

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* (blue-fin tuna/great shearwater) constellation mid-century 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 macrohynchus*). 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 demographics. 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.

References

Addink, M. & C.S. Smeenk 1999. The harbour porpoise *Phocoena phocoena* in Dutch coastal waters:

- analysis of stranding records for the period 1920-1994. *Lutra* 41: 55-80.
- Andersen, L.W., D.E. Ruzzante, M. Walton, P. Berggren, A. Bjørge & C. Lockyer 2001. Conservation genetics of the harbour porpoise, *Phocoena phocoena*, in eastern and central North Atlantic. *Conservation Genetics* 2: 309-324.
- ASCOBANS 2014. Report of the 3rd Meeting of the North Sea Group. 21st ASCOBANS Advisory Committee Meeting, Gothenburg, Sweden, 29 September – 1 October 2014. AC21/Doc 2.2. 1.a (WG).
- Baker, J.R. & A.R. Martin 1992. Causes of mortality and parasites and incidental lesions in harbour porpoises (*Phocoena phocoena*) from British waters. *Veterinary Record* 130: 554-558.
- Banguera-Hinestroza, E., A. Bjørge, R.J. Reid, P. Jepson & A.R. Hoelzel 2010. The influence of glacial epochs and habitat dependence on the diversity and phylogeography of a coastal dolphin species: *Lagenorhynchus albirostris*. *Conservation Genetics* 11: 1823-1836.
- Beare, D.J., S. Batten, M. Edwards & D.G. Reid 2002. Prevalence of boreal Atlantic, temperate Atlantic and neritic zooplankton in the North Sea between 1958 and 1998 in relation to temperature, salinity, stratification intensity and Atlantic inflow. *Journal of Sea Research* 48: 29-49.
- Beineke A., U. Siebert., M. MacLachlan, R. Bruhn, K. Thron, K. Failing, G. Müller & W. Baumgärtner 2005. Investigations of the potential influence of environmental contaminants on the thymus and spleen of harbor porpoises (*Phocoena phocoena*). *Environmental Science and Technology* 39: 3933-3938.
- Bjørge, A., R.L. Brownell, G.P. Donovan & W.F. Perrin 1994. Significant direct and incidental catches of small cetaceans. A report by the Scientific Committee of the International Whaling Commission to the United Nations Conference on Environment and development (UNCED). Report of the International Whaling Commission (special issue) 15: 75-130.
- Brandt, M.J., A. Diederichs, K. Betke & G. Nehls 2011. Responses of harbour porpoises to pile driving at the Horns Rev II offshore wind farm in the Danish North Sea. *Marine Ecology Progress Series* 421: 205-216.
- Brandt, M.J., A.-C. Dragon, A. Diederichs, A. Schubert, V. Kosarev, G. Nehls, V. Wahl, A. Michalik, A. Braasch, C. Hinz, C. Ketzner, D. Todeskino, M. Gauger, M. Laczny & W. Piper 2016. Effects of offshore pile driving on harbour porpoise abundance in the German Bight. Assessment of Noise Effects. Final Report. IBL Umweltplanung GmbH, Institut für Angewandte Ökosystemforschung GmbH / BioConsult SH GmbH, Husum, Germany.
- Bruhn, R., N. Kannan, G. Petrick, D.E. Schulz-Bull & J.C. Duinker 1999. Persistent chlorinated organic contaminants in harbour porpoises from the North Sea and Arctic waters. *The Science of the Total Environment* 237-238: 351-361.
- Camphuysen, C.J. 1994. The harbour porpoise *Phocoena phocoena* in the southern North Sea, II: a come-back in Dutch coastal waters? *Lutra* 37 (1): 54-61.
- Camphuysen, C.J. 2004. The return of the harbour porpoise (*Phocoena phocoena*) in Dutch coastal waters. *Lutra* 47: 113-122.
- Camphuysen, C.J. 2007. Foraging humpback whale (*Megaptera novaeangliae*) in the Marsdiep area (Wadden Sea), May 2007 and a review of sightings and strandings in the southern North Sea, 2003-2007. *Lutra* 50 (1): 31-42.
- Camphuysen, C.J. & M.F. Leopold 1993. The harbour porpoise *Phocoena phocoena* in the southern North Sea, particularly the Dutch sector. *Lutra* 36 (1): 1-24.
- Camphuysen, C.J. & G. Peet 2006. Whales and dolphins of the North Sea. Fontaine Uitgevers, Kortenhoef, the Netherlands.
- Camphuysen, C.J., Smeenk, C., Addink, M.J., van Grouw, H. & O.E. Jansen 2008. Cetaceans stranded in the Netherlands from 1998 to 2007. *Lutra* 51 (2): 87-122.
- Canning, S.J., M.B. Santos, R.J. Reid, P.G.H. Evans, R.C. Sabin, N. Bailey & G.J. Pierce 2008. Seasonal distribution of white-beaked dolphins (*Lagenorhynchus albirostris*) in UK waters with new information on diet and habitat use. *Journal of the Marine Biological Association of the United Kingdom* 88 (6): 1159-1166.
- Cheney, B., R. Corkrey, J.W. Durban, K. Grellier, P.S. Hammond, V. Uslas-Villanueva, V.M. Janik, S.M. Lusseau, K.M. Parsons, N.J. Quick, B. Wilson &

- P.M. Thompson 2014. Long-term trends in the use of a protected area by small cetaceans in relation to changes in population status. *Global Ecology and Conservation*, 2: 118-128.
- Cheney, B.J., P.M. Thompson, S.N. Ingram, P.S. Hammond, P.T. Stevick, J.W. Durban, R.M. Culloch, S.H. Elwen, L. Mandleberg, V.M. Janik, N.J. Quick, V. Islas-Villanueva, K.P. Robinson, M. Costa, S.M. Einfeld, A. Walters, C. Philips., C.R. Weir, P.G.H. Evans, P. Anderwald, R.J. Reid, J.B. Reid & B. Wilson 2012. Integrating multiple data sources to assess the distribution and abundance of bottlenose dolphins (*Tursiops truncatus*) in Scottish waters. *Mammal Review* 43: 71-88.
- Clausen, B. & S. Andersen 1988. Evaluation of by-catch and health status of the harbour porpoise (*Phocoena phocoena*) in Danish waters. *Danish Review of Game Biology* 13: 1-20.
- Dähne M., A. Gilles, K. Lucke, V. Peschko, S. Adler, K. Krügel, J. Sundermeyer & U. Siebert 2013. Effects of pile-driving on harbour porpoises (*Phocoena phocoena*) at the first offshore wind farm in Germany. *Environmental Research Letters* 8: 2.
- Das, K., U. Siebert, M. Fontaine, T. Jauniaux, L. Holsbeek & J.M. Bouqueneau 2004. Ecological and pathological factors related to trace metal concentrations in harbour porpoises *Phocoena phocoena* from the North Sea and adjacent areas. *Marine Ecology Progress Series* 281: 283-295.
- Das K., A. Vossen, K. Tolley, G. Vikingsson, K. Thron, G. Müller, W. Baumgärtner & U. Siebert 2006. Interfollicular fibrosis on the thyroid glands of the harbour porpoise (*Phocoena phocoena*): An endocrine disruption? *Archive of Environmental Contamination and Toxicology* 51: 720-729.
- Deaville, R. & P.D. Jepson 2011. UK Cetacean Strandings Investigation Programme. Final report for the period 1st January 2005 – 31st December 2010. Institute of Zoology, Zoological Society of London, London, UK.
- De Smet, W.M.A. 1974. Inventaris van de walvisachtigen (Cetacea) van de Vlaamse kust en de Schelde. Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen 50 (1): 1-156.
- De Smet, W.M.A. 1979. Geschiedenis en huidige toestand van het onderzoek over Cetaceeën in België. *Lutra* 21: 25-36.
- De Smet, W.M.A. 1981. Gegevens over de walvisachtigen (Cetacea) van de Vlaamse kust en de Schelde uit de periode 1969-1975. Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen 54 (4): 1-34.
- Donovan, G.P. & A. Bjørge 1995. Harbour porpoises in the North Atlantic: edited extract from the report of the IWC Scientific Committee, Dublin 1995. Reports of the International Whaling Commission (special issue) 16: 3-25.
- Edwards, M., P. Reid & B. Planque 2001. Long-term and regional variability of phytoplankton biomass in the Northeast Atlantic (1960-1995). *ICES Journal of Marine Science* 58: 39-49.
- Edwards, M., G. Beaugrand, P.C. Reid, A.A. Rowden & M.B. Jones 2002. Ocean climate anomalies and the ecology of the North Sea. *Marine Ecology Progress Series* 239: 1-10.
- Evans, P.G.H. 1976. An analysis of sightings of Cetacea in British waters. *Mammal Review* 6: 5-14.
- Evans, P.G.H. 1980. Cetaceans in British Waters. *Mammal Review* 10: 1-52.
- Evans, P.G.H. 1990. European cetaceans and seabirds in an oceanographic context. *Lutra* 33: 95-125.
- Evans, P.G.H. 1997. Ecology of sperm whales (*Physeter macrocephalus*) in the Eastern North Atlantic, with special reference to sightings & strandings records. In: G. Jacques & R.H. Lambertsen (eds). Sperm whale deaths in the North Sea. Science and management. Bulletin de l'Institut royal des Sciences naturelles de Belgique / Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen, Biologie 67 - supplément: 37-46.
- Evans, P.G.H. & L. Borges 1995. Associations between porpoises, seabirds and their prey in South-East Shetland, N. Scotland. *European Research on Cetaceans* 9: 173-178.
- Evans, P.G.H. & A. Bjørge 2013. Impacts of climate change on marine mammals. *Marine Climate Change Impacts Partnership (MCCIP) Science Review* 2013: 134-148. Published online 28 November 2013 DOI:10.14465/2013.arc15.134-148.
- Evans, P.G.H. & J. Teilmann (eds) 2009. Report of ASCOBANS/HELCOM Small Cetacean Population Structure Workshop. ASCOBANS/UNEP Secretariat, Bonn, Germany.
- Evans, P.G.H., P. Anderwald & M.E. Baines 2003. UK

- Cetacean Status Review. Report to English Nature and the Countryside Council for Wales. Sea Watch Foundation, Oxford, UK.
- Evans, P.G.H., P. Fisher, I. Rees & J. Wainwright 1993. Ecological studies of the Harbour Porpoise in Shetland, North Scotland. Report to World Wide Fund for Nature. Sea Watch Foundation, Oxford, UK.
- Evans, P.G.H., S. Harding, G. Tyler & S. Hall 1986. Analysis of Cetacean Sightings in the British Isles, 1958-1985. Nature Conservancy Council, Peterborough, UK.
- Evans, P.G.H., C.C. Kinze, R.H.H. Kroger & C. Smeenk 1987. Statement of Concern. The decline of the Harbour Porpoise in the North Sea. European Cetacean Society, Oxford, UK.
- Fraser, F.C. 1974. Reports on Cetacea stranded on the British coasts from 1948 to 1966, 14. British Museum (Natural History), London, UK.
- Galatius, A. & C.C. Kinze 2016. *Lagenorhynchus albirostris* (Cetacea: Delphinidae). Mammalian Species 48 (933): 35-47.
- Gilles, A., M. Scheidat & U. Siebert 2009. Seasonal distribution of harbour porpoises and possible interference of offshore wind farms in the German North Sea. Marine Ecology Progress Series 383: 295-307.
- Gilles, A., S. Adler, K. Kaschner, M. Scheidat & U. Siebert 2011. Modelling harbour porpoise seasonal density as a function of the German Bight environment: implications for management. Endangered Species Research 14: 157-169.
- Gilles, A., S. Viquerat, E.A. Becker, K.A. Forney, S.C.V. Geelhoed, J. Haelters, J. Nabe-Nielsen, M. Scheidat, S. Sveegaard, F.M. van Beest, R. van Bemmelten & G. Aarts 2016. Seasonal habitat-based density models for a marine top predator, the harbour porpoise, in a dynamic environment. Ecosphere 7 (6): e01367. 10.1002/ecs2.1367.
- Haelters, J. & C.J. Camphuysen 2009. The harbour porpoise in the southern North Sea. Abundance, threats and research & management proposals. IFAW EU Office, Brussels, Belgium / IFAW Dutch Office, Den Haag, the Netherlands.
- Hammond, P.S., P. Berggren, H. Benke, D.L. Borchers, A. Collet, M.P. Heide-Jørgensen, S. Heimlich, A.R. Hiby, M.F. Leopold & N. Øien 2002. Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. Journal of Applied Ecology 39: 361-376.
- Hammond, P.S., K. Macleod, P. Berggren, D.L. Borchers, M.L. Burt, A. Cañadas, G. Desportes, G.P. Donovan, A. Gilles, D. Gillespie, J. Gordon, L. Hiby, I. Kuklik, R. Leaper, K. Lehnert, M. Leopold, P. Lovell, N. Øien, C.G.M. Paxton, V. Ridoux, E. Rogan, F. Samarra, M. Scheidat, M. Sequeira, U. Siebert, H. Skov, R. Swift, M.L. Tasker, J. Teilmann, O. Van Canneyt & J.A. Vázquez 2013. Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. Biological Conservation 164: 107-122.
- Hughes, S.L., J. Tinker & S. Dye 2017. Temperature. MCCIP Science Review 2017: DOI: 10.14465/2017.arc10.003.tem.
- ICES WGMME 2014. Report of the Working Group on Marine Mammal Ecology. 10-13 March 2014, Woods Hole, Massachusetts, USA.
- Jansen, O.E., M.F. Leopold, E.H.W.G. Meesters & C. Smeenk 2010. Are white-beaked dolphins *Lagenorhynchus albirostris* food specialists? Their diet in the southern North Sea. Journal of the Marine Biological Association of the United Kingdom 90: 1501-1508.
- Juniaux, T., D. Petitjean, C. Brenez, M. Borrens, L. Brosens, J. Haelters, T. Tavernier & F. Coignoul 2002. Post-mortem findings and causes of death of harbour porpoises (*Phocoena phocoena*) stranded from 1990 to 2000 along the coastlines of Belgium and Northern France. Journal of Comparative Pathology 126: 243-253.
- Jepson, P.D. (ed.) 2005. Trends in cetacean strandings around the UK coastline and cetacean and marine turtle post-mortem investigations, 2000 to 2004 inclusive (contract CRO 238). Report to Defra. UK Cetacean Strandings Investigation Programme, Institute of Zoology, London, UK.
- Jepson, P.D., J.R. Baker, T. Kuiken, V.R. Simpson, S. Kennedy & P.M. Bennett 2000. Pulmonary pathology of harbour porpoises stranded in England and Wales between 1990 and 1996. Veterinary Record 146: 721-728.
- Jepson, P.D., P.M. Bennett, R. Deaville, C.R. Allchin, J.R. Baker & R.J. Law 2005. Relationships between polychlorinated biphenyls and health status in

- harbour porpoises (*Phocoena phocoena*) stranded in the United Kingdom. *Environmental Toxicology and Chemistry* 24 (1): 238-248.
- Jepson, P.D., R. Deaville, J.L. Barber., A. Aguilar, A. Borrell, S. Murphy, J. Barry, A. Brownlow, J. Barnett, S. Berrow, A.A. Cunningham, N.J. Davison, M. ten Doeschate, R. Esteban, R. Ferreira, A.D. Foote, T. Genov, J. Giménez, J. Loveridge, A. Llavona, V. Martin, D.A. Maxwell, A. Papachlimitzou, R. Penrose, M.W. Perkins., B. Smith, R. de Stephanis, N. Tregenza, P. Verborgh, A. Fernandez & R.J. Law 2016. PCB pollution continues to impact populations of orcas and other dolphins in European waters. *Nature Scientific Reports* 6: 18573. DOI: 10.1038/srep18573.
- Kayes, R.J. 1985. The decline of porpoises and dolphins in the southern North Sea: a current status report. Political Ecology Research Group, Oxford, UK.
- Kinze, C.C. 1985. Intraspecific variation in Baltic and North Sea harbour porpoises (*Phocoena phocoena* L. 1758). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 146: 63-74.
- Kinze, C.C., M. Addink, C. Smeenk, M. García Hartmann, H.W. Richards, R.P. Sonntag & H. Benke 1997. The white-beaked dolphin (*Lagenorhynchus albirostris*) and the white-sided dolphin (*Lagenorhynchus acutus*) in the North and Baltic Seas: Review of available information. *Reports of the International Whaling Commission* 47: 675-681.
- Kinze, C.C., T. Jensen, S. Tougaard & H.J. Baagøe 2010. Danske hvalfund (strandinger) i perioden 1998-2007. *Flora og Fauna* 116 (4): 91-99.
- Kock, K.-H. & H. Benke 1996. On the by-catch of harbour porpoise (*Phocoena phocoena*) in German fisheries in the Baltic and the North Sea. *Archive of Fishery and Marine Research* 44 (1/2): 95-114.
- Kompanje, E.J.O. 2001. Review of strandings and catches of *Tursiops truncatus* (Mammalia: Cetacea, Odontoceti) in the Netherlands between 1754 and 2000. *Deinsea* 8: 169-224.
- Kremer, H. 1987. Untersuchungen zur Alterbestimmung am Schweinswal (*Phocoena phocoena* Linné1758). MSc Thesis. University of Kiel, Germany.
- Kroger, R.H.H. 1986. The decrease of harbour porpoise populations in the Baltic and North Sea. University of Linköping, Sweden / University of Hamburg, Germany.
- Law R.J., P. Bersuder, J. Barry, R. Deaville, R.J. Reid & P.D. Jepson 2010. Chlorobiphenyls in the blubber of harbour porpoises (*Phocoena phocoena*) from the UK: levels and trends 1991-2005. *Marine Pollution Bulletin* 60: 470-473.
- Learmonth, J.A., S. Murphy, P.L. Luque, R.J. Reid, I.A.P. Patterson, A. Brownlow, H.M. Ross, J.P. Barley, M.B. Santos & G.J. Pierce 2014. Life history of harbour porpoises (*Phocoena phocoena*) in Scottish (UK) waters. *Marine Mammal Science* 30 (4):1427-1455.
- Lockyer, C. 2003. Harbour porpoises (*Phocoena phocoena*) in the North Atlantic: Biological parameters. *NAMMCO Scientific Publications* 5: 71-89.
- Lowry, N. & J. Teilmann 1994. By-catch and by-catch reduction of the harbour porpoise (*Phocoena phocoena*) in Danish Waters. In: W.F. Perrin, G.P. Donovan & J. Barlow (eds). *Gillnets and Cetaceans*: 203-209. International Whaling Commission, Special Issue, 15. Cambridge, UK.
- Murphy, S., J.L. Barber, J.A. Learmonth, F.L. Read, R. Deaville, M.W. Perkins, A. Brownlow, N. Davison, R. Penrose, G.J. Pierce, R.J. Law & P.D. Jepson 2015. Reproductive failure in UK harbour porpoises *Phocoena phocoena*: Legacy of pollutant exposure. *PLoS ONE* 10 (7): e0131085. DOI:10.1371/journal.pone.0131085.
- Northridge, S. 1988. Marine Mammals and Fisheries: a study of conflicts with fishing gear in British waters. Report to Wildlife Link, London, UK.
- Northridge, S.P. & P.S. Hammond 1999. Estimation of porpoise mortality in UK gill and tangle net fisheries in the North Sea and west of Scotland. Paper presented to the Scientific Committee of the International Whaling Commission, Grenada, May 1999. SC/51/SM42.
- Northridge, S., A. Cargill, A. Coran, L. Mandleberg, S. Calderan & R.J. Reid 2010. Entanglement of minke whales in Scottish waters: an investigation into occurrence, causes and mitigation. Final report to Scottish government CR/2007/49. Sea Mammal Research Unit, University of St. Andrews, UK.
- Northridge, S.P., M.L. Tasker, A. Webb & J.M. Williams 1995. Distribution and relative abundance of harbour porpoises (*Phocoena phocoena* L.), white-beaked dolphins (*Lagenorhynchus albirostris* Gray), and minke whales (*Balaenoptera acu-*

- trostrata* Lacepède) around the British Isles. ICES Journal of Marine Science 52: 55-66.
- Perry, A.L., P.J. Low, J.R. Ellis & J.D. Reynolds 2005. Climate change and distribution shifts in marine fishes. Science 308: 1912-1915.
- Peschko, V., K. Ronnenberg, U. Siebert & A. Gilles 2016. Trends of harbour porpoise (*Phocoena phocoena*) density in the southern North Sea. Ecological Indicators 60: 174-183.
- Pierce, G.J., M.B. Santos, R.J. Reid, I.A.P. Patterson & H.M. Ross 2004. Diet of minke whales *Balaenoptera acutorostrata* in Scottish (UK) waters with notes on strandings of this species in Scotland 1992-2002. Journal of the Marine Biological Association of the UK 84: 1241-1244.
- Pierce, G.J., M.B. Santos, C. Smeenk, A. Saveliev & A.F. Zuur 2007. Historical trends in the incidence of strandings of sperm whales (*Physeter macrocephalus*) on North Sea coasts: An association with positive temperature anomalies. Fisheries Research 87: 219-228.
- Rayner, N.A., D.E. Parker, E.B. Horton, C.K. Folland, L.V. Alexander, D.P. Rowell, E.C. Kent & A. Kaplan 2003. Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late Nineteenth Century. Journal of Geophysical Research 108 (D14), 4407. DOI:10.1029/2002JD002670.
- Reid, J.B., P.G.H. Evans & S.P. Northridge 2003. Atlas of cetacean distribution in North-west European waters. Joint Nature Conservation Committee, Peterborough, UK.
- Reijnders, P.J.H. 1992. Harbour porpoises, *Phocoena phocoena*, in the North Sea: numerical responses to changes in environmental conditions. Netherlands Journal of Aquatic Ecology 26: 75-85.
- Reijnders, P.J.H., A. Aguilar & G.P. Donovan (eds) 1999. Report of the workshop on chemical pollution and cetaceans. Chemical Pollutants and Cetaceans. Journal of Cetacean Research and Management (Special Issue 1). International Whaling Commission, Cambridge, UK.
- Richardson, W.J., C.R. Greene, C.I. Malme & D.H. Thomson 1995. Marine Mammals and Noise. Academic Press, San Diego, CA, USA.
- Ryan, R., R. Leaper, P.G.H. Evans, K. Dyke, K.P. Robinson, G.N. Haskins, S. Calderan, N. van Geel, O. Harries, K. Froud, A. Brownlow & A. Jack 2016. Entanglement: an emerging threat to humpback whales in Scottish waters. IWC SC/66b/HIM/01.
- Santos, M.B., G.J. Pierce, J.A. Learmonth, R.J. Reid, H.M. Ross, I.A.P. Patterson, D.G. Reid & D. Beare 2004. Variability in the diet of harbor porpoises (*Phocoena phocoena*) in Scottish waters 1992-2003. Marine Mammal Science 20: 1-27.
- Scheidat, M., K-H. Kock & U. Siebert 2004. Summer distribution of harbour porpoise (*Phocoena phocoena*) in the German North and Baltic Sea. Journal of Cetacean Research and Management 6: 251-257.
- Scheidat, M., H. Verdaat & G. Aarts 2012. Using aerial surveys to estimate density and distribution of harbour porpoises in Dutch waters. Journal of Sea Research 69: 1-7.
- Scheidat, M., J. Tougaard, S. Brasseur, J. Carstensen, T. van Polanen-Petel, J. Teilmann & P. Reijnders 2011. Harbour porpoises (*Phocoena phocoena*) and wind farms: a case study in the Dutch North Sea. Environmental Research Letters 6. 025102.
- Sheldrick, M.C. 1976. Trends in the strandings of Cetacea on the British coasts 1913-72. Mammal Review 6: 15-23.
- Sheldrick, M.C. 1989. Stranded whale records for the entire British coastline, 1967-1986. In: G. Pilleri (ed.). Investigations on Cetacea. Vol. XXII: 298-329. G. Pilleri (privately published), Berne, Switzerland.
- Sheldrick, M.C., J.D. George, P.J. Chimonides & S. Phillips 1992. An analysis of cetaceans stranded around the British Isles between 1967 and 1990. Report to the UK Department of the Environment. The Natural History Museum, London, UK.
- Sheldrick, M.C., P.J. Chimonides, A.I. Muir, J.D. George, R.J. Reid, T. Kuiken, C. Iskjaer-Ackley & A. Kitchener 1994. Stranded cetacean records for England, Scotland and Wales, 1987-1992. In: G. Pilleri (ed.). Investigations on Cetacea. Vol. XXV: 259-283. G. Pilleri (privately published), Berne, Switzerland.
- Siebert, U., C. Joiris, L. Holsbeek, H. Benke, K. Failing, K. Frese & E. Petzinger 1999. Potential relation between mercury concentrations and necropsy findings in cetaceans from German waters of North and Baltic Seas. Marine Pollution Bulletin 38 (4): 285-295.

- Siebert, U., A. Gilles, K. Lucke, M. Ludwig, H. Benke, K.-H. Kock & M. Scheidat A decade of occurrence of harbour porpoises in German waters: Aerial surveys, incidental sightings and strandings. *Journal of Sea Research* 56: 65-80.
- Siebert, U., A. Wünschmann, R. Weiss, H. Frank, H. Benke & K. Frese 2001. Post mortem findings in harbour porpoises (*Phocoena phocoena*) from the German North and Baltic Sea. *Journal of Comparative Pathology* 124: 102-114.
- Smeenk, C. 1987. The harbour porpoise *Phocoena phocoena* (L., 1758) in the Netherlands: stranding records and decline. *Lutra* 30: 77-90.
- Smeenk, C. 1997. Strandings of sperm whales *Physeter macrocephalus* in the North Sea: history and patterns. In: G. Jacques & R.H. Lambertsen (eds). Sperm whale deaths in the North Sea. Science and management. *Bulletin de l'Institut royal des Sciences naturelles de Belgique / Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen, Biologie* 67 - supplément: 15-28.
- Smeenk, C., M. Addink & C.J. Camphuysen 2003. De eerste bultrug voor Nederland. *Zoogdier* 14: 3-4.
- Sonntag, R.P. & T. Lütkebohle 1998. Potential causes of increasing sperm whale strandings in the North Sea. *Deutsche Hydrographische Zeitschrift Supplement* 8: 119-124.
- Tolley, K.A., P.E. Rosel, M. Walton, A. Bjørge & N. Øien 1999. Genetic population structure of harbour porpoises (*Phocoena phocoena*) in the North Sea and Norwegian waters. *Journal of Cetacean Research and Management* 1: 265-274.
- Tougaard J., J. Carstensen & J. Teilmann 2009. Pile driving zone of responsiveness extends beyond 20 km for harbour porpoises (*Phocoena phocoena* (L.)). *Journal of the Acoustical Society of America* 126: 11-14.
- van Bree, P.J.H. 1977. On former and recent strandings of cetaceans on the coast of the Netherlands. *Zeitschrift für Säugetierkunde* 42: 101-107.
- van der Kooij, J., G.H. Engelhard & D. Righton 2016. Climate change and squid range expansion in the North Sea. *Journal of Biogeography* 43 (11): 2285-2298. DOI: 10.1111/jbi.12847.
- van de Meij, S.E.T. & C.J. Camphuysen 2006. Distribution and diversity of whales and dolphins (Cetacea) in the southern North Sea: 1970-2005. *Lutra* 49: 3-28.
- Van Gompel, J. 1991. Cetacea aan de Belgische kust, 1975-1989. *Lutra* 34: 27-36.
- Van Gompel, J. 1996. Cetacea aan de Belgische kust, 1990-1994. *Lutra* 39: 45-51.
- Vanselow, K.H. & K. Ricklefs 2005. Are solar activity and sperm whale *Physeter macrocephalus* strandings around the North Sea related? *Journal of Sea Research* 53: 319-327.
- Vanselow, K.H., S. Jacobsen, C. Hall & S. Garthe. 2017. Solar storms may trigger sperm whale strandings: explanation approaches for multiple strandings in the North Sea in 2016. *International Journal of Astrobiology*. DOI: 10.1017/S147355041700026X.
- Vanselow, K.H., K. Ricklefs & F. Colijn 2009. Solar driven geomagnetic anomalies and sperm whale (*Physeter macrocephalus*) strandings around the North Sea: An analysis of long term datasets. *The Open Marine Biology Journal* 3: 89-94.
- Verwey, J. 1975. The cetaceans *Phocoena phocoena* and *Tursiops truncatus* in the Marsdiep area (Dutch Waddensea) in the years 1931-1973. *Nederlands Instituut voor Onderzoek der Zee* 17a, b: 1-153.
- Vinther, M. 1999. Bycatches of harbour porpoises (*Phocoena phocoena* L.) in Danish set-net fisheries. *Journal of Cetacean Research and Management* 1 (2): 123-135.
- Vinther, M. & F. Larsen 2004. Updated estimates of harbour porpoise by-catch in the Danish bottom set gillnet fishery. *Journal of Cetacean Research and Management* 6 (1): 19-24.
- Wilson, B., P.M. Thompson & P.S. Hammond 1997. Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology* 3: 1365-1374.
- Wilson, B., P.S. Hammond & P.M. Thompson 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecological Applications* 9 (1): 288-300.
- Wilson, B., R.J. Reid, K. Grellier, P.M. Thompson & P.S. Hammond 2004. Considering the temporal when managing the spatial: a population range expansion impacts protected areas-based management for bottlenose dolphins. *Animal Conservation* 7: 331-338.
- Witte, R.H., H.J.M. Baptist & P.V.M. Bot 1998. Increase

of the harbour porpoise *Phocoena phocoena* in the Dutch sector of the North Sea. *Lutra* 40: 33-40.

Wright, A.J. 2005. Lunar cycles and sperm whales (*Physeter macrocephalus*) strandings on the North Atlantic coastlines of the British Isles and Eastern Canada. *Marine Mammal Science* 21: 145-149.

Wünschmann, A., U. Siebert, K. Freise, R. Weiss, C. Lockyer, M.P. Heide-Jørgensen, R. Weiss, G. Mül-

ler & W. Baumgärtner 2001. Evidence of infectious diseases in harbour porpoises (*Phocoena phocoena*) hunted in the waters of Greenland and by-caught in the German North and Baltic Sea. *Veterinary Record* 148: 715-772.

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