bredanensis* te ontwarren wordt een chronologisch overzicht gegeven van de totstandkoming van die naamgevingen. Op basis van dit overzicht wordt *Delphinus rostratus* beschouwd als een senior synoniem van *Inia geoffrensis* en niet als een junior synoniem van *Delphinus gangeticus* Lebeck, 1801. F. Cuvier meende in 1836 te weten dat de naam Cuvier beschikbaar was voor de snaveldolfijn waarbij hij ten onrechte zijn broer G. Cuvier 1812 en niet Shaw 1801 de credits gaf. De juiste naam voor de snaveldolfijn is echter *Steno bredanensis* (Lesson, 1828) met als type-lokaliteit de Scheldemonding. Aangezien het type-exemplaar van Shaws *Delphinus rostratus* niet kan worden gelokaliseerd om opnieuw onderzocht te worden, lijkt het meest voor de handliggend de naam te beschouwen als een 'nomen dubium', omdat de beschrijving niet voldoet aan de normen voor een juiste identificatie. Alternatief kan zijn de *International Commission on Zoological Nomenclature* te vragen de naam uit te sluiten.

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