Status, ecology and life history of harbour porpoise (*Phocoena phocoena*), in Danish waters

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ABSTRACT

A review of historical harbour porpoise catches in Danish waters, together with current distribution, are provided. Most information on distribution is derived from historical catch data with a total of about 100,000 animals taken in Little Belt alone and 40,000 from Isefjord area during the 19th century. Recent sightings surveys and tagging indicate extensive movements of animals within and between Inner Danish Waters and the Skagerrak / North Sea. Biological information is reviewed for the region, drawing on directed catches, bycatches and strandings from a database comprising nearly 1,900 records from 1834 through 1998. Diet, parasites, pollutants, biological parameters (age and reproduction) and body condition are reported, focusing mainly on the period 1996-98 when comprehensive data were collected. In 1980s samples, gadoids were the most important prey items (found in 62% of stomachs) followed by clupeoids (35%), gobiids (30%), and ammodytids (30%). Some dietary differences were observed between North Sea and Inner Danish waters. Pollutant analyses indicated a decline in sumDDT concentrations yet an increase in sumPCB and HCH levels in Danish porpoises, with comparatively higher levels here than in Baltic and Norwegian waters. Heavy metal concentrations appear higher than in Baltic porpoises. Biological parameters indicate a longevity of up to 23 years in both sexes but with fewer than 5% living beyond 12 years. Sexual maturity occurred at slightly over age 3 years in both females and males, with corresponding lengths of about 135 cm in males and 143 cm in females. The data indicate a size range at birth of 65 - 75 cm (weight 4.5 – 6.7 kg), with a minimum of 60 cm and 3.4 kg, and a likely gestation time of 10 months. Conception most likely occurs during August, with peak births in June. Directed catches comprised adult animals whereas bycaught and stranded porpoises comprised predominantly juveniles. In data from all sources, males outnumbered females. Directed catches occurred in winter months, strandings year-round with a peak in late summer, and bycatches year-round with most in September and the later part of the year.

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INTRODUCTION

The harbour porpoise (*Phocoena phocoena*) is the most common cetacean in all Danish waters (Melchior 1834, Eschricht 1849, Tauber 1880, 1892, Wulff 1881, Winge 1908, Degerbøl 1935, Jensen 1946, Møhl-Hansen 1954, Heel 1962, Kinze 1990) and was particularly renowned for its pronounced seasonal migrations through the Danish straits into the Baltic proper (ICES area IIId) in spring, and out again in late autumn and winter (Wolk 1969, Andersen MS 1972). For centuries, considerable numbers of porpoises were caught in a drive fishery in the northern Little Belt and in special porpoise traps in the Isefjord area (Kinze 1995). In more recent years, large areas in the Baltic and the southern Belt Sea and Sound (Øresund) have been lost or depopulated, causing a near cessation of the annual migration (Andersen 1982). Most investigations have focused on the inner waters, while the North Sea stocks have only recently received attention (Clausen and Andersen 1988, Kinze 1985a, 1990, Danielsen *et al.* 1992). Yet until 1983, there was no detailed knowledge on distribution, seasonal abundance, habitat, calving and breeding areas in Danish waters, or on aspects of life history such as age structure, growth, reproduction and feeding biology. This paper provides a review of the current status of our knowledge, and includes additional new information gleaned from sampling bycatches and strandings in the Danish waters in more recent years, especially during the BY-CARE project, an EU-funded multinational programme of research (BY-CARE 1999) investigating diverse aspects of small cetacean bycatches in the North-eastern Atlantic and western Baltic Sea.

DISTRIBUTION AND ABUNDANCE

Methods

The fishery areas used by the International Council for the Exploration of the Sea (ICES) are applied in this review (Fig. 1). Danish waters comprise the eastern central North Sea (ICES area IVb), the Skagerrak (ICES area IIIan), the Kattegat (IIIas), the Sound (IIIb), the Belt Sea (IIIc), and waters around Bornholm in the western part of the Baltic proper (IIId). ICES areas IIIas through IIId may be termed Inner Danish waters.

A review of literature and unpublished sources such as newspaper cuttings, published accounts, and archival files was conducted, and the collections in the Zoological Museum, University of Copenhagen, were examined in order to extract information on distribution (directed catches, incidental catches, strandings, qualitative sightings), abundance (systematic sighting surveys), as well as habitat, breeding and calving areas. The results are presented chronologically from the earliest subfossil finds to present day information on distribution and abundance.

Results

Subfossil finds

A caudal vertebra of a harbour porpoise was found in the Eem-interglacial marine deposits at Lerby on the island of Ærø, documenting the presence of the species in Denmark 100,000 years ago (Aaris-Sørensen 1988). Finds from 23 mesolithical sites indicated exploitation, and hence a common occurrence of the species in the inner waters (Møhl 1970).

Historical records

Much of the knowledge on the historical distribution of the harbour porpoise in Danish waters originates from the taxation of the porpoise catches. In the Little Belt, the catches may have commenced on a larger scale as early as 1357, and in the Isefjord as early as 1402 (Klausen 1867, Jensen 1946, Møller 1961). Besides these 2 major catch areas, minor catches also took place all along the coasts.

16th century

The information for this century is very scanty. Large catches were taken in the Little Belt around 1545 (Petersen 1969).

17th century

A directed catch was carried out at several places in the country, documenting the species from the Little Belt and the Isefjord area (Møller 1961). Lauritsøn-Wolf (1654) reported an annual take of several hundred porpoises in the Middelfart area.

18th century

Olavius (1787) reported on the occurrence of porpoises near the town of Skagen and proposed to initiate a catch operation similar to the drive catch in the Little Belt. The occurrence of harbour porpoises in the Little Belt area can be deduced from information on the reported catch activities (Petersen 1969). The catch season 1711-12 was poor while the period 1713-14 to 1737-38 yielded increasingly good catches. Pontoppidan (1730) reported a contemporary annual catch of about 1,000 animals. The catch of 1749 was likewise good, probably in the order of 500 to 700. In 1761, the catch was estimated at 320 animals, which was a rather poor season; and for 1773, the catch was at the same level with 330 animals, which is a two-thirds reduction of the contemporary catch. The years 1775 – 1777 yielded only poor takes of 100-125 animals, and in 1780, 120 animals were caught. The catch probably declined even further, and the last tax payment to the church was

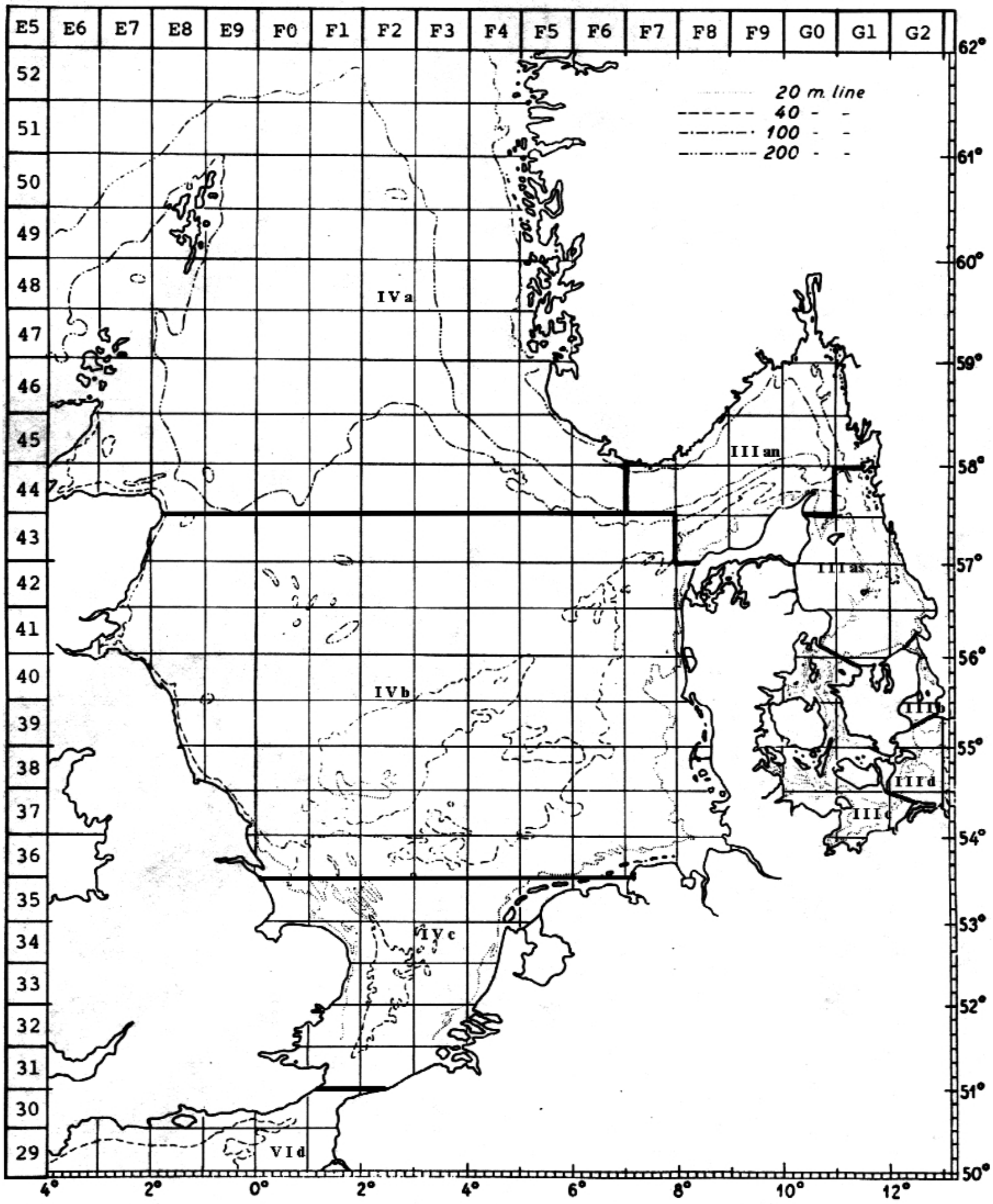


Fig. 1. Map of the North Sea and Inner Danish waters, together with ICES areas and squares, latitude North and longitude West and East.

made in the season 1798-99. Ice conditions severely hampered the catch activities in 1709, 1740, 1770, 1771, 1775, 1784 and 1789 and may eventually have contributed significantly to the closure of the site. A rough estimate of the total catch in this century is 42,000 animals in all, calculated from mean annual catches of 1,000 animals (25 seasons: 1715-16 – 1739-40), 600 animals (15 seasons: 1740-41 – 1754-55), 300 animals (20 seasons: 1755-56 – 1774-75) and 100 animals (20 seasons: 1775-76 – 1794-95).

In the Isefjord at Bramnæsvig there was a maximum catch of 165 in the second half of the century (With 1804).

19th century

Directed catch

Melchior (1834), Irminger (1846), and Eschricht (1849) describe the occurrence of the species as regular. Catch statistics document the occurrence of the species in the Little Belt and Isefjord areas (Kinze 1995). The Zoological Museum, Copenhagen, (ZMUC) collection holds specimens from these areas and the Sound. Kinze (1995) reviewed the catch sites, the size of the catch and its fluctuations for the Little Belt and Isefjord areas. Additional information about the catch in the Little Belt can be found in Erslev (1855-57) and Both (1876).

In the Little Belt area, minimum catch figures are known for 51 of the 81 seasons between 1819-20 and 1891-92 when the guild discontinued the catch. The catches range from 244 to 2,200 with a mean of 1,035. For the years 1889-96 additional catches were taken outside the jurisdiction of the guild and also after the guild activities were discontinued. The preponderance of the catch shifted from the Little Belt area to the Isefjord area. The total catch for the entire century is estimated to be of the order of 100,000 animals (Kinze 1997). The ZMUC collection holds a number of foetuses collected from the area in the years 1853, 1857, 1858, 1860 and 1863.

Table 1. Earlier published catch reports from the Isefjord area.

Period	Isefjord combined	Bramsnæsvig	Jægerpris	Source
1840s			300-400	Eschricht 1849
1860s			>100	Brammer 1872
1870s	300	-	-	Tauber 1880
1880s	800			Tauber 1892
1920s	several 100s			Stuberg 1936

Table 2. Detailed historical logbook catch reports of harbour porpoises by year, in the Isefjord area.

Year	Bramsnæsvig	Jægerpris	Total
1885	29	103	132
1886	987	429	1,416
1887		156	156
1888	1,443	530	1,973
1889	236	75	311
1890	231	139	370
1891	43	62	105
1892	115	115	230
1893	82	57	139
1894	104	180	284
1895	2,125	165	2,290
1896	134	215	349
1897	184	112	296
1898	137	120	257
1899	155	156	306
1900	263	306	569
All years	6,268	2,915	9,183
mean	418	182	574
min	29	57	105
max	2,125	530	2,290

For the Isefjord area, catch data are available for the catch sites at Jægerpris/Kulhuse and Bramsnæsvig respectively (Table 1). A review of the Danish Fishery Reports (Fiskeriberetninger) for the period 1885-1900 has revealed additional catch statistics for the 4 Jægerpris seasons 1888-90 and 1893, and for the 14 Bramnæsvig seasons 1886 and 1888-1900 (see Table 2). Noteworthy are the fluctuations found in the Bramnæsvig catch, with extremely high takes of 987, 1,443, and 2,125 porpoises for the seasons 1886, 1888, and 1895, respectively. The total catch for the Isefjord area can be estimated as roughly 40,000 animals or 400 animals per season. The ZMUC collection holds a number of skeletons and foetuses from Jægerpris.

An additional few hundred animals were taken at Holsteinsborg and Karrebæksminde, and similar sized catches occurred in the Sejrøbugt at Nekselø. For the period 1885-1899, minor catches in various nets were reported for the Mariager Fjord, Odder, Aså, Snekkersten and Vordingborg. A total minimum take of 39 animals is estimated during the period.

<u>Incidental catches</u>
Tauber (1880, 1892) estimated an annual bycatch in fishing nets as a few hundred in the 1880s and 1890s. He also mentioned a catch in salmon nets in the waters off Bornholm.

The ZMUC collection holds specimens that originated from fishing nets from the Sound in June 1838 and February 1884, Frederikshavn in April 1895, and Lyø in September 1895. Another specimen taken at Taarbæk in the Sound in 1863 is now in the collection of the Uppsala Zoological Museum in Sweden.

<u>Breeding and calving areas</u>
The ZMUC collection holds a newborn specimen from the Sound (ICES IIIb) from 7 June 1838, indicating that this species bred here during the 19^{th} century.

20th century
<u>Directed catches</u>
During World War One (1916-19), 1,600 animals were caught in the Little Belt area and during World War Two (1939-45) the catch seasons there yielded 980 porpoises (Kinze 1995). Møhl-Hansen (1954) collected specimens and data from the Little Belt, which are now in the collection and archives of the ZMUC. The catch in the Isefjord continued throughout the 1920s and was revived during World War Two.

<u>Ice entrapments</u>
Larger numbers of dead harbour porpoises were reported from Bornholm after severe ice conditions in February 1929. Also in January 1942, substantial numbers suffocated in the waters east of the island of Als.

<u>Seasonal migrations</u>
Andersen (1982) suggested that the migrations of former times had almost ceased after the depletion of the inner Baltic stocks. Kinze (1985a) found a more diffuse pattern and a possible mixing in the northern North Sea. More recent studies applying satellite telemetry have found evidence of substantial movements over rather short periods (Teilmann *et al.* MS 1998).

<u>Incidental catches:</u>
Stuberg (1936) and Jensen (1946) do not mention incidental catches of harbour porpoises but only refer to the dwindling directed catch in the Isefjord. However, the ZMUC collection holds specimens that document incidental catches or strandings of the species for the following years and localities: 2 December 1909 at Snekkersten in the Sound, March 1917 on Anholt, 1926 at Fredericia, 1929 at Gildbjerg Hoved, 2 July 1934 at Agersø, 1934 and 1941 at Taarbæk in the Sound, 1959 on Samsø, 1965 at Køge Bugt, 1969 at Hornbæk and 1979 at Storstrømbroen.

Andersen and co-workers were the first to collect information on a larger scale. They received animals from pound-nets and gill-nets from all Danish waters during the 1960s and early 1970s (Andersen 1974, 1978). Clausen and Andersen (1988) reported on incidental catches primarily in gill-nets. Incidentally-caught harbour porpoises were reported to the Ministry of Fisheries for the period 1978-86, and between 1986 and 1990 specimens were collected by the Danish harbour porpoise project (Kinze 1994).

The harbour porpoise was apparently abundant in the North Sea. Clausen and Andersen (1988) estimated a total annual bycatch in the North

Sea in the so-called wreck fisheries of 3,000 animals. Kinze (1994) reported an estimated bycatch of 750 from a single harbour alone. Vinther (1996) estimated that the Danish gill-net fisheries in the North Sea took up to 7,000 animals annually. For the inner Danish waters there are only very crude estimates of the size of the incidental catches. Andersen (MS 1972) mentioned a possible annual take of the order of 1,000 animals.

Strandings

Recording of and collection of data from stranded harbour porpoises in Denmark commenced in 1986, and 495 strandings or bycatch records exist from 1986-89 (Kinze 1990). Strandings and bycatch records were reported from all Danish waters, with the lowest numbers found in areas where few or no sightings were made. Harbour porpoises were found stranded or incidentally-caught in all months of the year.

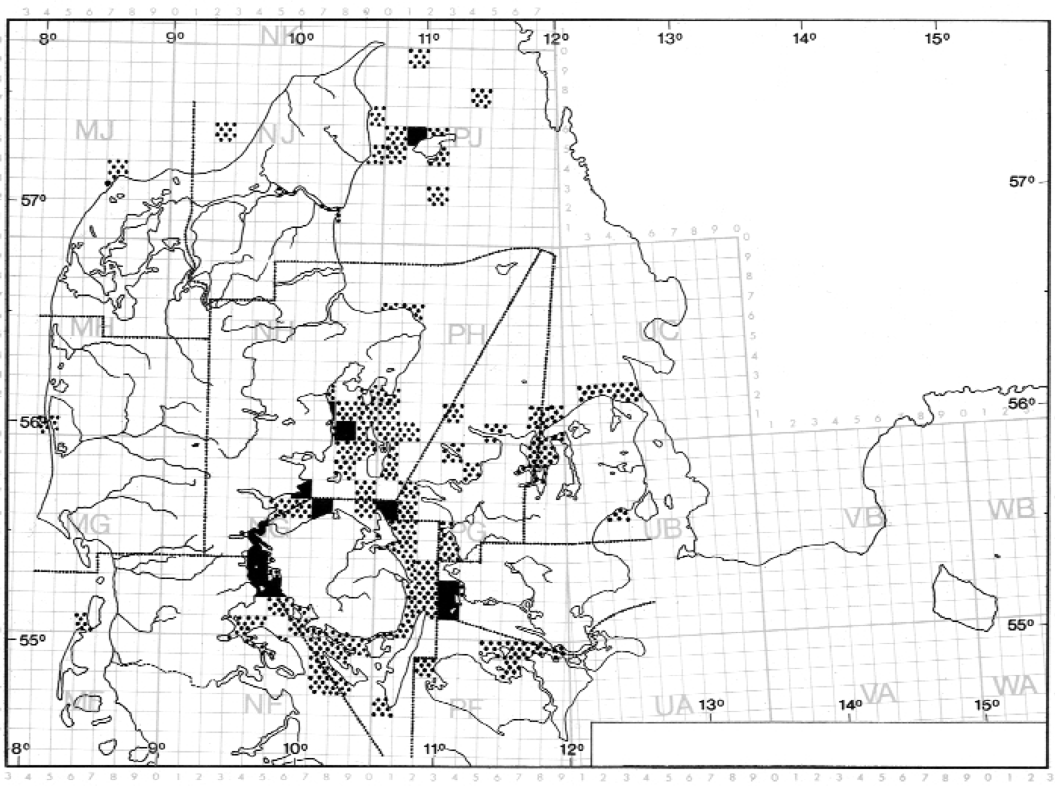
Lindroth (1962) provided evidence of a more common occurrence in the Bornholm area during the 1960s. Newspaper cuttings held in the ZMUC archives report specimens from 1967. Other specimens have been reported for the years 1982, 1985, 1988, 1989. The annual record is estimated to be 10-15 individuals in the mid-1980s.

Qualitative sighting records

Kinze (1990) reported 9,067 sightings from ferry boats and sailing yachts in the Inner Danish waters (predominantly Belt seas) for the period 1963-89. Of these sightings, 4,921 were reported from ferry boats for the period 1983-89 and 4,146 records originated from yachtsmen and other sources during the period 1963-89 (although the period 1963-83 only accounts for 209 sightings or about 4% of all sightings). For the more recent years, data sheets exist but have not been reviewed.

Harbour porpoises were sighted throughout Danish waters except off Bornholm. Few sightings were reported from the Sound, the south-western part of the Baltic Sea, or the central part of the Limfjorden. Harbour porpoises were

Fig. 2. *Distribution of porpoise sightings during 1984-89 (after Kinze 1990). Black squares = sightings of calves during 3 or more years.*



sighted in all months of the year but with few sightings from January to March, and numbers increased markedly in April.

School sizes varied from single to many animals (Kinze 1990). Singletons were the most commonly reported school size from both ferry boats and yachts (41.3% and 44.7% respectively), while pairs were found in 35.1% and 35.7% of all cases respectively. Schools of 10 animals and more accounted for 1.7% and 1.0% of all schools reported from ferry boats and yachts, respectively. The largest school, reported to contain approximately 100 individuals, was observed in July 1987. School sizes reported from the field cruises were very similar in distribution. The overall average school size was 2.11 (2.33 from yachts and 1.96 from ferry boats). Average school size varied by month. The highest figures were found in March, April, and November for sightings from yachts, whilst the average school size was always lower for sightings from ferry boats. The largest reported aggregation of harbour porpoises containing calves consisted of 17 individuals including 5 calves.

Breeding and calving areas:
Information on near-term foetuses and newborn calves was retrieved from the data records in order to elucidate the whereabouts of calving areas. Prior to 1962 the information is very scanty. Records of newborn calves or near-term foetuses (65 - 95 cm) from the ZMUC fall broadly into the time period May to August. Sightings of newborn calves (Fig. 2), and combinations of newborn calves and near-term foetuses have been recorded for the following areas: the northern part of the Little Belt, the waters north of Funen, the Sejrø Bight, the Great Belt, the Smålandsfarvandet, and the archipelago south of Funen (Kinze 1990). Live sightings of calves were reported from April through October. Highest numbers were found in July and this is supported by the results of small cetacean-dedicated cruises in 1987-89 (Kinze 1990), and 1994 (Hammond *et al.* 1995) (Fig. 3).

Fig. 3. *Distribution of porpoise calf sightings during July 1994 (after Hammond et al. 1995), showing ratio of calf sightings to all porpoise sightings for each leg of survey effort. The black dot size is proportional to the calf ratio. Open dots indicate zero ratio.*

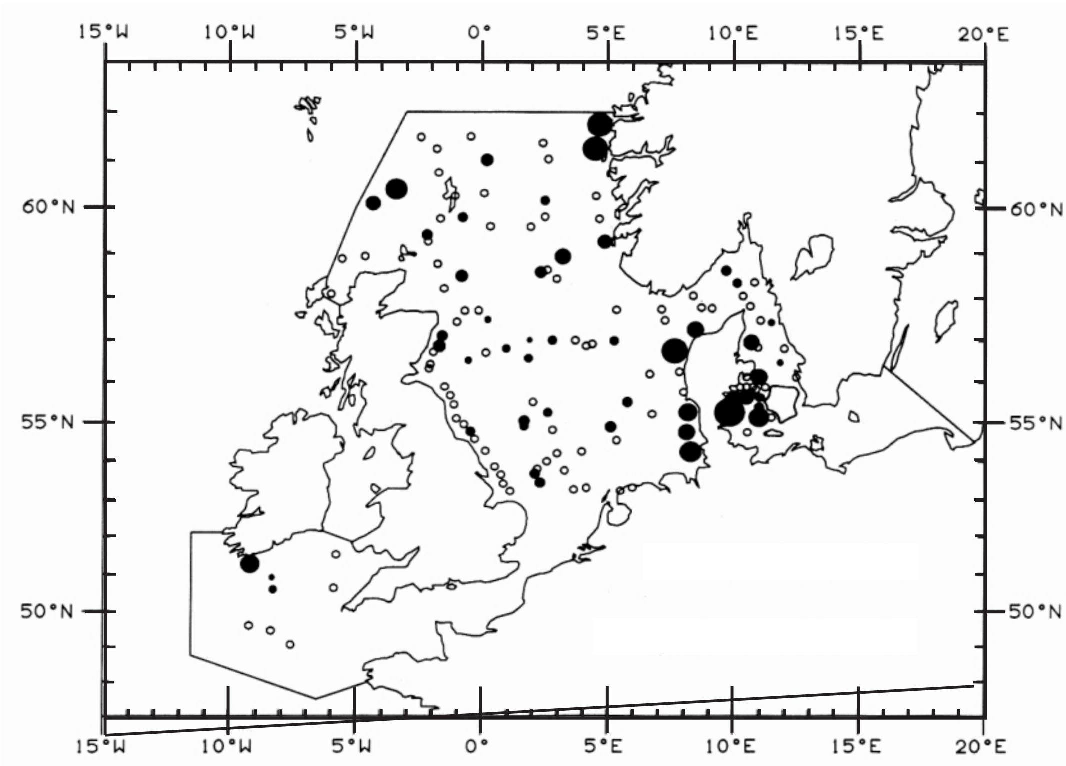


Table 3. Composition of schools including calves by years (observations combined).

School Size	No. Calves	No. of Schools 1983	1984	1985	1986	1987	1988	1989	Sum	%
2	1	3	9	11	10	18	13	24	88	49.4
3	1	1	7	6	7	9	9	18	57	32.0
4	1	0	1	2	1	3	1	6	14	7.9
4	2	0	1	2	2	1	1	0	7	3.9
5	2	0	2	0	0	1	1	0	4	2.2
6	1	0	0	0	0	1	0	1	2	1.1
6	2	0	0	0	0	0	1	0	1	0.6
7	1	0	0	0	0	0	1	0	1	0.6
7	3	0	0	0	1	0	0	0	1	0.6
8	2	0	0	0	0	0	0	1	1	0.6
15	4	0	0	0	1	0	0	0	1	0.6
17	5	0	0	0	0	1	0	0	1	0.6
Sum									178	

The percentage of newborn calves increased from May (9.1%) to June (6.9 - 10.6%) and reached a peak in July (11.5 - 23.8%) and August (18.2 - 23.5%) (Kinze, 1990). Cow and calf pairs were most common (49.4%), followed by groups of 3 animals including 1 calf (32.0%); other combinations were rare (Table 3). The small cetacean-dedicated cruises showed a similar frequency of mother-calf pairs but groups of 3 (Table 4) were less frequent (19.4%). The overall sample size in Table 4 is much smaller than in Table 3, and the differences are likely not significant. Calf percentages calculated from EU-funded SCANS (Small Cetacean Abundance in the North Sea) survey data show similarly very high percentages in the inner Danish waters and the Wadden Sea area (Hammond *et al.* 1995).

Ferry survey 1991

Kinze and Jensen (MS 1991) compared the sighting frequencies during the summer months on 4 different ferry lines. The ferry route Frederikshavn-Læsø had a relative frequency of 0.04 animals km^{-1} track, whilst Svenborg-Ærøskøbing and Spodsbjerg-Tårs had 0.06 km^{-1} track and 0.11 km^{-1} track respectively. The highest frequency was found on the route Hov-Samsø with 0.20 km^{-1} track.

Small cetacean-dedicated cruises 1987-1989

The dedicated cruises in the area north of Funen resulted in 277 primary sightings (96 in 1987, 103 in 1988, 78 in 1989) during the months April to August. These cruises showed an increase in density from April through July with a decline in August (Kinze 1990).

Systematic sighting surveys 1987-94

Danielsen *et al.* (1992) conducted shipboard cruises in 1987 and 1988 in the Danish sector of the North Sea and the northern Kattegat. Heide-Jørgensen *et al.* (1992, 1993) conducted aerial surveys in the Inner Danish waters whilst the SCANS project covered all Danish waters with a combination of aerial and shipboard surveys.

Danielsen *et al.* (1992) estimated the population of porpoises in the Danish sector of the North Sea as 7,000 individuals (95% CI 2,800-11,200) in October-November 1987 and 7,500 individuals (95% CI 3,599-11,700) in 1988.

Table 4. Compositions of schools including calves observed during the small cetacean-dedicated cruises 1987-89.

Size of school	Number of calves	Number of observations	%
2	1	16	51.6
3	1	6	19.4
4	1	2	6.5
4	2	2	6.5
5	1	5	16.3

The SCANS surveys conducted in the summer of 1994 provided an estimate of 5,912 (cv 0.27) for the German Bight with adjacent Danish waters outside the Wadden Sea area (area Y), 11,870 (cv 0.47) for coastal waters of Jutland (area L), 36,046 for area I (Eastern Skagerrak, Kattegat, and Belt Sea), 5,262 (cv 0.25) for the Inner Danish waters (area I´, which is contained in area I) and 588 (cv 0.48) animals for area X (Little Belt and southwestern Belt sea) – see Fig. 6.1, p. 127, in Hammond *et al.* (1995) for details of SCANS area definitions. No sightings were made in the waters around Bornholm. For the whole area K there were too few sightings to provide an abundance estimate. Berggren (1995a) later gave a preliminary estimate of 655 animals from part of this area (area A in Berggren 1995a).

Discussion

Trends in distribution

No systematic surveys are available before 1987, but a general decline was noted by several authors (Andersen 1982, Kinze and Sørensen 1984). Kinze (1990) collected qualitative data from ferry boats and yachtsmen, and together with data collected from 4 ferry lines (Kinze and Jensen MS 1991), found the species to be rare in the southern and southeastern-most part of the Inner Danish waters, and in the Limfjord. Aerial surveys conducted for the Danish Ministry of the Environment (Heide-Jørgensen *et al.* 1992) support this.

The harbour porpoise is abundant in the Belt Sea and Kattegat but rarely seen in the Sound, the westernmost part of the Baltic, and off Bornholm where the most recent bycatch was reported in 1982 (appendix in Kinze and Sørensen 1986). The boundary of frequent encounters can be drawn slightly further to the south than suggested by Kinze (1985b). No marked migration pattern has been found, concurring with earlier findings of Andersen (MS 1972) for Danish waters in general and Kinze (1985b) for the Kattegat. During the summer, harbour porpoises have been found to be rather sedentary (Kinze MS 1986, 1989; Watson 1976). The largest average school sizes are found in March, April and November, probably reflecting migrating animals. Northern ferry lines have harbour porpoise sightings all year round, whilst more southerly ones lack sightings in the first quarter of the year. This may indicate southward migration with animals arriving in the southern waters in April and a northward migration in early winter. During the winter months, large concentrations of harbour porpoises have been found in the northern Kattegat around Læsø (Danielsen *et al.* 1992) indicating an offshore migration taking place in the late autumn months.

The Baltic population has been severely reduced and a relic may now be largely confined to Inner Danish waters. This is supported by latest figures from neighbouring Baltic countries (Schulze 1987, Lindstedt and Lindstedt 1988, Skora *et al.* 1988). The pronounced migrations of past decades have ceased (Andersen MS 1972). These migrations have been considered an adaptation of the stock to the special hydrographic conditions of the Baltic proper (*e.g.* Eschricht 1849). Along with the shrinking of the distribution area, the migratory behaviour has changed and become more diffuse and may now resemble the onshore/offshore pattern commonly found in the species (Gaskin and Blair 1977). Large winter aggregations may no longer be observed because the number of animals entering Danish waters from the Baltic proper is low. Kinze (1985b, MS 1986), when analysing observed directions of animals, found no clear-cut tendencies and suggested a complex pattern of movements back and forth in the Kattegat and through the Danish straits.

Initially the only information on calving areas came from qualitative sightings of calves and collected specimens. Dedicated cruises were conducted in the central part of the distributional range of the species in Danish waters and in an area where calves have been reported in earlier years. Collected information from the sighting scheme and dedicated cruises from the same area accord well with each other. The dedicated cruises revealed further areas with newborn calves, which may, therefore, be considered breeding areas.

Calves have been observed from April to October, with peaks in July and August. Births are believed to take place mainly in late June and early July, with nursing lasting 8 or more months (Møhl-Hansen 1954, Lockyer 2003a). The present results, given later in this paper, with near-term foetuses found in June and July and newborn calves in August, are in good agreement with these findings.

Conclusions

In conclusion, the harbour porpoise is the most common cetacean species in all Danish waters. The range of the species has been reduced, affecting the western Baltic Sea in particular, and the southern Belt Sea. There is a substantial incidental catch continuing, the effects of which may be significant and complex on the population(s) affected, depending on the degree of cross-boundary migrations and stock mixing between areas.

LIFE HISTORY AND BIOLOGICAL INVESTIGATIONS

Database

A database containing biological information on harbour porpoise collected during dissections of carcasses taken from waters around Denmark (the North Sea and Inner Danish waters - chiefly ICES areas IVb, IIIas, IIIan, IIIb and IIIc – Fig. 1) was compiled during the period 1996-1998 under the project BY-CARE. It has since been maintained and now includes data on nearly 1,900 individuals from 1834 to the present. Photographs of the specimens examined since 1996 have been collated and since 1998 are also stored digitally on computer. These data, in an Access format, form the basis of all new analyses herein. Throughout the database, the number of males (1,043) exceeds that of females (799). There are of course a few animals for which no sex category was recorded. The majority of records are from catch and incidental take, the implications of which will be discussed below. The catch records do not include biological data apart from length, body weight and foetal information, and are therefore not included in most of the biological analyses.

Diet, parasites and toxicology

The diet of the harbour porpoise is closely intertwined with the occurrence of parasites and the accumulation of persistent organic pollutants and heavy metals. Therefore, these subjects are treated under the same heading. The following reviews earlier studies and it also includes new data derived from the BY-CARE project.

Diet

Prey species identified

Early accounts of the diet of the harbour porpoise in Danish waters are very general. Eschricht (1839) stated that fish formed the main part of the diet, and in 1849 he reported herring (*Clupea harengus*) to be the main prey species. Melchior (1834) and Tauber (1892) reported herring, cod (*Gadus morhua*), garfish (*Belone belone*) and, near Bornholm, also salmon (*Salmo salar*) (Wulff 1881, Winge 1908) as comprising the diet of the species.

Møhl-Hansen (1954) took a large sample of stomach contents from the Little Belt area, which were later analysed by Källquist (1973, 1974). She found gadoids to be the most common fish type, especially whiting (*Merlangius merlangus*). Andersen (1965) listed a number of prey species for the harbour porpoise in Danish waters. However, neither Källquist nor Andersen apparently differentiated between the North Sea and the Inner Danish waters.

For the period 1985-90 stomach contents of Danish harbour porpoises were examined by Aarefjord *et al.* (1995) (n = 57), Santos (1998) (n = 58), Enghoff (Zoological Museum, Copenhagen, unpublished data, n = 2) and Thomas (Zoological Museum, Copenhagen, unpublished data, n = 4).

For the most recent period, stomach content data are available from 24 bycaught porpoises taken during the acoustic deterrent pinger trials in the North Sea in autumn 1997, carried out as part of the BY-CARE project. These animals showed a high prevalence of sandeel (*Ammodytes tobianus*). In 10 of 16 cases the stomachs contained *Ammodytidae* (species not certain) and in 9 cases this group was the dominant prey type. The second important prey group were *Gadidae* that were found in 8 stomachs, and as the sole or dominant species in 2 specimens, with *Clupidae* in third position. In total, 21 species of fish and 2 species of squid have been identified as prey items (Table 5). Comparisons of prey preferences in porpoises from several areas are presented by Lockyer (2003b).

Importance of prey species

The diet of Danish harbour porpoises has been studied by several authors (see above), and animals examined cover all Danish waters. Overall, between the mid-1980s and present, gadoids were the most important prey items (found in 62% of the stomachs examined: 52 of 84) followed by clupeoids (35% of all stomachs), gobiids (30%), and ammodytids (30%). Squid were found in only 7% of the examined stomachs. There were regional differences in the diet reflecting the general occurrence of the prey species (see Table 5), and also differences over time when compared with reports from the 19th century when herring was the most frequently observed food item (see above). No stomachs from the Baltic proper, however, were available.

Quantity of food

During the period 1996-98, porpoises from both the North Sea and Inner Danish waters, derived from bycatches and strandings, were examined for stomach contents. These were both weighed and sorted as to prey type (as indicated above). The results indicated that stomachs of stranded animals rarely contained food remains, and that in the bycaught animals, the prey composition was not necessarily similar to the fish species targeted in the net fishery in which they were taken. The amounts present in the stomach (chiefly the first chamber) are presented in Table 6, and indicate that a maximum stomach fill approximates 1 kg whole food in animals >120 cm in length.

Table 5. Diet of harbour porpoises from Danish waters by ICES areas, in the period 1985-1997, including previous analyses and new data

Prey taxon	ICES IVb	ICES IIIan	ICES IIIas	ICES IIIb	ICES IIIc
FISH					
Lycodes esmarkii Eelpout		x	x		x
Anguilla anguilla Eel		x	x		x
Ammodytes sp. Sandeel	x	x	x		x
Belone belone Garfish					x
Gobiidae sp. Gobies	x	x	x	x	x
Gadidae sp. Codfish	x	x	x	x	x
Gadus morhua Cod	x	x	x	x	x
Merlanogrammus æglefinus Haddock	x	x	x		
Trisopterus sp. Small codfish	x	x			
T. esmarkii Norway pout		x			
T. minutus Poor cod	x	x	x		
Pollachius pollachius Pollack	x		x		
Micromesistius poutassou Blue whiting		x	x		
Merluccius merluccius Hake	x		x		
Merlangius merlangus Whiting	x	x	x		x
Clupeidae sp. Herring and Anchovies	x		x	x	x
Clupea harengus Herring		x	x		x
Sprattus sprattus Sprat	x	x	x		
Maurolicus muelleri Pearlside		x	x		
Scomber scombrus Mackerel	x				
Labridae sp. Wrasse		x			
Pleuronectidae Flatfishes					x
SQUIDS					
Allotheuthis	x		x		
Sepietta		x			

Table 6. Quantities of food remains found in harbour porpoise stomachs in Danish waters, both North Sea and Inner Danish, 1996-98, by actual observed wet weight.

Origin of animal	Mean wet weight food (g ± S.E.)	Range wet weight food (g)	No stomachs examined
Stranded females	14.3± 6.7	0–31.0	4
Stranded males	11.3± 5.9	0.02–43.0	18
Bycaught females	217.5±63.6	0.03–983.0	8
Bycaught males	145.1±31.4	0–717.0	30
Total	172.3±30.9	0–983.0	60

Geographical and age dependent differences

Aarefjord *et al.* (1995) divided their sample, derived from Norway, Sweden and Denmark into seven geographical areas, 3 of them being Danish waters. They observed no significant geographical difference in prey species preference (but see above). However, pregnant females may have a more diverse prey preference in order to build up reserves for nourishing their calf (Aarefjord *et al.* 1995). The diet is diversified with age, *i.e.* calves tend to eat few prey species while older animals gradually broaden their menu.

Parasites

The information on the parasite load falls into 3 levels. At level 1 only the presence or absence is noted without any quantification of the infestation. Level 2 is an attempt to do a 'quick and dirty' semi-quantitative assessment by dividing the infestation into 'light', 'medium', and 'high' (Clausen and Andersen 1988). The third level includes counts of parasites. Infestation comes through the diet, and therefore is age-dependent. Also, the body condition may have an influence on the parasite burden which may also fluctuate seasonally. Møhl-Hansen (1954) estimated that all animals over 25 kg (*i.e.* post-weaning) would be infested. The organs that have been examined for parasites have included ears, lungs, heart, stomach, liver, kidneys and intestines from 1985-98, all of these except stomach, kidneys and intestines were examined in 1943-44, all except kidneys in 1962-65, and all except kidneys and intestines in 1980-81. These organs are detailed below. In our recent studies (1996-98), the soft organs were carefully opened and heart, lungs, liver and kidneys sliced through serially; the ears and sinuses and blowhole were examined, also the trachea and bronchi, and the intestines were cut along the length and the inside wall examined. The stomach contents were washed out in the investigation for food and drained through various grades of sieves from which items were retrieved. The stomach lining was also examined.

Parasites of the ear sinuses and the brain

Principal parasites of the ear sinuses are *Stenurus minor* and *Crassicauda* sp., the latter species also infesting the brain. *Stenurus minor* was found to be present in 82.9% of the animals in the 1940s (Møhl-Hansen, unpublished data). No clear pattern of infestation emerges, since both non-infested and infested animals include small and large animals. Unfortunately the age is known of only one animal: a 9 year-old female which was infested.

There are only few comparable data from the 1960s and these suggest a similar high infestation rate (5 out of 6), as do the findings of Clausen and Andersen (1988). New results from 1996-98 indicate a moderate infestation rate of 67.6% (Table 7), and include both sexes and all ages. *Crassicauda* sp. was only recently recognised in Danish porpoise, but subcutaneously, not in the brain nor in the ear sinuses.

Lung parasites

Of the principal parasites of the lung the following 3 species have been found in Danish porpoises. The earliest evidence of parasite infestation in Danish harbour porpoises dates back to Bartholin (1654), who mentioned nematodes in the lungs. Eschricht (1839) reported a high infestation rate in the lungs, worms being present in such high numbers that he thought the diving capability of the animals was compromised. Wesenberg-Lund (1947) gave a general description of the occurrence of 2 species of lung worms (*Pseudalius inflexus* and *Torynurus convolutus*) based on samples collected by Møhl-Hansen (1954). Of a sample size of 50 animals 'more than 90%' were infested.

Dissections during the 1960s and 1970s likewise found high infestation rates in the lungs (S. Andersen pers. comm.): 33.3% (2 of 6) in animals less than 125 cm and 100% (14 of 14) in animals larger than 125 cm. Further, the species *Halocercus invaginatus* was added to the list (Andersen 1965). Clausen and Andersen (1988) found infestation rates of 30.9% for animals less than 1 year old and 96.8 % for animals older than 1 year. The comparable figures for the period 1985-89 are 53.6% and 97.9% respectively (Kinze unpublished). Investigations in 1996-98 indicated a moderate infestation rate of 59.5% for lungworms (Table 7). This included many young animals of age 0-2 years, and may explain why the infestation rate was lower than that observed previously for post-weaning animals.

Heart parasites

Pseudalius inflexus may also be found in the ventricle of the heart. The primary data from Møhl-Hansen (1954) indicate a rather common occurrence of this parasite with an infestation rate of 48.4% (31 out of 64 animals). Later studies found much lower rates: 18.2% (4 out of 22; S. Andersen pers.comm.), 0.7% (1 out of 149; Clausen and Andersen 1988) and 11.5% (3 out of 26) for the period 1985-89 (Kinze unpublished). It is not known whether these figures are directly comparable, but if so, they may reflect larger changes over time or geographical differences. The Møhl-Hansen sample from the 1940s originated from the Little Belt and the winter period and may have been of pure Baltic origin, while the other samples originated mainly from the North Sea. The incidence of heart parasites in animals examined in 1996-98 showed a low infestation rate of 14.3% (Table 7) comparable with earlier reports, but this organ was examined in relatively few animals.

Stomach parasites

The principle parasite species of the stomach is *Anisakis simplex* (Herreras *et al.* 1996). In the 1960s the species was reported by Andersen (1965). During the period 1996-98, 60% of stomachs observed had a moderate infestation of nematodes (Table 7). A gross comparison between parasite loads in Danish animals and animals from other areas was provided by Harreras *et al.* (1997).

Liver parasites

The principle liver parasite is *Campula oblonga*. Møhl-Hansen (1954) mentions its occurrence and the infestation rate given is rather high at 80.6%. The fluke-like parasite causes the formation of cysts which frequently become fibrous and calcified. The figures for the 1960s and early 1980s were 68.1% and 61.7% respectively (Kinze unpublished). During 1996-98, 50% of animals had a mainly light infestation (Table 7), and those with heavy infestation appeared to be otherwise healthy. There is a suggestion of a decline over time in infestation rate, but all factors such as age, sex, locality and season should be considered in the interpretation.

Parasites of the intestines

A number of tapeworms and nematodes are known from this host organ. Andersen (1965) lists a *Diphylobothrium* species which was also found once in the survey conducted by Clausen

Table 7. Parasitic infestation rates of harbour porpoises from mainly North Sea and a few from Inner Danish waters, recorded during 1996 – 1998. Infestation: 1 - light; 2 - moderate; 3 – high; ND – not described.

	Ear and sinuses	Lungs and bronchi	Stomach chambers	Heart	Liver and ducts	Kidneys	Intestines
No.sampled	71	74	20	7	74	10	38
No. infested	48	44	12	1	37	2	2
% infested	67.6	44.0	60.0	14.3	50.0	20.0	5.3
Infestation	1-2, v. few 3	1-2, v. few 3	1-2, v. few 3	ND	1 few 2-3	ND	ND

and Andersen (1988) and is also reported by Herreras *et al.* (1997). The only systematic survey conducted so far was by Herreras *et al.* (1996, 1997). Intestinal parasites (unspecified cestodes and ancanthocephalans) were recorded in only 5.3% of animals, despite a thorough search throughout the length of the intestine (about 10-13 m) during 1996-98 (Table 7).

Kidneys and subcutaneous tissue
Crassicauda sp. has been found in the kidney and subcutaneously by J.A. Raga and co-workers of the University of Valencia, Spain (pers. comm.) and recently (1996-98) encysted in post-ventral blubber during dissections at the Zoological Museum. During 1996-98, 20% of only a few animals examined contained parasites (Table 7). Cysticercoid cysts (tapeworm) have also been observed in very few animals between 1996-98, when the cysts were observed in the post-ventral blubber adjacent to the perineal area.

General discussion and conclusions
Danish harbour porpoises generally become infested with parasites in the ear sinuses (*Stenurus minor*), the lungs (*Pseudalius inflexus, Torynurus convolutus, Halocercus invaginatus*), the stomach (*Anisakis sp.*), the liver (*Campula oblonga*) and the intestines (*Diphylobothrium* sp.) (see Table 8). The infestation rate increases with age and it is conceivable that in some cases, infection may develop into a fatal condition if organ failure occurs. There are no apparent differences between the seas around Denmark, and there are no apparent long term tendencies towards higher present day infestation rates (Tables 7 and 8). Danish harbour porpoises appear to have been consistently heavily infested with lung worms from the documentation in 1654, 1839, 1945 (see above) and in more recent surveys. Detailed comparisons on parasitic infection in porpoises from other areas is presented by Lockyer (2003b).

Pollutants
<u>Chlorinated hydrocarbons</u>
Levels of total DDT concentrations may be decreasing while PCB and HCH loads have increased in Danish porpoises. Too few animals have been analysed to allow comparison between various Danish waters.

Organochlorine loads of Danish harbour porpoises were reported by Otterlind (MS 1976), Andersen and Rebstorff (1976), Clausen and Andersen (1988) and Granby and Kinze (1991). The latter found evidence for a decline in sumDDT, but higher loads of sumPCB. Kleivane *et al.* (1995) compared organochlorine loads in young males from the Danish Kattegat (Gilleleje) and Norwegian waters (Vestlandet and Tufjord) and found the Danish animals to have higher loads. In addition, reports from the Swedish Skagerrak and Kattegat for male por-

Table 8. Parasites found in Danish harbour porpoises 1943-90 (citations in text).

Species	North Sea			Inner Danish Waters		
	1943-1944	1962-1965	1985-1990	1943-1944	1962-1965	1985-1990
Nematoda						
Stenurus minor	x	x	x	x	x	x
Pseudalius inflexus		x	x	x	x	x
Torynurus convolutus		x	x		x	x
Crassicauda sp.						
Halocercus invaginatus		x	x			x
Anisakis simplex		x	x	x	x	x
Trematoda						
Campula oblonga		x	x	x	x	x
Cestoda						
Diphylobothrium stemmacephalum		x	x			

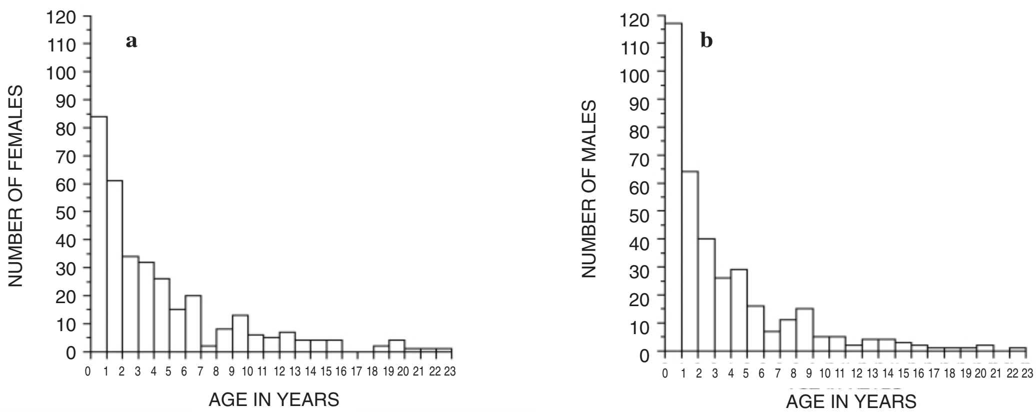


Fig. 4. *Age frequency distribution for stranded and bycaught harbour porpoises. a. females; b. males.*

poises indicated higher levels of sumDDT, sumPCB and sum non-ortho PCB than in the Baltic, but that levels have declined between 1978-81 and 1988-91 (Berggren *et al.* 1995).

<u>Heavy metals</u>
Mercury and cadmium burdens are only known from the early and mid-1980s and are considered to be low. Heavy metal burdens were reported by Clausen and Andersen (1988) and Joiris *et al.* (1991). More recently, Szefer *et al.* (MS 1998) have reported on cadmium levels of 0.12-0.25 ug g^{-1} dry weight of liver and 0.14-1.84 ug g^{-1} dry weight of kidney from Danish porpoises, both higher levels than observed in true Baltic animals (Polish coast), yet considerably lower than for West Greenland porpoises.

Comparisons on contaminant load in porpoises from other areas are presented in Lockyer (2003b).

Age, growth and reproduction
Age and length distributions
Methods
Teeth were collected from each individual and prepared for age determination as described by Lockyer (1995a, b) and Bjørge *et al.* (1995). This method entails collecting teeth (usually about 5) from the lower jaw, of which 2 are decalcified in *RDO* (a proprietary decalcifying agent manufactured by Apex Engineering Products Corp., Illinois) after fixing in 10% neutral formalin solution. The 2 teeth are sectioned, each in a different longitudinal plane, on a freezing microtome at 25 micron thickness through the crown and central pulp cavity and stained with Erhlich's acid haematoxylin (Lockyer 1995a). Growth layer groups (GLGs) are counted in dentine and also cementum under low power magnification with transmitted light. GLGs are taken as representing years (Bjørge *et al.* 1995, Lockyer 1995a, b). All tooth sections used in this study were read independently of biological information about the specimen on at least 2 separate occasions. The age data so derived were entered as rounded down to the nearest year. Total body length was measured as described in Lockyer (1995b, c, d). The data (all sub-sets: catches, strandings, bycatches) have been combined for all years and locations but separated by sex.

Age distribution by sex
Age structure is shown as age frequency distributions in Fig. 4 which represents strandings and bycatches only. The largest age group is 0 years in both sexes, whilst longevity is 22-23 years regardless of sex. The age class frequency declines rapidly from birth to age 2 years, and then declines more slowly. These data suggest an especially high mortality in the first year of life, except that the decline is much greater in males than females. The data could also be indicative of segregation by age and sex. Less than 5% animals live beyond age 12 years. These findings almost exactly echo the age structure of British harbour porpoises (Lockyer 1995b). Table 9 presents means ± s.e. for animals from different sources and in different periods. Table 10 provides the numbers of porpoises recorded by source by year. It should be noted, however, that ages and lengths are not consistently available for all animals. Generally such data are available only from the 1940s onwards.

Table 9. Calculated mean lengths, ages and various indicators of body condition (according to Lockyer, 1995c), by sex and data subset.

	Mean Length ± S.E. (cm)	Age ± S.E. (Years)	Body Weight ± S.E. (kg)	Muscle Weight ± S.E. (kg)	Blubber Weight ± S.E. (kg)	Blubber Thickness, D3 ± S.E. (mm)	Mid-Girth, G3 ± S.E. (cm)
Females *All years incl. BY-CARE*							
Catch - all years, areas	150.7 ± 1.1 (*n*=202)	8.1 ± 2.5 (*n*=10)	54.3 ± 0.9 (*n*=287)				
Incidental catch - all years, areas	132.1 ± 1.1 (*n*=277)	3.1 ± 0.3 (*n*=233)	37.4 ± 0.9 (*n*=215)				
Strandings - all years, areas	127.9 ± 2.7 (*n*=114)	5.2 ± 0.6 (*n*=79)	25.8 ± 3.4 (*n*=35)				
Males *All years incl. BY-CARE*							
Catch - all years, areas	141.0 ± 0.8 (*n*=277)	9.0 ± 4.3 (*n*=4)	54.5 ± 0.5 (*n*=437)				
Incidental catch - all years, areas	124.0 ± 0.8 (*n*=334)	2.5 ± 0.2 (*n*=248)	31.5 ± 0.6 (*n*=260)				
Strandings - all years, areas	120.1 ± 2.0 (*n*=129)	4.2 ± 0.5 (*n*=86)	24.7 ± 2.0 (*n*=45)				
Females *BY-CARE, 1996-98*							
Incidental catch	128.5 ± 3.6 (*n*=33)	2.1 ± 0.6 (*n*=30)	35.8 ± 2.4 (*n*=30)	8.9 ± 0.9 (*n*=29)	11.2 ± 0.7 (*n*=29)	22.0 ± 1.6 (*n*=26)	83.7 ± 1.9 (*n*=29)
Strandings	111.6 ± 9.4 (*n*=16)	3.1 ± 1.3 (*n*=14)	17.4 ± 4.0 (*n*=11)	3.0 ± 0.9 (*n*=9)	7.2 ± 1.2 (*n*=9)	22.9 ± 3.7 (*n*=8)	62.7 ± 5.6 (*n*=9)
Males *BY-CARE, 1996-98*							
Incidental catch	123.5 ± 2.2 (*n*=47)	3.5 ± 0.7 (*n*=40)	33.3 ± 1.5 (*n*=42)	8.2 ± 0.7 *n*=38)	10.8 ± 0.5 (*n*=38)	22.4 ± 1.4 (*n*=38)	84.5 ± 2.0 (*n*=36)
Strandings	110.5 ± 5.0 (*n*=27)	3.0 ± 0.9 (*n*=26)	22.1 ± 2.9 (*n*=21)	7.6 ± 1.4 (*n*=17)	9.6 ± 1.0 (*n*=16)	22.9 ± 2.5 (*n*=17)	74.0 ± 4.0 (*n*=16)

Length distribution by sex

These data are presented as frequencies in Table 11 and means in Table 9. These data also include several neonates and near-term foetuses. There are clearly differences in mean lengths between animals derived from different sources, and these are influenced by skewed length distributions; the catches comprising predominantly larger mature animals, whilst the bycatches tend to be predominantly immature small animals. Strandings also include many smaller immature animals, but also some very large (old) animals. In general, the most represented sizes range from 135-165 cm in females and 120-150 cm in males.

Growth

The data of length and weight at age have been combined for all years, locations and sources, but separated by sex. In this analysis, bias from combining different data subsets should not be present.

Length at age by sex

Lengths at age by sex have been plotted in Fig. 5, and preliminary curves derived by logarithmic fit. There is considerable scatter in length at age in all age classes, but especially the younger age classes, and thus it is important to observe that the "fitted" mean curve may not be representative for many individuals. It is clear however, that maximum length in females exceeds that for males. This is anticipated from data from other sources (van Utrecht 1978, Gaskin *et al.* 1984, Read and Gaskin 1990, Sørensen and Kinze MS 1990, 1994, Kull and Berggren MS 1995, Lockyer 1995b, d). Mean adult lengths for females and males appear to be about 160 cm and 145 cm respectively - the same as for British animals (Lockyer 1995b, d), porpoises from the Swedish Skagerrak and Kattegat (Berggren 1995b), but larger than the Canadian Bay of Fundy animals (Read and Gaskin 1990). Maximum lengths recorded are 189 cm for females and 167 cm for males (see also Lockyer 2003a). Berggren (1995b) reported a maximum size of 167 cm in females and 154 cm in males in the Swedish Skagerrak and Kattegat.

Weight at age by sex

Weight at age data have been plotted for individuals in Fig. 6 , and preliminary curves derived by logarithmic fit. As in the length at age plots, there is considerable scatter. The origin of this may be not only due to individual variation, but also season, source and reproductive status. It is clear that females are heavier than males at any given age. Mean adult body weight is about 65 kg in females and 50 kg in males. The

Table 10. Records of harbour porpoise in the database, from 1838 to 1998 inclusive, according to source where specified. There are animals listed in the database for which the source is not known.

Year	Catches	Incidental Catches	Strandings
1838	1		
1847	13		
1941	116		
1942	135		
1943	290		
1944	175		
1950			1
1957	5		
1958	6		
1962		2	
1963		36	
1964		2	
1965		1	
1969		1	
1971			1
1978		1	
1980		148	
1981		4	
1982		1	
1985		3	5
1986	1	21	24
1987		22	30
1988		37	50
1989		19	14
1990		29	8
1991		52	63
1992		102	5
1993		39	1
1994		25	4
1995		3	1
1996		9	12
1997		55	27
1998		32	14
Total	742	644	259

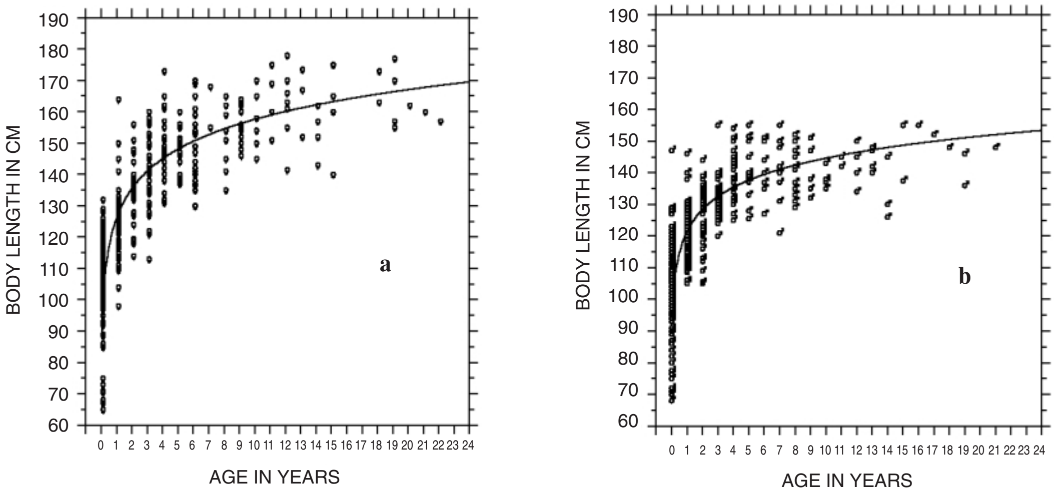


Fig. 5. Body length at age of porpoises from strandings and bycatches. a. females; b. males.

absolute maximum weight recorded for each sex was 89 kg for females and 79.5 kg for males (not shown in Fig. 6b). These are rather higher than hitherto recorded anywhere, but the database comprises some 537 female weights and 742 male weights, perhaps one of the largest databases in Europe for harbour porpoise. Kull and Berggren (MS 1995) reported a maximum weight of 77.1 kg for females and 53.2 kg for males in the Swedish Skagerrak and Kattegat.

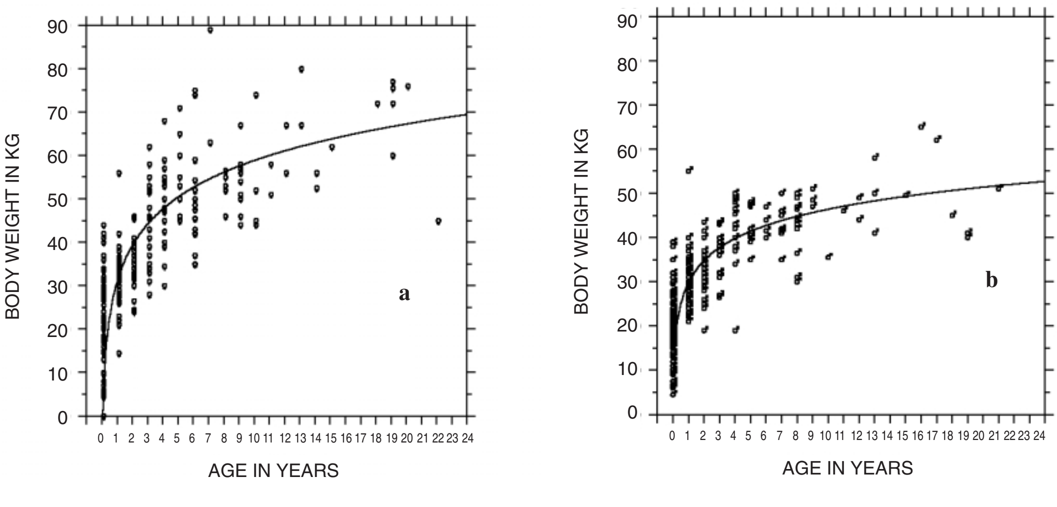
Body condition

Body condition here is equated with nutritional status, and indicators of body condition include overall body weight at length, relative blubber and muscle masses, body girth, blubber thickness relative to body size and lipid content of the blubber. The lattermost is not considered here at all and forms the subject of another investigation. However, the body weight relationships are investigated here, although blubber and muscle mass, girth and blubber thickness were only collected during 1996-98. These factors are considered later in this paper and are summarised in Table 9.

Weight at length

The body weight / total length relationship is similar for both sexes, and a least-squares logarithmic regression of weight on length (Zar

Fig. 6. Body weight at age of porpoises from strandings and bycatches. a. females; b. males.



1984) for both sexes combined is:

(1) $W = 0.000081 * L^{2.67}$

where W = body weight in kg, L = body length in cm. Standard error for the exponent is $\pm$ 0.03; R^2 (correlation coefficient) is 0.91.

Comparison with similar data for a much smaller sample (200) from the British Isles (Lockyer 1995c) indicates that this relationship of weight at length is virtually identical to the much larger Danish sample of 983 animals.

Reproduction

Data are available on gonad size and presence of *corpora* (*lutea* and *albicans*) in the ovaries, but the data set is very small relative to the accumulated number of records. This is because most information is available only from the period 1996-98. The general conclusions therefore, that can be made from these data are somewhat preliminary.

Male

Testes weights have been recorded, but no histological examination has been made for presence of sperm, spermatogonia or tubule diameter and character (open /closed).

Testes weight and sexual maturity

The testes weights for 135 males are recorded in the database. Fig. 7 shows the combined testes weights at body length. The testes start to increase in size from about 120 cm body length, and taking the combined weight criterion of 200 g as a guide to sexual maturation (Lockyer 1995b), one might consider most males as pubertal until 135 cm length when the majority of testes exceed 200 g.

In Fig. 8, the combined testes weights are plotted against age. Again, using the 200 g criterion, the switch from immature to mature appears to occur between 3 - 4 years. Both the implied average length and age at sexual maturation are comparable with data for harbour porpoises from elsewhere (Gaskin *et al.* 1984, Lockyer 1995b) and with previous estimates for Danish porpoises (Sørensen and Kinze MS 1990, 1994).

Female

Ovarian *corpora* (Perrin *et al.* 1984) were detected from the surface scar on the ovaries, cut open and measured for diameter and classified according to type when examined under a binocular microscope. The ovaries were in any case sliced in 1 mm thick sections.

Ovarian corpora and sexual maturity

The presence of at least one *corpus luteum/albicans* was used as a criterion for sexual maturity (Lockyer 1995b). Other criteria used for assessing maturity were evidence of pregnan-

Fig. 7. *Testes weight at body length in male porpoises*

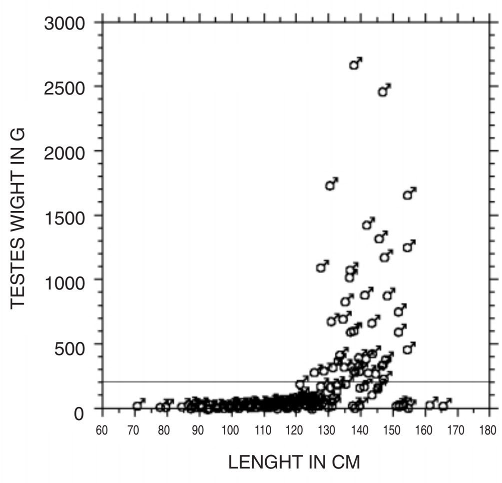
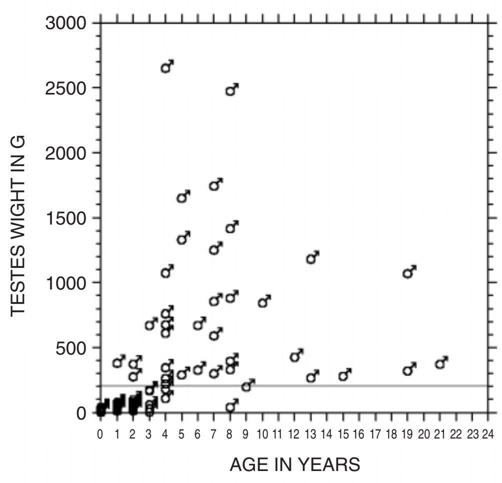


Fig. 8. *Testes weight at age in male porpoises*



cy and/or lactation. The youngest animal with a corpus was 3 years, and the oldest recorded was 19 years with 12 corpora. In a fitted least-squares linear regression (Zar 1984) of ovarian corpora number against age for just 25 animals, the following relationship is derived. Only females with 1 corpus or more were included in this calculation:

(2) Number of corpora = 0.61 * Age - 1.15

where the standard error for the age coefficient is ± 0.08, and for the constant is ± 0.71; R^2 is 0.71.

The line cuts the age axis at 3.5 years, a similar age at first ovulation as observed for Bay of Fundy porpoises (Read 1990a). A previous estimate of sexual maturation in females was given as 4 years (Sørensen and Kinze 1994). Read (1990a) observed an ovulation rate of 0.66 derived from *corpora* at age analysis, similar to results here. The implied ovulation interval is about every one and half years. In reality, because the data indicate a strong seasonality of reproduction (see below), females may either ovulate each year or every two years. Read (1990a) observed a decline in ovulatory activity in older females relative to those newly mature, in that multiple ovulations settled to a more regular apparently annual ovulation rate so that actual fecundity might not necessarily be affected by increased age. However, the data reported here do not really support an annual pregnancy, although the potential certainly exists. Based on the data here, a female with longevity to 20 years might expect to deliver a maximum of 11-12 calves in a lifetime. However, as we see from the age frequency distribution in Fig. 4a earlier, most do not survive that long, and a more reasonable estimate is about 10 - 12 years, in which case only 4 - 6 young per female are likely in a lifetime.

Sørensen and Kinze (1994) observed a peak ovarian follicular activity at the end of July and active *corpora lutea* during August for Danish porpoises. However, both these earlier findings (based on 59 females) and current results are considered preliminary, and can only be taken as a guide to fecundity. More data are needed for a concise estimate of reproductive parameters. The age at first reproduction corresponds to a length of about 143 cm (Fig. 5a).

Foetus

There are numerous records of foetuses in the database from early times and most include sex, length and weight as well as date.

<u>Foetal weight / length</u>

The weight at length of 124 foetuses of both sexes were investigated using logarithmic linear regression (Zar 1984). Data for males and females were similar but with relatively few animals of large size and weight compared to early foetuses. The relationship is described by the formula:

(3) $W = 0.050 * L^{2.72}$

where W = body weight in g, L = body length in cm. Standard error for the exponent is ± 0.06; R^2 is 0.94.

The predicted birth weight using this formula is 3.4 kg at a length of 60 cm. This is likely to be a minimum weight. The Danish data indicate a wide overlap of lengths for near-term foetuses and neonates from 60 - 89 cm, although the maximum was 80 cm apart from one individual of 89 cm described below. This single large foetus was recorded from a dead-stranded female on Funen during summer 1998. The foetus was 89 cm and weighed nearly 10 kg, while the 13 year old mother was 173.5 cm in length and weighed 80 kg. The reason for the death of the mother was diagnosed as birth difficulties because although the foetus still remained within the uterus, the uterus had ruptured with ensuing problems. It is considered that most neonates are within the size range 65 - 75 cm (weight 4.5 - 6.7 kg), based on Danish neonate records (the largest recorded foetuses of 80 cm would weigh about 8 kg using the above formula), and discussion presented by Lockyer (1995b). Animals of >80 cm and weighing about 8.5 kg may present difficulties to the mother, and the quoted size range of 70 - 85 cm (Møhl-Hansen 1954, and other authors – see Lockyer 2003a) seems to extend beyond the likely maximum size.

Sex ratio and relative size

Foetal sex ratio indicates that males consistently appear to outnumber females 1.1:1.0, and the larger number of males in the first year class (Fig. 4b) also supports a bias to males. However, the difference is not significant. The length frequency distribution of foetuses over a similar time span shows 2 peaks in the distribution. The primary one corresponds to a modal size of 25 - 30 cm in females and 30 - 35 cm in males; the second to a modal size of 60 - 65 cm in females and 65 - 70 cm in males, so that males appear to be slightly larger.

Breeding and birthing seasons

The reproductive season can be estimated from an analysis of seasonal development in testicular tissue, and also size analysis of foetuses by month.

Seasonal testes weight

Fig. 9 shows the seasonal hypertrophy of testes in the male harbour porpoise. All males are included, even immatures, because Desportes *et al.* (2003) showed seasonal hypertrophy in the testes of a sub-adult male porpoise taken from Inner Danish waters and held in human care. The peak is in August which also coincides with Desportes *et al.*'s observations. The maximum size of testes in mature males in season is 2.65 kg. This peak coincides well with the observations for British porpoises (Lockyer 1995b), and suggests that mating, and probably conception, may be especially likely at this time. Earlier results for Danish waters (Sørensen and Kinze 1994) observed a peak testicular development in July – August, but their sample size was only 60 males. These data are different to the Bay of Fundy male porpoises where Read (1990b) found a decline in testicular activity between June and September.

Foetal growth by month

A histogram plot of foetal lengths by month (Fig.10), where both sexes are combined, indicates a peak in size in June, and minimum size in September. This would indicate a likely gestation time of 10 months, and the size distribution fits with the onset of male fertility in August.

The timing of mating, conception and parturition may be a little protracted, so that births could occur in March through to August as observed for the Swedish Skagerrak and Kattegat (Kull and Berggren MS 1995). Sørensen and Kinze (1994) reported a parturition season of June – July in Danish waters. Evidence from stranded neonate frequency in the British Isles indicated that births peaked in June (Lockyer 1995b). Read (1990b) observed that peak births in Bay of Fundy occurred in mid-May and the smallest foetuses were undetectable until August. However, his analysis of ovarian activity indicated a likely conception in June in the Canadian porpoises, and suggested a pre-implantation period of pregnancy of up to 7 weeks. Delayed implantation is not generally considered a feature of cetacean reproduction, however, and has not been reported elsewhere for harbour porpoises.

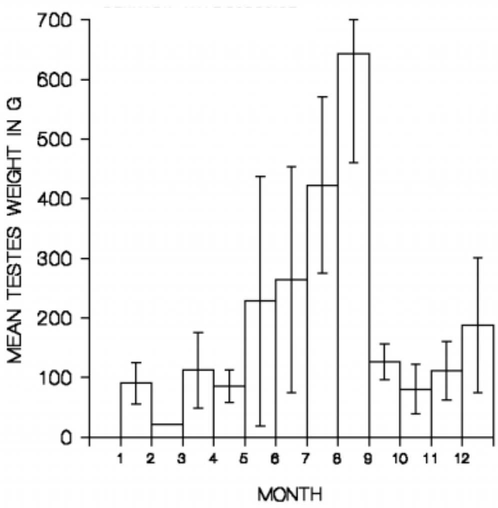


Fig. 9. *Mean monthly testes weights for male porpoises*

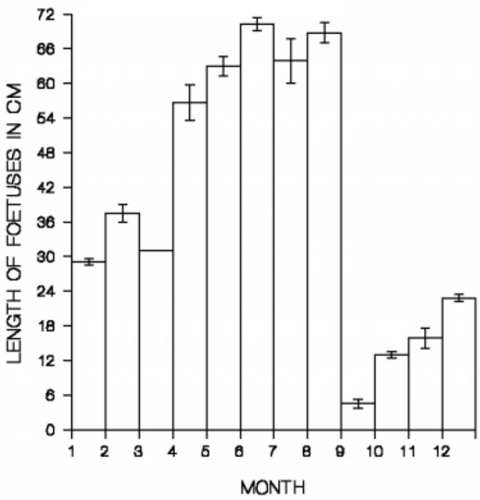


Fig. 10. *Mean monthly lengths of porpoise foetuses.*

GENERAL CONCLUSIONS

It is clear that harbour porpoises in Danish waters appear very similar in most characteristics to those around the British Isles. Size and body condition are similar to British porpoises. Longevity is recorded up to 23 years, and in both sexes, the first year suffers the highest mortality, but apparently more males die than females in the second year. Sexual maturity occurs at slightly over age 3 years in both females and males, as reported earlier by Sørensen and Kinze (1994). These ages correspond to lengths of about 135 cm in males and about 143 cm in females. Limited data suggest an average ovulation interval of about 1.5 years or a reproductive interval of alternately 1 or 2 years. A fertile female might expect to produce 5 young in a lifetime of 10 years. Conception most likely occurs during August, and peak births take place in June after about 10 months gestation. There may be a predominance of males in the foetal stage, and they appear to be slightly larger than females at any given time during gestation.

Selectivity on length and age by fisheries

As pointed out earlier, the number of males (1,043) exceeds that of females (799) in the database. This imbalance suggests several scenarios: a bias in sex selectivity by the fisheries, segregation of the sexes by geography or season, or a possible natural excess of males. The directed fisheries might have been expected to target the removal of more females because of their greater size (Table 9), but this does not seem to be the case in practice. The sex ratio in the directed takes is 1.5:1.0 (males:females). However, the predominance of males in the bycatches (ratio 1.2:1.0) indicates that this bias might be rooted either in behavioural differences between the sexes where the males are wider-ranging and may even feed in a different area/depth stratum than females, or that males are less receptive generally to hazards in their environment. A disproportionate ratio in the sexes usually indicates some kind of segregation, and might reflect the general hypothesis that males are more mobile and wider-ranging than females (Walton 1997). The strandings, in fact, have a ratio of 1.1:1.0 (males:females), which is similar to the sex ratio of foetuses.

Biases in age and length

A sub-set of the database is listed in Table 10, where the sources of the data are known *i.e.* directed catch, bycatch and strandings. There are many animals for which the source is not known. All data, presented as numbers by length and age according to source, month and sex, are in Table 11.

Catches

Directed takes of harbour porpoises are recorded in the database and date back to 1834 but come mainly from the 1940s, after which they cease – see Table 10. There are no age data to analyse except for a mere handful (see Tables 9 and 11), but sex and lengths are available. These length data are presented as frequency tables in Table 11 by sex. The distribution is heavily skewed to large adult animals with a mean length of about 151 cm in females and 141 cm in males (Table 9). This emphasises the clear preference for larger animals (maximum lengths of females are up to 189 cm, but only 167 cm in males) and is perplexing in light of the overall preponderence of males (Tables 9 and 11) as discussed above.

Strandings

There are fewest records for stranded animals, but for these there exist most basic biological data. Strandings records in the database were not officially recorded until 1950, and the majority come from the period 1985 – 1998 (Table 10), when considerable interest in bycatches prompted collection of records. It is possible that strandings before this time were seen as providential and if fresh would probably have been consumed locally. The length frequencies are presented in Table 11, where it is clear that the size range is much wider than for catches, with many smaller and younger animals. The maximum size is also considerably smaller. Table 9 gives mean lengths of about 128 cm for females and 120 cm for males, both sizes that are representative of juvenile animals. Age frequencies are shown in Table 11, and emphasise again the preponderence of males, especially in the first year class and subsequent high mortality. Table 9 gives a mean age of about 5 years in females and 4 years in males.

Incidental takes / bycatches

The bycatch data records form the largest segment of the database. Records of bycatches of harbour porpoises date from 1962 until the present (Table 10), and the fluctuation in recordings may be more a reflection of current enthusiasm rather than any real environmental trend. However, bycatch records commenced after directed catches ceased with the latter ending in the late 1950s and bycatches becoming more visible from the early 1960s. The length frequencies, shown in Table 11, have a slightly higher mean (132 cm in females, 124 cm in males - Table 9), but are barely significantly different from strandings. However, the distributions are much less spread out than strandings, and very small and large animals are less represented in the bycatches. The age frequencies in Table 11 are very similar to those for strandings, but mean ages are about 3 years in females and 2.5 years in males (Table 9).

BY-CARE data, 1996 - 98
The data collected from 1996 - 98 have also been examined separately as strandings and bycatches, but the general results are similar to those for all years combined. Table 9 provides the mean lengths and ages, but the datasets are very small by comparison to the others discussed above. On initial inspection, the mean lengths of strandings are definitely smaller in the most recent years, despite a small sample size. The reason for this is unclear but may reflect the current and very recent focus on retrieving all beach-cast harbour porpoises. This would enhance the recovery of many small neonates that might previously have been overlooked. However, neither the mean lengths for bycatches, nor ages for both bycatches and strandings appear to be significantly different to those from the larger corresponding datasets.

Assessment of body condition status
Since the beginning of 1996, organ and tissue weights have been recorded as well as girth and blubber thickness measurements, according to the criteria in Lockyer (1995c). Only total body weights are available for earlier years. Table 10 provides mean values for body weights for all subsets, and blubber and muscle weights, girth and blubber thickness for all recent subsets. In general, as anticipated, bycaught animals are heavier, have more blubber, muscle, and are bigger in girth than stranded animals. The blubber thickness is similar in both stranded and bycaught specimens, even though it is well known that smaller juveniles have thicker blubber than older larger animals (Lockyer 1995c, Read 1990c). Therefore, blubber thickness is not necessarily a useful characteristic for detecting trends in nutritional status and body condition in populations unless the sample size is large enough to permit grouping of data by body length, reproductive status, and season – all of which can have significant effects on blubber thickness (see Lockyer 1995c, Lockyer *et al.* 2003). Focusing only on the bycaught animals from Table 10, Read (1990c) found generally similar indicators of body condition in similarly-sized bycaught Bay of Fundy porpoises of 108–134 cm length: average blubber weights of 11.6 - 13.2 kg , blubber thickness of 19.0 - 24.4 mm, and mid-girth of 76.8 - 87.2 cm.

Segregation of animals
The argument for possible segregation of animals by sex has been raised above, and it is important to note that Tables 9 and 11 indicate that in all subsets, males predominate. This suggests that geographical segregation may be the more likely cause than active selectivity by fisheries (directed or incidental) because strandings also reflect this bias. It is also possible that males may naturally be in slight excess, although the 1.1:1 ratio at birth is not as pronounced as the overall 1.3:1 ratio observed in the post-natal database, unless females have a higher mortality after maturity. However, longevity appears similar in both sexes (Fig. 4).

In Fig. 11, length data have been analysed by ICES areas (Fig. 1). Unfortunately the sample sizes so derived are small, and both sexes have been combined. The data show a low mean length in area IIIb (Sound) relative to adjacent areas, and in particular to the North Sea (IVb). Areas IIIc (Belt Seas and southern Inner Danish waters) and the few data from IIId (western Baltic, Bornholm) also appear smaller than IVb and IIIa (Skagerrak and Kattegat). It is tempting to imagine that IIIb and IIIc may offer nursery areas to harbour porpoise because of the smaller animals observed here. Certainly porpoises do breed around these areas (Inner Danish waters and the Sound) as indicated by the neonates recovered during the summer months. Sightings also indicate mothers and calves in these areas (Hammond *et al.* 1995, and see earlier discussion in this report).

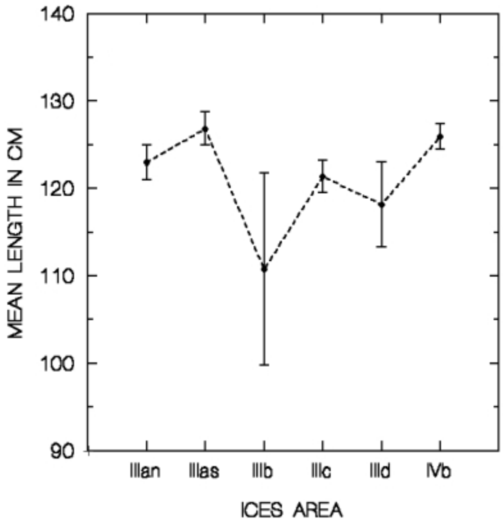


Fig. 11. *Mean lengths ± S.E. of porpoises by ICES area for all years. Sample sizes are IIIan:112, IIIas:100, IIIb:10, IIIc:224, IIId:6, and IVb:238*

Biases in abundance by month

Catches

The frequencies of females and males in the catches by month are shown in Table 11. The distributions are highly seasonal and focus on the winter months (November to February) almost exclusively. This is because of the now historic winter migration of harbour porpoise through this area and the associated drive fisheries for porpoises (Andersen MS 1972, Kinze 1995).

Strandings

The frequencies of stranded females and males by month are shown in Table 11. Unlike the catch records, the peak numbers are in the summer and autumn months with highest numbers in July and August. This coincides with the period identified as the likely breeding and parturition season, when females move to coastal areas, and also may be the time that the young of the year are becoming most numerous but also vulnerable to hazards in the waters close to shore with the attendant natural mortality of neonates and young calves. It is also possible that reporting in general may increase in this season because of the presence of more people on the beaches, but we have no evidence for this. Certainly reports peak in August and are absent between February and April.

Incidental takes / bycatches

The monthly frequencies of incidental catches of females and males are shown Table 11. The distribution here is unlike both that for catches and strandings, and shows that there are bycatches throughout the year. Bycatch numbers are lower in the first half of the year, but the highest numbers are late in the year with a peak in September. The lowest numbers are in December through February. This partly reflects the fishery and bycatch analyses for the Danish North Sea over a 6-year period (1992 - 98) by Vinther (1999), where highest numbers of bycatches were observed in the cod and turbot bottom-set gillnets in the third quarter of the year, although bycatch rates per km of netting were highest both in the first and third quarters of the year. This seasonal bycatch pattern is thus influenced both by porpoise presence and fishery activity.

Biases in porpoise size by month

Body size has been analysed by weight, which has been recorded for 917 males and 696 females. The datasets are therefore large, and can tolerate subdivision by month and according to origin (Table 11).

Catches

Mean monthly records of body weight ± S.E. are shown by sex in Table 11. The data obviously reflect the monthly catching activity, but the mean sizes are adult sizes of 41 - 59 kg.

Strandings

Similar data are shown for strandings in Table 11. Here the lowest mean body weights of 15 - 18 kg are seen in June and July, although mean body weight in other months is generally in the range 20 - 48 kg and much lower than for catches. The largest animals are in May (females) and in the winter (males). However, most means are not significantly different from each other. The small body size in June / July probably reflects the increase in number of neonates and calves at this time.

Incidental takes / bycatches

The data for bycatches show a more even distribution of body size throughout all months (Table 11). Any pattern of size variation is less easy to detect and most monthly means are not significantly different from each other. The

Table 11. Age and length distributions by sex, and frequencies and mean body weights by month and sex, by source of data.

CATCHES								BY-CATCHES								STRANDINGS							
Age		Length		Month		Body weight		Age		Length		Month		Body weight		Age		Length		Month		Body weight	
(yr)	*n*	cm	*n*		*n*	Month	Mean±S.E.	(yr)	*n*	cm	*n*		*n*	Month	Mean±S.E.	(yr)	*n*	cm	*n*		*n*	Month	Mean±S.E.
Females																							
0	1	65		January	125	January	54.05±1.38	0	62	65		January	8	January	45.33±11.29	0	19	65	4	January	2	January	57.00
1	2	70		February	47	February	58.43±2.09	1	47	70		February	2	February	60.00	1	8	70	5	February	2	February	
2		75		March		March		2	29	75		March	20	March	46.61±4.38	2	4	75	2	March	1	March	
3		80		April	7	April		3	23	80		April	21	April	34.36±3.07	3	9	80		April	3	April	41.88±12.93
4	2	85		May		May		4	17	85		May	30	May	43.18±3.82	4	5	85	6	May	9	May	48.33±15.84
5		90		June	3	June	15.00	5	9	90	3	June	29	June	36.94±3.78	5	5	90	1	June	10	June	25.40±10.87
6	1	95		July		July		6	14	95	5	July	19	July	38.22±3.33	6	4	95	1	July	40	July	16.33±5.75
7	1	100		August		August		7	1	100	12	August	8	August	34.09±6.25	7		100	6	August	17	August	23.56±6.87
8		105	2	September		September		8	5	105	9	September	50	September	37.22±1.88	8	3	105	5	September	8	September	20.00±11.00
9		110	1	October		October		9	6	110	21	October	34	October	36.02±1.84	9	6	110	4	October	17	October	27.00±11.42
10		115	5	November	14	November	43.93±3.69	10	4	115	27	November	44	November	35.54±1.97	10	2	115	5	November	.	November	
11		120	8	December	101	December	54.34±1.55	11	3	120	29	December	10	December	34.43±4.10	11	2	120	4	December	2	December	35.00
12		125	12					12	4	125	25					12	3	125	8				
13		130	7					13	2	130	26					13	2	130	6				
14		135	19					14	3	135	20					14	1	135	11				
15		140	11					15	1	140	22					15	3	140	5				
16		145	11					16		145	22					16		145	9				
17		150	24					17		150	16					17		150	11				
18		155	23					18	1	155	18					18	1	155	6				
19	2	160	36					19	2	160	14					19		160	6				
20	1	165	26					20		165	3					20		165	5				
21		170	13					21		170	5					21	1	170	1				
22		175	2					22		175						22	1	175	3				
23		180	1					23		180						23		180					
24		185	1					24		185						24		185					
		190								190								190					

CATCHES								BY-CATCHES								STRANDINGS							
Age		Length		Month		Body weight		Age		Length		Month		Body weight		Age		Length		Month		Body weight	
(yr)	*n*	cm	*n*		*n*	Month	Mean±S.E.	(yr)	*n*	cm	*n*		*n*	Month	Mean±S.E.	(yr)	*n*	cm	*n*		*n*	Month	Mean±S.E.
Males																							
0		65		January	164	January	46.97±0.81	0	84	65		January	6	January	28.67 ±3.76	0	28	65	1	January	8	January	30.75±4.62
1	1	70		February	40	February	41.78±1.47	1	50	70		February	7	February	34.00	1	10	70	3	February		February	
2	1	75		March		March		2	32	75	1	March	22	March	34.82±2.38	2	3	75	4	March	3	March	41.00
3		80		April	6	April		3	19	80	1	April	33	April	34.26±1.80	3	4	80	3	April	6	April	27.50±4.50
4		85		May		May		4	20	85	2	May	15	May	29.25±2.91	4	8	85	5	May	6	May	31.00
5		90		June		June		5	10	90	6	June	29	June	27.40±2.41	5	5	90	2	June	12	June	15.26±4.56
6		95		July		July		6	4	95	6	July	24	July	30.92±2.23	6	3	95	7	July	30	July	17.50±9.21
7		100		August		August		7	5	100	12	August	18	August	33.99±3.15	7	6	100	5	August	24	August	26.75±5.67
8		105	2	September		September		8	11	105	27	September	66	September	31.81±1.41	8	4	105	8	September	13	September	22.63±7.38
9		110	5	October		October		9	3	110	34	October	46	October	29.89±1.24	9	2	110	13	October	18	October	22.90±6.57
10		115	11	November	19	November	47.68±2.54	10	3	115	37	November	56	November	30.32±1.25	10	2	115	5	November	5	November	33.25±2.96
11		120	16	December	218	December	49.58±0.82	11		120	48	December	13	December	35.30±3.15	11	2	120	12	December	3	December	
12		125	25					12	2	125	42					12	2	125	9				
13		130	24					13	2	130	26					13	2	130	10				
14		135	27					14		135	37					14	3	135	13				
15		140	39					15	1	140	25					15	1	140	9				
16	1	145	51					16		145	14					16		145	9				
17	1	150	38					17		150	12					17		150	8				
18		155	21					18		155	3			1		8		155	3				
19		160	17					19	1	160	1			1		9	1	160					
20		165	1			2		0		165						20		165					
21		170						21	1	170						21		170					
22		175						22		175						22		175					
23		180						23		180						23		180					
24		185						24		185						24		185					
		190								190								190					

ranges of mean body size is 34 - 47 kg in females and 27 - 35 kg in males, and are therefore larger than for the strandings (see also Table 9). In females, smallest size is noted in April, August and December, and largest size in January through March, and in May. The tendency to larger females in the early part of the year may reflect the intrusion onto the fishing grounds of adult females that gave birth the previous summer. However, this is mainly speculative, but might reinforce the question of possible segregation. The males offer a slightly different picture with body size remaining between 29 - 35 kg in all months except for a dip in June – the month of peak births (see discussion above).

CONCLUSION

There are clearly many factors which can introduce bias into some analyses of the database records. For obvious reasons, estimates of natural mortality have not been attempted. The records from the historical catches were clearly biased to only adult animals, especially males, and also limited in season. The strandings emphasise the neonate, calf and juvenile component of the population(s) and bycatches probably emphasise the male segment and sub-adult animals. The fisheries areas of operations have been examined by Vinther (1999). However, the observer effort in recording bycatches during BY-CARE has predominantly focused on the North Sea, while historical records also come from Inner Danish waters. In general, it appears that bycatches recover animals of broadly similar size and exclude neonates and very young (pre-weaned) calves. However, the male predominance exists here in the ratio 1.2:1.0. Whilst the strandings indicate a consistent ratio with that at birth, the slight increase in the bycatch sex ratio might indicate that males are more at risk than females. This may result from the interaction between seasonal segregation of the sexes and also area of fishing operation.

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