The return of the harbour porpoise (*Phocoena phocoena*) in Dutch coastal waters

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Abstract: The harbour porpoise (*Phocoena phocoena*) became virtually extinct in Dutch coastal waters in the early 1960s. A systematic method to record seabird passage along the coast became established in the early 1970s and was used ever since. These observations allowed a reconstruction of the return of the elusive harbour porpoise in Dutch coastal waters. A small, but gradually increasing number of sightings in the mid-1980s to early 1990s was followed by a proportional rate of increase of 41% per annum over the last 15 years. At first, only full-grown animals were seen and the occurrence was virtually restricted to mid-winter. In later years, numbers sharply increased in winter, and more and more animals were seen also in summer and autumn, including mother-calf combinations. Both the historic decline and the recent increase are concurrent with similar trends in strandings and at-sea survey data. Unambiguous explanations for the initial decline have never been given and it is equally difficult to fully understand the come-back. There is evidence, however, that distributional shifts rather than population fluctuations underlie the trends observed. The re-distribution of harbour porpoises in the North Sea may have been triggered by local reductions or shifts in principal prey availability.

Keywords: harbour porpoise, *Phocoena phocoena*, sightings, The Netherlands, population trends, historical decline, distribution shift.

Introduction

In the 1950s, or even in the 1940s, a decline in sightings of the harbour porpoise (*Phocoena phocoena*) in Dutch coastal waters occurred. The first reports indicating fewer sightings date back to 1939 (Viergever 1955), but it was immediately after the Second World War that the decline became more obvious (Verwey 1975). Not everyone was immediately convinced that harbour porpoises had declined (van Deinse 1952, Vader 1956, van Deinse 1959), since numerous corpses of porpoises littered the Dutch beaches. When a general consensus was reached that porpoises were less common than they used to be, the animal had become a rarity. Unfortunately, from reported sightings, the decline is poorly documented. Smeenk (1987) and Addink & Smeenk (1999) reconstructed the decline from strandings records and encountered a similar problem. At first, porpoises were so abundant that corpses on the beach were not systematically recorded (van Deinse 1925, van Deinse 1931, van Deinse 1946). Only since 1951 porpoises were included in a recording scheme of beached marine mammals, a scheme that collapsed in the early 1960s as a consequence of the death of its organiser in 1964. Hence, strandings were recorded when the decline was already prominent and the final phase, when the animals became rare, was not documented. Very few harbour porpoises were seen in The Netherlands in the 1960s, 1970s, and early 1980s and strandings were at a very low level compared to the first half of that century (Camphuysen 1982, Smeenk 1987). The harbour porpoise, once a very common cetacean in Dutch coastal waters and "a typical summer animal" (Viergever 1955) had gone.

Amateur ornithologists developed an interest in seabirds somewhere in the late 1960s and early 1970s. High powered, but relatively cheap binoculars became available in these years and

with those mounted on a tripod, a revolution in bird recording took place. Many more true seabirds could be seen than anyone had realised before, and violent autumn storms attracted crowds of observers at strategic lookouts to witness the spectacle (Camphuysen & van Dijk 1983, Camphuysen 1985). Spring migration turned out to be equally spectacular and not before long, "seawatchers" were observing seabirds almost every day, throughout the year, at the more popular sites. The establishment of the "Club van Zeetrekwaarnemers" in 1972 formalised seawatching and the development of a standard record card was the foundation of a highly successful scheme for the years to come, until the present day. Although seabirds formed the motivation for these coastal observations, marine mammals were also recorded and included as "highlights" in bi-annual, reports. The seawatching scheme became established when marine mammals were extremely rare in Dutch coastal waters and very few were recorded in the first ten years (Camphuysen 1982).

In the mid-1980s, the number of harbour porpoise sightings gradually increased. While only 20 harbour porpoises were recorded between 1972 and 1985, during 39,704 hours of observation (one every 2000 hours), 75 porpoises were observed between 1986 and 1990 during a further 14,565 hours of observation (one every 190 hours; a tenfold increase). Between 1991 and 1995, 222 porpoises were recorded during 17,732 hours of observation (one every 80 hours), or another 2.5 fold increase compared to the preceding years. Camphuysen & Leopold (1993) and Camphuysen (1994) published early accounts of what they thought might be a comeback of the harbour porpoise in Dutch coastal waters. These reviews were largely based on seawatching data from the Dutch coast, but with additional information on the distribution of porpoises from ship-based and aerial surveys in the Dutch sector of the North Sea. This paper, ten years later, intends to be an update based largely on the continuing seawatching results.

Methods

Harbour porpoise abundance was analysed by extracting sightings from the seawatching database of the Nederlandse Zeevogelgroep (NZG/CVZ database; 1972-2004). A second dataset used is a series of incidental sightings obtained directly from the observers or extracted from numerous smaller publications in local, regional or even national journals and, more recently, from websites. Both data sets are restricted to sightings from coastal sites; records (even incidental sightings) from ships and aircraft have been excluded. The seawatching data set is the more important collection of sightings, because the observer effort is known. Observers record the date, the duration (start- and end-time), and weather characteristics for each set of data and usually record their sightings per hour of observation. Equally important, the observers were considered trained and experienced in cetacean identification. It is from these data that reliable long-term trends can be calculated and the seasonal patterns analysed. Incidental sightings come from a variety of sources and outliers have been checked individually in order to exclude erroneous sighting reports. The identification of cetaceans, including porpoises, is not easy (Camphuysen 1987, Camphuysen 1991) and people who rarely see them have a tendency to just guess what it might have been. The greatest additional value of the data presented here is above all the contribution to our knowledge of the geographical distribution: seawatchers work from a small number of sites, while porpoises are much more widespread.

The effort-corrected data from systematic seawatches in this paper are expressed as "number per hour of observation" (n h^{-1}). Considering the observer effort, some assumptions had to be made, for not all data have yet fully been submitted (and there will always be a backlog in that). Sightings of porpoises during seawatching have been promptly reported by nearly all observers *before* all observational and effort data are logged on record cards and subsequently entered into the database. With only part of the record

cards being processed and, hence, observer effort in 2001-2004 not (yet) completely known, this has been assumed to be similar as in the preceding five-year period (table 1). Future reports using the same source, but with an updated database, may therefore report slightly different levels of abundance for the most recent years. However, with the activity of most observers currently well known (e.g. reported at www.trektellen.nl), it is unlikely that later adjustments will lead to substantial changes in the results.

Results

Between 1970 and 2004, 3024 harbour porpoises have been reported; 626 as 'incidental reports' and 2398 during systematic seawatching (table 2). The results show that the animals were near-absent between 1970 and 1985, that their numbers slowly increased in the late 1980s and that an exponential increase occurred in the 1990s and early 21st century (figure 1). Over the last 15 years, the numbers of harbour porpoises seen during systematic seawatching have increased significantly at a proportional rate of 41% per annum ($\ln(n\ h^{-1}) = 0.3438x - 6.054$, $r^2 = 0.91$).

Initially, during 1970-1985, when porpoises were still rare, they could be seen in any month (table 2). Of 34 recorded individuals, twelve were recorded in winter (Dec-Feb, 35%), nine in spring (Mar-May, 26%), six in summer (Jun-Aug, 18%), and seven in autumn (Sep-Nov, 21%). During 1986-1990, when the frequency of sightings increased, 67% were observed in winter, and another 26% in spring (n=84 animals recorded). Since then, harbour porpoises became winter/early spring visitors, arriving around October and disappearing around April with a peak from December through March (table 2, figure 2). The largest numbers were seen in March 1997 (108 individuals), February-March 2001 (137, 160), March 2002 (141), March 2003 (123), March 2004 (147), and December 2004 (297).

In June harbour porpoises were seldom reported, indicating a near-complete contraction away from the Dutch coast in early summer. In the most recent years, increasing numbers were seen in late summer/early autumn (Jul-Sep). Apparently, we are currently witnessing the development of a (late) summer population along the coast. Harbour porpoises can now be seen virtually everywhere along the coast.

Discussion

Harbour porpoises in the past: seasonal pattern and decline

Harbour porpoises have historically been described as 'summer visitors' in The Netherlands (van Deinse 1925, van Deinse 1931, IJsseling & Scheijgrond 1943, Viergever 1955, Verwey 1975). According to Verwey (1975), who recorded sightings of harbour porpoises in the western Wadden Sea during 1931-1945, a *"striking scarcity or even complete absence"* in March-April occurred, followed by a marked increase in "*May and (or) June*". Verwey (1975) explained this 'spring dip' (Mar-Apr) by a contraction of the wintering population away from the coast. Despite published claims that porpoises were

Table 1. Observer effort during seawatching from Dutch coastal sites, 1972-2004 (hours of observation; all sites combined). The amount of effort for the last period (2001-2004) is not exactly known due to a backlog in data processing, but is assumed to be similar as in the preceding five years (see text).

	J	F	M	A	M	J	J	A	S	O	N	D	total
1972-1985	1533	1355	2536	4541	3881	2024	2660	5020	5775	5646	2967	1764	39704
1986-1990	725	712	886	1582	1394	536	911	1634	1929	1915	1368	973	14565
1991-1995	1156	1012	1482	1837	1675	936	1238	2177	2069	1845	1334	971	17732
1996-2000	739	761	1226	1549	1309	751	825	1220	1245	1355	788	664	12432
2001-2004	740	760	1225	1550	1300	750	835	1220	1245	1350	790	665	12420

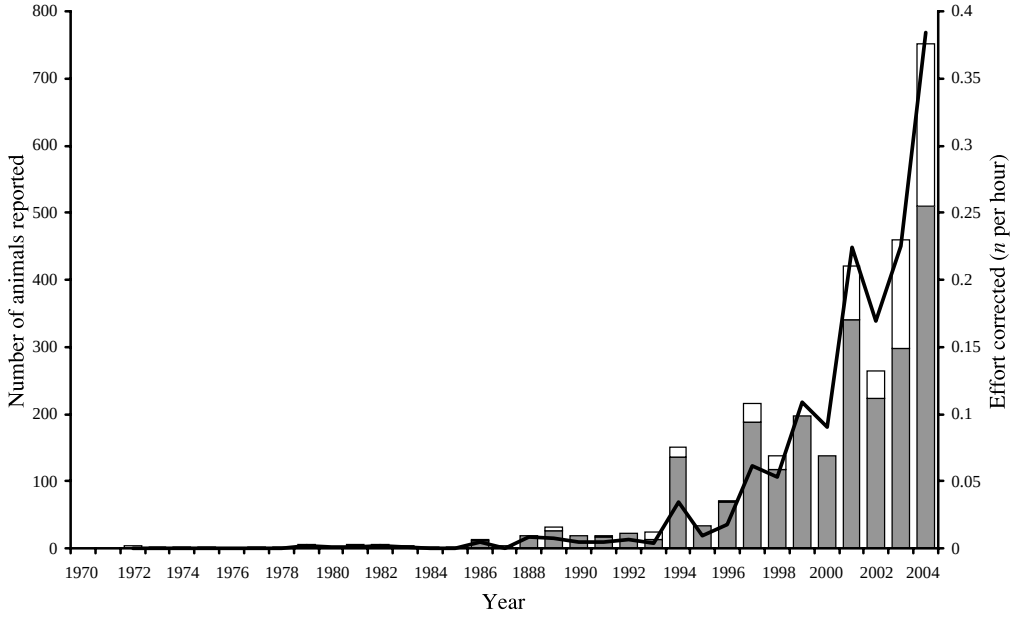

Figure 1. Numbers of harbour porpoises observed in Dutch coastal waters since 1970 from incidental sightings (white bars) and systematic seawatching results (grey bars), and long-term trend (n h^{-1}) based on seawatching results (black line).

normally seen on warm summer days, they could be numerous in autumn and winter too, perhaps with the exception of very cold seasons (with ice cover in the Wadden Sea; Verwey 1975). The increase in summer was explained by *"the fact"* that the animals were seeking the coast at that time and it coincided with an increase in newly born young. IJsseling & Scheygrond (1943), actually citing Van Deinse (1931), highlighted the summer as the period of highest abundance and claimed that pregnant female porpoises entered river mouths in summer, apparently attracted by salmon (*Salmo salar*). The annual return of harbour porpoises in early summer in the western Waddensea coincided with the arrival of herring (*Clupea harengus*), entering the Wadden Sea and Zuiderzee (currently the IJsselmeer, and now a fresh water lake) through the Marsdiep area. Heinsius (1914), observed numerous harbour porpoises in summer in the Zuiderzee targeting shoals of anchovy (*Engraulis encrasicolus*) and garfish (*Belone belone*).

There was considerable debate in the 1950s if a decline had taken place (Vader 1956). Sightings reports in the late 1950s were rather confusing, with for example 'high numbers' in summer and autumn 1957, and Jan-Feb 1958 in the western Wadden Sea (van Deinse 1959). A keen observer, F.J. Appelman, recorded porpoises during 10 out of 15 beach visits at Loosduinen (The Hague) in summer 1958 (van Deinse 1959), while numerous visits by the same observer in 1959-1962 did not produce a single sighting (van Deinse 1964). From the data collected by Verwey (1975) after the war (1945-1961) around Den Helder (circa 121 animals), some 49% were seen in January, 8% in February, 4% in March, 14% in April, 17% in November (remarkably, none in December) and only 8% in summer and early autumn (May-Oct). There was no evidence for a summer influx of pregnant females in coastal waters. Viergever (1955), in the Delta area, observed that harbour porpoises had become very scarce immediately after the Second World War and had his opinion confirmed by "field experiences" of local skippers and fishermen. Harbour

Table 2. Harbour porpoises per month in Dutch coastal waters, 1970-2004. (A) Incidental sightings (number of individuals), (B) sightings during systematic seawatching (number of individuals) and (C) relative abundance from seawatching results (number per observation hour).

	J	F	M	A	M	J	J	A	S	O	N	D	total
(A) Incidental sightings (*n*)													
1970-1985	3	1	2	2	1	1	1	0	1	0	0	2	14
1986-1990	0	0	4	0	1	0	0	0	0	0	0	4	9
1991-1995	2	0	10	1	12	0	0	0	0	0	0	4	29
1996-2000	3	3	37	3	0	0	1	1	0	0	0	2	50
2001-2004	27	91	150	54	4	1	14	12	28	25	17	101	524
													626
(B) Systematic observations (*n*)													
1972-1985	0	4	2	2	0	1	3	0	4	2	0	2	20
1986-1990	34	5	10	7	0	0	5	1	0	0	0	13	75
1991-1995	27	19	65	55	6	0	0	0	1	12	18	19	222
1996-2000	69	160	293	59	6	1	4	0	7	11	36	63	709
2001-2004	162	206	421	59	16	3	18	48	30	58	70	281	1372
													2398
	J	F	M	A	M	J	J	A	S	O	N	D	mean
(C) Effort corrected systematic sightings (n h^{-1})													
1972-1985	0	0.00	0.00	0.00	0	0.00	0.00	0	0.00	0.00	0	0.00	0.00
1986-1990	0.05	0.01	0.01	0.00	0	0	0.01	0.00	0	0	0	0.01	0.01
1991-1995	0.02	0.02	0.04	0.03	0.00	0	0	0	0.00	0.01	0.01	0.02	0.01
1996-2000	0.09	0.21	0.24	0.04	0.00	0.00	0.00	0	0.01	0.01	0.05	0.09	0.06
2001-2004	0.22	0.27	0.34	0.04	0.01	0	0.02	0.04	0.02	0.04	0.09	0.42	0.11

porpoises were distinctly less abundant than they had been prior to the war, but it was the scarcity of porpoises in summer immediately after the war that may well have been the first signal of an overall decline. In the 1960's and 1970's, it was highly unusual to see a porpoise alive in The Netherlands anywhere and at any time of year.

Harbour porpoises in recent years: a recent come-back

We are very lucky to have been able to document the return of the harbour porpoise, as a side-product of a scheme that aimed at recording seabird migration. Certainly in the 1970s and early 1980s, it would have made no sense to set up a porpoise monitoring system, when waiting for a single sighting required on average 2000 hours of watch on a wind-swept look-out. Today, harbour porpoises are winter visitors in the Southern Bight (i.e. the North Sea between the French Channel in the south and 53°30'N in the north), and only the last few years can they be seen virtually year-round, but still with low numbers in June. Harbour porpoises can now be so numerous and close to the coast that a keen observer can spot some even during a winter walk along the beach. It is only because these elusive animals are so notoriously difficult to detect that relatively few 'incidental sightings' occur. Mother-calf combinations have been reported and are seemingly increasingly common (difficult to quantify, for most sightings are of unaged animals). From ship-based surveys in recent years, we have evidence that in peak periods (winter), thousands of porpoises may occur within the 20 m depth contour along the mainland coast of Noord-Holland alone (circa 3000 were estimated to occur between IJmuiden and Texel, winter 2003/2004; Leopold et al. 2004).

When studying the recent sightings data in more detail, the occurrence of harbour porpoises is highly irregular, with influxes at times

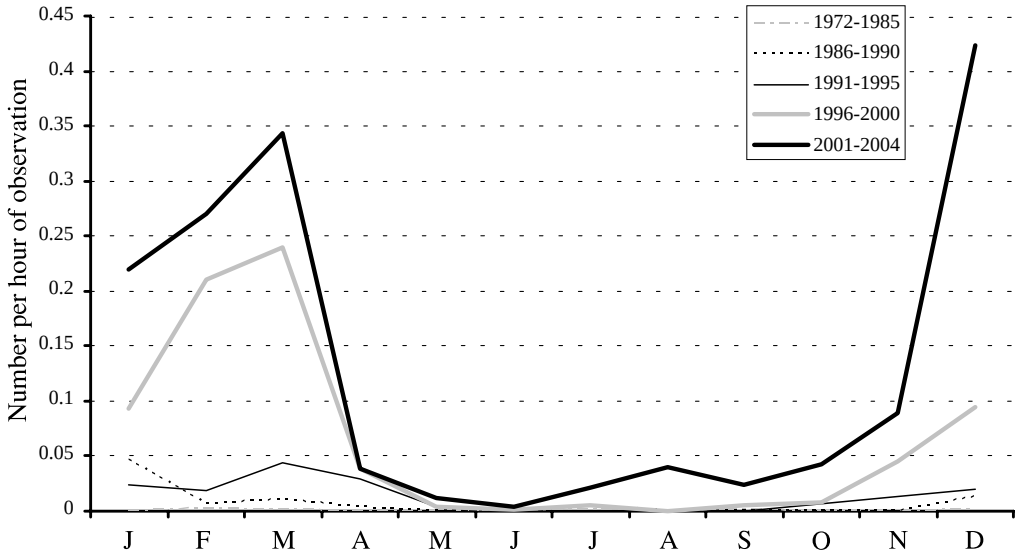

Figure 2. Numbers of harbour porpoises per hour per month observed in Dutch coastal waters since 1972 from systematic seawatching results. At this scale, the seasonal pattern in the earliest sightings (1972-1985) is hardly visible, but porpoises could be seen in virtually every month, if recorded at all. In recent years, the U-shape curve developed more and more strongly, while a mid-summer peak in occurrence is in fact from a very recent date, i.e. 2003-2004.

(recorded everywhere along the Dutch coast, but of a few days or weeks duration at most) followed by periods of absence. Movements to and from the coast are the most likely explanation for the variability in abundance between seasons and between months. We have no evidence for regular north-south or vice versa movements along the Dutch coast; the animals tended to arrive and disappear everywhere simultaneously at times. Possible reasons for inter-annual and within-season differences in abundance and distribution may include changes in availability of primary prey species, or movements among population units with the North Sea at large.

So what happened?

Is this a return to the 'original' situation (whatever that might have been), is this a population recovery following the near-extinction of a local stock, or are we receiving animals from abroad that are for example seeking alternative foraging areas? These questions are easier asked than answered. We have very few empirical data on demography, foraging ecology, migration routes and (offshore) population fluctuations of porpoises in the southern North Sea. Both the historical decline and the recent increase are therefore subject to major speculation. Some remarks can be made, however.

Woodley & Read (1991) estimated the natural rate of increase of harbour porpoises at 4% or less per annum. Barlow & Boveng (1991), using demographic models, produced an estimate of 9.4% for the maximum potential rate of increase of these animals. Caswell et al. (1998) used a series of rescaled mortality schedules and a Monte Carlo sampling procedure to estimate the potential rates of increase for harbour porpoise. Their distribution of potential rates of increase had a median of about 4%, and it was concluded that a rate of more than 10% per year would be highly unlikely. So, even when the reproductive success of harbour porpoises in the southern North Sea has been exceptionally high in the past decades, it could not have accounted for the 41% increase per annum as currently ob-

Harbour porpoises, Eemshaven, 21 February 2004. *Photograph: Klaas Kreuijer.*

served in Dutch coastal waters. Shifts in distribution, or immigration, must therefore have been underlying the observed trend.

In order to try and understand why harbour porpoises would have returned to Dutch coastal waters during the last 15 to 20 years, it is essential to know something of their spatial distribution patterns and feeding ecology. A North Sea wide census in 1994 resulted in an estimated 263,000 harbour porpoises (Hammond et al. 2002), 70% of which were found in the northwest North Sea and around Orkney and Shetland. Few porpoises were found in the Channel area, while they were locally abundant in the German Bight. These patterns are similar to those described by Reid et al. (2003). In a recent comparative study of harbour porpoise diets, based on stranded or drowned individuals collected in Scotland, Denmark, and The Netherlands, principal prey and the dietary diversity differed significantly between areas (Santos 1998). In Scotland, whiting (*Merlangius merlangus*) and sandeels (Ammodytidae) were the most important prey categories, making up >84% of prey mass. In Denmark, cod (*Gadus morhua*), viviparous blenny (*Zoarces viviparus*) and whiting made up almost two thirds of the total prey mass. In porpoises stranded in The Netherlands, whiting made up more than 75% of the total estimated prey mass, and other important species were sandeels and gobies (Gobiidae).

In the northern North Sea, starting in Shetland, several piscivorous seabirds have had highly variable reproductive success since a major crisis in seabird breeding occurred in the late 1980s as a result of failed sandeel recruitment (Monaghan et al. 1992, Wright & Bailey 1993). Breeding success of seabirds during 2002, 2003, and 2004 were the worst on record, apparently as a result of declines of northwest North Sea sandeel stocks. Food shortages resulting from sandeel recruitment failures have been reported from an growing part of the northwest North Sea, including the Orkneys and Scottish east coast in 2003 and 2004. Based

on the most recent estimates, the International Council for the Exploration of the Seas (ICES, Copenhagen) classified the North Sea sandeel stock as having reduced reproductive capacity and for 2004 the population was estimated to be at a historic low value (325,000 ton) due to a historic low recruitment in 2002.

Low recruitment and reduced stocks of planktivorous fish have been linked with climate change, found to cause a drop in the quality and quantity of plankton in the North Sea (Beaugrand et al. 2003). This decline in plankton has been attributed to a rise in surface water temperatures causing warm-water plankton species to move north, displacing cold-water species. That reduced the number and size of the plankton and it also caused major plankton blooms to be out of synchrony with the larval stage development of fish, meaning fewer fish larvae were reaching adulthood. The decoupling of phenological relationships will have important ramifications for trophic interactions, altering food-web structures and leading to eventual ecosystem-level changes (Edwards & Richardson 2004). Sandeel recruitment was found to be reduced in warm winters, and Frederiksen et al. (2004) proposed that this explains the temperature effects on breeding success of some Scottish seabirds.

It is currently unclear what is going on in the northern North Sea, but the summering humpback whales (*Megaptera novaeangliae*) in Shetland disappeared and minke whales (*Balaenoptera acutorostrata*) were found to concentrate in summer feeding areas further to the south and in larger numbers than previously (Camphuysen et al., in press). Apparent redistributions of large cetaceans and poor breeding of piscivorous seabirds may be interpreted as signals of shifts in prey availability in the affected area. Declines in prey availability in the northwest North Sea may have triggered distribution shifts even in species with a mixed diet, such as harbour porpoises.

Conclusions

We have witnessed a return of an animal that had nearly completely disappeared from the Dutch coastal waters after the Second World War. The return cannot be interpreted as a population recovery, but rather as a shift in distribution. The Netherlands have been avoided during several decades for reasons we don't quite understand, but are increasingly used by porpoises in recent years, at first mainly during winter and at present during most of the year. The reason for the re-appearance is possibly a reduction in principal prey stocks further north in the North Sea. There are no signs as yet that the increase in sightings is levelling off and we should therefore continue monitoring, by using the same methods, in the years to come. Meanwhile, if we are to gain understanding of the foraging and breeding opportunities for porpoises in the Dutch waters, or if we simply wish to monitor their well-being in the southern North Sea, it is time to set up dedicated research programmes. The animals are numerous enough by now to make them attractive study objects.

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References

Addink, M.J. & C. Smeenk 1999. The harbour porpoise *Phocoena phocoena* in Dutch coastal waters: analysis of stranding records for the period 1920-1994. Lutra 41 (1-2): 55-80.

Barlow, J.P. & P. Boveng 1991. Modeling age-specific mortality for marine mammal populations. Marine Mammal Science 7: 50-65.

Beaugrand, G., K.M. Brander, J.A. Lindley, S. Souissi & P.C. Reid 2003. Plankton effect on cod recruitment in the North Sea. Nature 426: 661-664.

Camphuysen, C.J. 1982. Zeezoogdieren langs de Nederlandse kust. Mededelingen Club van Zeetrekwaarnemers 5 (2): 6-8.

Camphuysen, C.J. 1985. Zeetrektellingen. In: M.F.H Hustings, R.G.M. Kwak, P.F.M. Opdam & M.J.S.M. Reijnen (eds.). Vogelinventarisatie: 215-219. Pudoc, Wageningen, The Netherlands.

Camphuysen, C.J. 1987. Het ontdekken en herkennen van Bruinvissen *Phocoena phocoena* op zee. Sula 1 (3): 66-72.

Camphuysen, C.J. 1991. Het herkennen van de Bruinvis *Phocoena phocoena* op zee. Huid & Haar 10 (1): 31-37.

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. & J. van Dijk 1983. Zee- en kustvogels langs de Nederlandse kust, 1974-79. Limosa 56 (3): 81-230.

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., B. Scott & S. Wanless, in press. Distribution and foraging interactions of seabirds and marine mammals in the North Sea: multi-species foraging assemblages and habitat-specific feeding strategies. In: I.J. Boyd, S. Wanless & C.J. Camphuysen (eds.). Management of Marine Ecosystems: monitoring change in upper trophic levels. Blackwell Science, London, UK.

Caswell H., S. Brault, A.J. Read & T.D. Smith 1998. Harbor porpoise and fisheries: an uncertainty analysis of incidental mortality. Ecological Applications 8: 1226-1238.

Deinse, A.B. van 1925. De bruinvisch. De Levende Natuur 29: 195-203.

Deinse, A.B. van 1931. De fossiele en recente Cetacea van Nederland. PhD thesis. Universiteit van Utrecht, Utrecht, The Netherlands.

Deinse, A.B. van 1946. De recente Cetacea van Nederland van 1931 tot en met 1944. Zoölogische Mededelingen Leiden 26 (1-4): 139-210.

Deinse, A.B. van 1952. De walvisachtige dieren in Nederland waargenomen in 1951, alsmede bijzonderheden omtrent onze oude en moderne walvisvaart. Zeepaard 12: 19-29.

Deinse, A.B. van 1959. Walvisnieuws 1958. Mededelingenblad van de Vereniging voor Zoogdierkunde 20 (= Lutra 1 (20)): 205-208.

Deinse, A.B. van 1964. Walvisnieuws over 1963. Lutra 6 (3): 61-66.

Edwards, M. & A.J. Richardson 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430: 881-884.

Frederiksen, M., S. Wanless, M.P. Harris, P. Rothery & L.J. Wilson 2004. The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. Journal of Applied Ecology 41: 1129-1139.

Hammond, P., 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 porpoises and other cetaceans in the North Sea and adjacent waters. Journal of Applied Ecology 39: 361-376.

Heinsius, H.W. 1914. Langs de Zuiderzee. De Levende Natuur 18: 282-286.

IJsseling, M.A. & A. Scheygrond 1943. De Zoogdieren van Nederland II. Thieme, Zutphen, The Netherlands.

Leopold, M.F., C.J. Camphuysen, C.J.F. ter Braak, E.M. Dijkman, K. Kersting & S.M.J. van Lieshout 2004. Baseline studies North Sea wind farms: lot 5 Marine Birds in and around the future sites Nearshore Windfarm (NSW) and Q7. Alterra Report 1048. Alterra, Wageningen, The Netherlands.

Monaghan, P., J.D. Uttley & M.D. Burns 1992. Effect of changes in food availability on reproductive effort in Arctic Terns *Sterna paradisaea*. Ardea 80: 71-81.

Reid, J.B., P.G.H. Evans & S.P. Northridge (eds.) 2003. Atlas of cetacean distribution in north-west European waters. Joint Nature Conservation Committee, Peterborough, UK.

Santos, M.B. 1998. Feeding ecology of harbour porpoises, common and bottlenose dolphins and sperm whales in the North East Atlantic. PhD thesis. University of Aberdeen, Aberdeen, UK.

Smeenk, C. 1987. The Harbour Porpoise *Phocoena phocoena* (L., 1758) in The Netherlands: stranding records and decline. Lutra 30 (1): 77-90.

Vader, W. 1956. Reuzen van de vloedlijn. Amoeba 32 (6-7): 101-103.

Verwey, J. 1975. The cetaceans *Phocoena phocoena* and *Tursiops truncatus* in the Marsdiep area (Dutch Wadden Sea) in the years 1931-1973, part 1 and 2. Publicaties & Verslagen Nederlands Instituut voor Onderzoek der Zee 17a: 1-98; 17b: 99-153.

Viergever, J. 1955. Hoe staat het met de bruinvis? Het Zeepaard 15: 90-91.

Woodley, T.H. & A.J. Read 1991. Potential rates of increase of a Harbour Porpoise (*Phocoena phocoena*) population subjected to incidental mortality in commercial fisheries. Canadian Journal of Fisheries and Aquatic Sciences 48: 2429-2435.

Wright, P.J. & M.C. Bailey 1993. Biology of sandeels in the vicinity of seabird colonies at Shetland. Fisheries Research Report 15/93. Marine Laboratory, Aberdeen, UK.

Samenvatting

De terugkeer van de bruinvis (*Phocoena phocoena*) in de Nederlandse kustwateren

De bruinvis (*Phocoena phocoena*) was zo goed als uitgestorven in de Nederlandse kustwateren in de jaren zestig van de vorige eeuw. Sinds het begin van de jaren zeventig wordt een systematische methode toegepast om verplaatsingen van kust- en zeevogels langs de Nederlandse kust te registreren. Aanvankelijk werden daarbij gedurende 40.000 waarnemingsuren vrijwel geen zeezoogdieren gezien. In de loop van de jaren tachtig werd door deze 'zeetrekwaarnemers' in winter en voorjaar steeds vaker melding gemaakt van bruinvissen voor de kust. Een geleidelijk toenemend aantal waarnemingen in de tweede helft van de jaren tachtig werd gevolgd door een toename met gemiddeld 41% per jaar tot aan 2004. Aanvankelijk werden uitsluitend volgroeide bruinvissen gezien, maar tegenwoordig komen hier ook veel moeder-kalf stelletjes voor. Werden aanvankelijk vooral veel bruinvissen gezien van oktober tot en met april, de laatste jaren worden daarnaast ook in de nazomer en vroege herfst en steeds regelmatiger groepjes opgemerkt. Zowel de historische afname, als de recente toename wordt weerspiegeld in de gegevens van gestrande bruinvissen op de Nederlandse kust. Voor de afname is nooit een ondubbelzinnige verklaring gevonden en ook de recente terugkeer is niet eenvoudig te begrijpen. De gegevens laten zien dat er sprake moet zijn geweest van een verschuivende populatie, omdat de toename veel te snel is gegaan om alleen door reproductief succes te kunnen worden verklaard. Het is mogelijk dat een afnemend voedselaanbod in het noorden van de Noordzee deze verplaatsing heeft veroorzaakt, waardoor bruinvissen in toenemende mate tot in de Zuidelijke Bocht van de Noordzee zijn doorgedrongen.

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