OPHELIA **55** (3):

REVIEW

CURRENT KNOWLEDGE ON HARBOUR PORPOISES (*PHOCOENA PHOCOENA*) IN THE BALTIC SEA

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ABSTRACT

Concern has been raised about the long-term viability of the harbour porpoise population in the Baltic Sea. By-catch at possibly unsustainable levels, contaminants, overfishing of prey species and disturbance have been identified as possible threats. This literature study summarises the current knowledge about harbour porpoises in the Baltic Sea and, on the basis of reviewed material, tries to identify critical remaining uncertainties and suggests management needs. Information on porpoise demography like distribution, abundance, migration, population structure, and factors affecting survival are presented.

The historic range of the harbour porpoise extended into the north-eastern parts of the Baltic Sea. During the second half of the 20th century, numbers of harbour porpoises have declined and the distribution range narrowed. Currently there is a considerable difference in abundance in the Kattegat and Belt Sea (0.73 - 0.99 animals km^{-2}) as opposed to the Baltic Proper (<0.01 animals km^{-2}).

Although recent morphometric, genetic and contamination studies of harbour porpoises in the Baltic Sea are somewhat inconsistent with respect to population structure, the existence of a distinct Baltic subpopulation appears to be a valid concept. Migrational patterns of Baltic Sea animals are still ambiguous. In historic times large numbers of harbour porpoises were hunted in the Danish straits during winter and spring. Therefore it was often concluded that porpoises escaped from ice cover in the eastern Baltic Sea in the winter and re-colonised the Baltic Proper in spring. Recent observations indicate that migration behaviour is much more complex and diffuse. There seems to be a tendency of animals from the Kattegat to migrate into the North Sea during winter. But also animals remaining in the western Baltic or Baltic Proper have been described.

Available nutritional studies suggest that harbour porpoises take a variety of different prey. Herring, sprat and cod are their most important prey items. Sexual maturity is attained at an age of 3 - 4 years. A larger proportion of females give birth to one calf every year (pregnancy rates were reported between 0.61 and 0.84). The average life span of harbour porpoises in the Baltic Sea is unknown. From existing data, a maximum age of 22 to 23 years seems to be a realistic assumption. However, a high mortality in the first years of age and a proportion of less than 5% of the animals living beyond 12 years have a significant impact on the potential for increase of the stocks. It is assumed that shallow areas play an important role for this species with respect to calving and nursing.

A variety of studies report heavy attacks from parasites such as *Anisakis simplex*, *Tonyurus convolutus*, *Stenurus minor*, *Halocercus invaginatus* or *Pseudalisus inflexus*. However, when compared to samples from Greenland these can be regarded as normal infestations.

Environmental contaminants most likely affect the long-term viability of Baltic Sea harbour porpoise stocks and might have been a major cause for the decline of Baltic Sea harbour porpoise stocks between the 1940s and the 1970s. Since then concentrations of PCBs and other organochlorine contaminants have declined. To date, the most important threat to Baltic Sea harbour porpoises is by-catch. Noise pollution has the potential to increasingly become a major threat due to the development of new activities in the Baltic Sea (offshore-windpower plants, fast ferries, etc.). This study lists a number of life history variables for which data is urgently needed. On the basis of the currently available knowledge, an effective management strategy must include political and technical means of mitigating threatening activities such as by-catch, disturbance to critical habitat, disposal of contaminants and over-fishing. In this respect it is important to establish marine protected areas and time- and area closures for certain fisheries which are likely to be unsustainable, to establish mandatory fishery observer programmes and to compile appropriate fisheries statistics.

Key words: harbour porpoise, Baltic Sea, distribution, abundance, by-catch, pollution, population structure, migration, reproduction, diet, habitat utilisation

INTRODUCTION

Growing concern has been raised about the status and the long-term viability of harbour porpoise (*Phocoena phocoena*) stocks in certain areas of their distributional range (Perrin *et al.* 1994). In many areas by-catch in the coastal set-net fishery occurs at presumably unsustainable levels. For the Baltic Sea information on by-catch and population size is sparse. Besides by-catch, other factors are discussed as threats to Baltic Sea harbour porpoises. Among these are environmental contaminants, depletion of fish stocks, disturbance by noise and boat traffic (Hammond *et al.* 1995).

For a comprehensive assessment of the status of harbour porpoises in the Baltic Sea knowledge on porpoise demography is necessary. This includes adequate information on (1) the distribution of porpoises, (2) their seasonal movements, (3) abundance, (4) population structure, (5) several life-history parameters and (6) factors affecting survival such as: by-catch, effects of pollutants on health and reproduction, habitat degradation, availability of food and possible effects of disturbance (traffic, exploration, military operations etc.) Although data for some of these factors have been collected for the Baltic Sea there is still a lack of information on the others. The *Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas* (ASCOBANS) recommends research on these issues in the Northeast Atlantic and the Baltic Sea (ASCOBANS 1994).

The purpose of this literature study is (1) to summarise the current knowledge about harbour porpoises in the Baltic Sea, (2) to identify the critical remaining uncertainties involved in assessing their status, (3) to suggest the types of studies required to resolve these uncertainties and (4) to conduct a preliminary assessment of the management needs on the basis of reviewed material. According to the definition of HELCOM (1992) the "Baltic Sea area" includes the internal Baltic waters and the entrance to the Baltic Sea bounded by the parallel at 57°44.43′N between the Kattegat and the Skagerrak. This definition is only arbitrary for this study since authors of reviewed papers might have used different definitions.

SOURCES OF INFORMATION

The main sources for this study were the existing peer reviewed and published literature. For some regions and for some questions no published information was available. In order to obtain additional information some unpublished papers (internal reports of ICES, IWC, ASCOBANS, reports to the European Commission, the German Federal Ministry for Education and Research (BMBF) and, exceptionally, conference reports of the ECS) were included where appropriate. To supplement the review, active researchers around the Baltic Sea were approached for recent, to date unpublished information.

DISTRIBUTION AND ABUNDANCE

Historic distribution (middle age to early 20th century).- Although there is ample anecdotal information regarding the historic and recent occurrence of harbour porpoises in different areas of the Baltic Sea, data do not allow precise abundance estimates. Nevertheless, from available sighting, stranding and by-catch data and from information on substantial numbers taken in several hunting localities in historical times it seems clear that the former range of the harbour porpoise extended into the easternmost and northernmost parts of the Baltic Sea.

In medieval times, harbour porpoises appeared to be quite numerous in different places along the Baltic coast. A catch existed for example in Middelfart (Little Belt), in Bramsnæsvig (Isefjord/Sjælland), different places around the Scanian peninsula, and even as far east as Hel (Gdansk Bay/Poland) (Kinze 1995; Otterlind 1976; Ropelewski 1957). Catches would not have been successful unless harbour porpoises were sufficiently abundant in these areas.

In the late nineteenth and early twentieth century the harbour porpoise was still believed to be common in the Baltic Sea, its distribution ranging from the Kattegat into the eastern part of the Baltic Proper (cf. Tomilin 1957). Greve (1909) noted that harbour porpoises inhabited the waters of Estonia and Latvia (sometimes even in the river Daugava near Riga) in summer and autumn. Levander (1905) reports sightings from the northern Gulf of Bothnia. Tomilin (1957) states that some solitary roaming individuals reached the eastern Gulf of Finland and penetrated into the river Neva as far as Lake Ladoga on occasions. Some authors assumed that the animals in the easternmost and northernmost regions were only vagrant (e.g. Tomilin 1957). From the existing notes it cannot be determined whether harbour porpoises were regular or rare visitors to the far eastern reaches of the Baltic Sea.

An indicator for residence in a certain area could be the occurrence of reproducing animals. Information on this is scarce, but there is a reference to reproducing animals from places as far east as Baltijsk (Pillau) at Gdansk Bay where Braun (1906) investigated five pregnant females by-caught in the local salmon fishery between March 1 and May 5, 1905. From this and from the fact that between 1922 and 1933 more than 700 harbour porpoises were caught in gillnets under a bounty scheme in that area (Skóra *et al.* 1988) and that porpoise liver oil was traditionally used for medical purposes along the Polish coast (Ropelewski 1957), it can be concluded that in the early days of the last century the species must have been fairly common in Polish waters. Further west along the coast of Mecklenburg-Prepomerania (Germany) harbour porpoises occurred on a regular basis each summer during the last 200 years or so, but probably were never numerous (Schulze 1991).

Most information on historical abundance in the western parts of the Baltic Sea are from catch statistics of Danish drive catches. Large numbers of harbour porpoises were reported performing seasonal movements at catch sites. Furthermore, mass deaths of harbour porpoises were reported in icy winters in the Baltic Proper, for example, in the cold winter of 1928/29 about 40 km east of Bornholm (Johansen 1929). This indicates that at least during particular periods of the year harbour porpoise abundance was very high in these places.

Recent distribution.- Many studies and even a crude examination of sighting and stranding data support the generally held view that numbers of harbour porpoises in the Baltic Sea have declined and that the distribution range has narrowed (Fig. 1). Certainly, stranding data are difficult to interpret since most strandings are of dead animals of unknown origin. Also sighting data must be treated with caution since the frequency of sightings is more certainly a function of effort. But at least, sighting data can serve as a source of information on recent distribution even though it does not provide us with sufficient information on abundance.

Also catch statistics are difficult to interpret since they might reflect changes in market demands of porpoise products like lamp oil rather than population trends. According to Kinze (1995) "fluctuations have occurred in the Danish catch [...], but a consistently increased take only occurred in the last half of the 19th century when the catch level doubled in the Little Belt area and may have led to an overexploitation and initiated the decline of the population". During the final phase of the catch the hunting season even had to be prolonged due to probably declining stocks (Kinze 1995). Mean annual catch numbers at Gamborg Fjord increased from 838 in the period between 1819 and 1845 (25 seasons for which data are available) to 1195 between 1871 and 1892 (20 seasons) and dropped to 533 during the First Word War (3 seasons) and to 327 during the Second World War (3 seasons).

Harbour porpoises still appear to be quite numerous only in the Kattegat and Belt Seas within the area covered by this review (cf. Hammond *et al.* 1995). Aerial surveys of the Great Belt, Little Belt and Kiel Bight (Heide-Jørgensen *et al.* 1993) as well as the analysis of incidental sightings (e. g., Benke *et al.* 1998) reveal a decline in density from the Danish islands towards the coast of Schleswig-Holstein (Germany). Furthermore, there is a sharp decline in porpoise sightings along the Swedish coast, from the Kattegat into the Baltic Proper (Berggren & Arrhenius 1995b).

Harbour porpoises are still considered regular visitors to the waters off Mecklenburg-Prepomerania in summer, where females are assumed to give birth in the shallow waters of coastal lagoons (Schulze 1991). Sightings and by-catches as well as numbers of stranded calves have apparently increased over the past 10 years in that area and are now in the order of 17 per year with gradually more reports from the western part of the area (Wismar Bay, Darß, Zingst, and the island of Hiddensee) (G. Schulze, pers. comm.). Due to prevailing westerly winds it remains unclear, however, whether stranded carcasses derive from porpoises inhabiting these waters. Since some of the specimens found were highly decomposed, Schulze (1991) assumes that a certain percentage of these died in Danish waters.

In the central Baltic Sea, harbour porpoises seem to have become rare visitors. Lindroth (1962) was able to collect 50 carcasses from that area with the help of salmon fishermen in 1961 (indicating that porpoises were still inhabiting the area) whereas the result of Otterlind (1976) in a similar salvage program

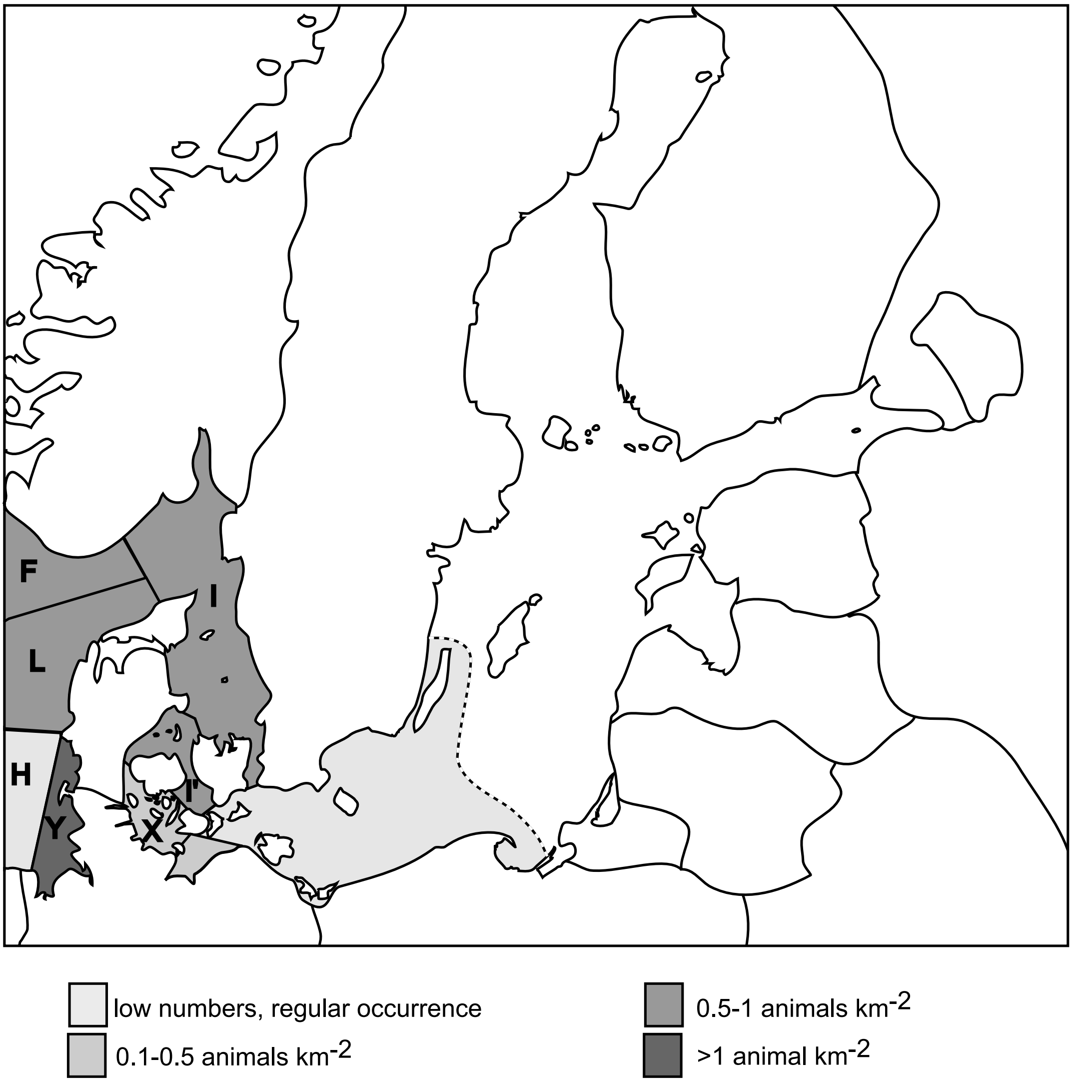

Fig. 1. Current assumed distribution and abundance of harbour porpoises in the Baltic Sea. Letters refer to SCANS areas (Hammond et al., 1995). Densities obtained from SCANS census were Y= 1.02; H=0.095; L=0.83; F=0.778; I=0.725; I'=0.987 and X=0.15 animals km^{-2}. The dotted line shows the possible current eastern limit of harbour porpoise distribution.

was 8 porpoises in 7 years. Sightings of harbour porpoises in the eastern Baltic Sea also have become rare. Over the past decades, the distributional limits of harbour porpoises gradually moved west and southward. For the presumed eastern border of the distributional range, a few reports are available on strandings, by-catch and live encounters of harbour porpoises (e. g., Skóra *et al.* 1988; Skóra 1991a). Today, harbour porpoises are very rarely encountered in Polish waters at any time of the year. Furthermore they are unknown to most coastal inhabitants. Only ten reports of harbour porpoises were listed by Skóra (1991a) between 1979 and 1990, most of them by-caught animals, and all from Puck Bay in the western part of Gdansk Bay. Barely 3 animals a year were sighted in the 1980s (Skóra 1991b). Currently still 4-6 annual by-catches occur year-round, whereas live encounters are very rare (Skóra, pers. comm.; IWC 1996). This suggests that harbour porpoises are still present in Polish waters during most parts of the year, but that their abundance is very low compared to the early 20th century. The same is true for the Swedish south and east coasts up to Gotland where harbour porpoises are still present, but where extremely low numbers are encountered (Berggren & Arrhenius 1995a,b).

The latest record from Lithuania dates back to 1938 (Timm *et al.* 1998). In Latvia harbour porpoises were reported in 1964 and 1974 as by-catch in gillnets in the Gulf of Riga (Taurins 1982; Pilats 1994). In Estonia the last record stems from 1961 (Timm *et al.* 1998). In the Finnish coastal areas no sightings have been reported in recent years. Määttänen (1990) showed that porpoise records in Finland have declined drastically between the 1930s (n=142) and the 1970s (n= 10) and essentially ceased in the 1980s (n=2). The last sightings date back to 1990 and 1991, when in total about a dozen porpoises were seen near the city of Kotka in the Gulf of Finland (Mattsson, pers. comm.). This implies the current eastern limit of regular occurrence of Baltic Sea harbour porpoises lies somewhere around Gdansk Bay and the northern limit close to Gotland (IWC 1996).

Current abundance.- There are considerable differences in harbour porpoise abundance between different areas of the Baltic Sea with comparably high numbers in the Kattegat and part of the Belt Sea and lowest numbers in the eastern reaches of the distributional range. First attempts to conduct a systematic survey of harbour porpoises in part of the Baltic Sea area were undertaken in the early 1990's: In 1992 Heide-Jørgensen and co-workers conducted aerial surveys in the southern Kattegat (around the island of Samsø), in the Great Belt, Little Belt and in Kiel Bight as well as in the North Sea off the island of Sylt (Heide-Jørgensen *et al.* 1993) - following a similar study in 1991 to evaluate their methodology (Heide-Jørgensen *et al.* 1992). They obtained relatively high densities in the North Sea study area (0.286 animals km^{-2}) and in the Great Belt (0.248 animals km^{-2}), low densities in Kiel Bight (0.021 animals km^{-2}) and intermediate densities in the southern Kattegat (0.12 animals km^{-2}) and the Little Belt (0.088 animals km^{-2}). Berggren & Arrhenius (1995a) found low densities in their summer 1991 survey in the eastern Kattegat (0.021 animals km^{-2}) as opposed to the findings of Heide-Jørgensen *et al.* (1993) in the southern Kattegat (0.142 animals km^{-2}). However, since these authors used different methodologies, their results are not directly comparable. Furthermore, these studies were able to detect relative abundances rather than absolute numbers since the study design did not take into account that porpoise schools might be missed on the transect line during their deep dives. Therefore, these studies can only be regarded as important pioneer work for a later survey, which was conducted during the summer of 1994.

The SCANS project (*Small Cetacean Abundance in the North Sea and Adjacent Waters*) was the largest harbour porpoise aerial and shipboard survey in the area covered by this review (Hammond *et al.* 1995). In tandem surveys (using two aeroplanes or two observer platforms on research vessels), for each group of porpoises the authors attempted to identify the probability that it would have been detected on the transect line. Thus, abundance calculations were corrected for porpoise groups which were missed because they passed the transect line during deep dives or responded to the research vessel. The area covered by SCANS in the Baltic Sea however, is only a small proportion of what is thought to be the range of harbour porpoises in these waters. Surveys were only conducted in the Kattegat and Belt Seas as well as in Kiel Bight where enough sightings were expected for a thorough statistical analysis. The SCANS survey found highest densities of harbour porpoises in the Kattegat (SCANS area I: 0.73 animals km^{-2}) and in the Great Belt and southern Kattegat (SCANS area I': 0.99 animals km^{-2}) and lowest densities in Kiel Bight (SCANS area X: 0.15 animals km^{-2}; cf. Table 1 and Fig. 1). This is consistent with Kinze (1990) who, from a sighting scheme and dedicated shipboard surveys suggested highest densities in the Great Belt and southern Kattegat (for methodological reasons no abundance data were provided).

Since the Baltic Proper was excluded by SCANS and the survey of the Mecklenburg Bight did not receive enough effort and was therefore postponed, two follow-up surveys were conducted (BMBF 1997). They obtained low densities of harbour porpoises in the autumn of 1995 and 1996 (0.1 animals km^{-2}) in an area bordered by the German coastline and the Danish islands of Als, Ærø, Langeland, Lolland and Falster.

POPULATION STRUCTURE

Recent studies on harbour porpoise population structure in the Baltic Sea are inconsistent:

Table 1. Results from aerial and shipboard surveys of harbour porpoises in the Baltic Sea.

area	time	size of area [km^2]	surveyed by	groups sighted	abundance (95 % CI)	density [animals * km^{-2}]	Reference
Kattegat (Block I)	summer 1994	49,485	ship	248	36,046	0.73	Hammond et al. (1995)
Great Belt and southern Kattegat (Block I')	summer 1994	8,170	aircraft	155	8,060	0.99	Hammond et al. (1995)
Kiel Bight (Block X)	summer 1994	5,810	aircraft	6	870	0.15	Hammond et al. (1995)
Kiel and Mecklenburg Bight	autumn 1995		aircraft	9	910 (360-2,520)	< 0.1	BMBF (1997)
Kiel and Mecklenburg Bight	autumn 1996		aircraft	15	1,830 (960-3,840)	0.1	BMBF (1997)
Around the island of Rügen	autumn 1995		aircraft		522 (233-2,684)	< 0.1	BMBF (1997)
Around the island of Rügen	autumn 1996		aircraft	0	not calculated	not calculated	BMBF (1997)

Although the existence of a Baltic subpopulation is a conceivable concept, with a number of studies showing differences between Baltic Sea and North Sea animals, a direct comparison of these studies is impossible because sampling areas and methods differ notably. The limits of a putative Baltic subpopulation and the amount of genetic exchange between regions have yet to be resolved. Migrational patterns are also still ambiguous.

Gaskin (1984) proposed three populations of harbour porpoises worldwide, based on differences in skull morphology and meristic characters as well as geographical isolation. According to his study, Baltic Sea animals form a sub-unit of the North Atlantic population. This view is supported by genetic analyses on an inter-oceanic scale (Rosel *et al.* 1995, 1999). However, for a thorough analysis of the species' status in certain areas of its distributional range it is inevitable to assess levels of intra-populational variation in order to accurately define management units below this large-scale approach. In the past two decades, research has been focused on the question whether there is a separate Baltic Sea subpopulation. Different attempts with a variety of methods have been made to answer this question.

Unfortunately, the conclusions from several different studies are contradictory. Thus, the population structure of harbour porpoises in the Baltic and North Sea remains poorly understood. In the present review, I will focus on the results of studies on non-metrical skull characters (Kinze 1985a, 1990; Huggenberger *et al.* in prep.), skull measurements (Kinze 1985a, 1990; Børjesson & Berggren 1997; Huggenberger *et al.* in prep.), tooth ultrastructure (Lockyer 1999), mitochondrial DNA (Andersen *et al.* 1995, 1997; Tiedemann *et al.* 1996; Wang & Berggren 1997), isozyme analysis (Andersen 1993; Andersen *et al.* 1997) as well as contaminant profiles (Bruhn 1997; Bruhn *et al.* 1999; Berggren *et al.* 1999a).

Yurick & Gaskin (1987) defined the term "population" as a large-scale unit assuming

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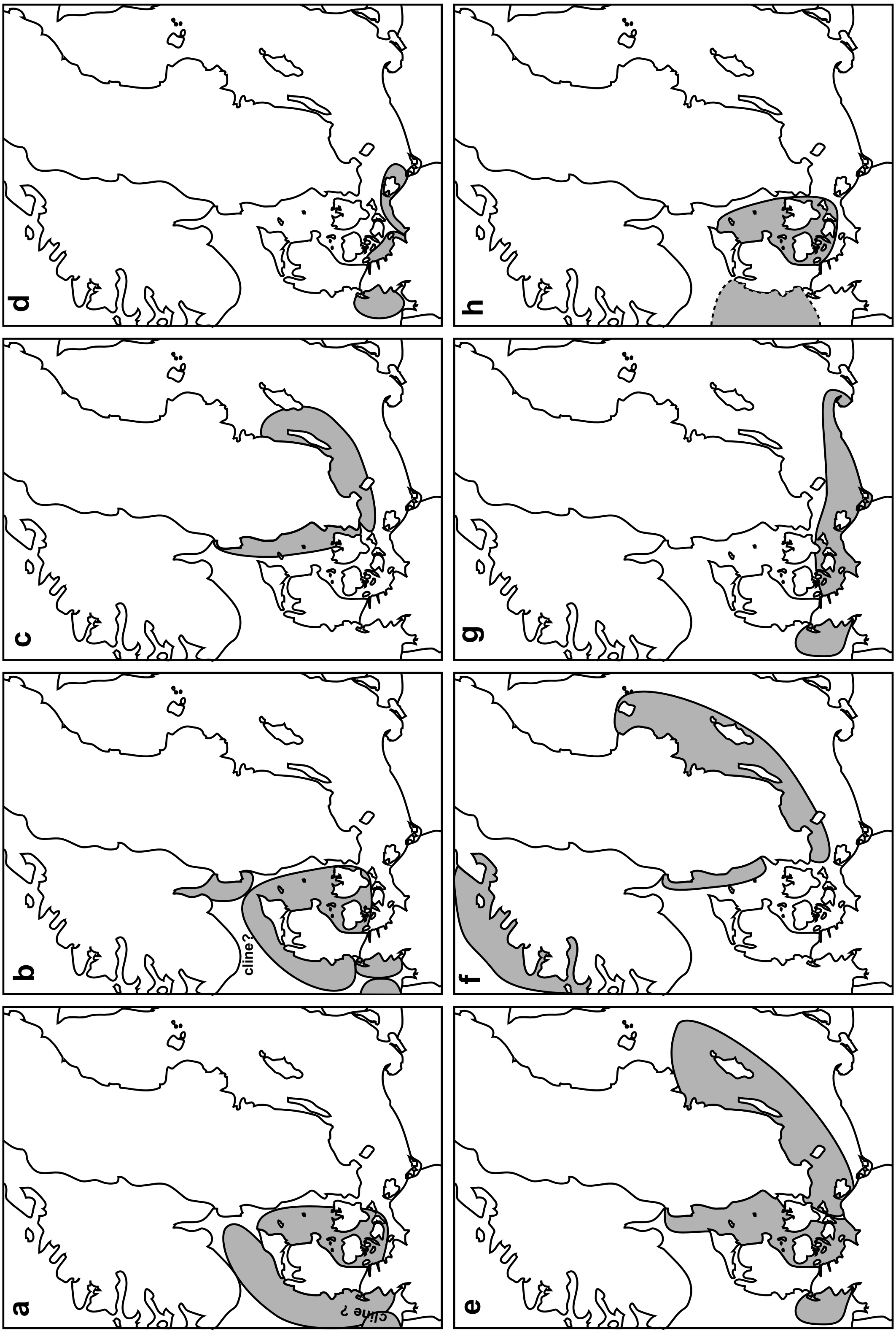
Fig. 2. Hypothetical harbour porpoise subpopulations from different morphometric and genetic studies. a) Kinze (1985) b) Kinze (1990) c) Børjesson & Berggren (1997) d) BMBF (1997) e) Huggenberger et al. (in prep.) f) Wang & Berggren (1997) g) Tiedemann et al. (1996) h) Andersen et al. (1997)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hierarchical segregation of the genetic pool below the species level. In this sense populations are isolated, e. g., by continental masses or wide ocean stretches. In the inhabited areas there will almost always be a tendency for seasonal aggregation in certain areas that favour optimal reproduction with genetic exchange taking place among the individuals that mate within each of these sub-units. Such a reproducing community is defined as a "subpopulation". In the present literature, however, the terms "stock", "population" or "subpopulation" are sometimes used equivalently. In the present paper the term "subpopulation" will be used for the putative sub-units of the greater North Atlantic population.

Morphometric studies.- In a first attempt to identify major subpopulations for the North Atlantic Yurick & Gaskin (1987) found trends suggesting some segregation between Dutch, eastern English and Baltic Sea animals. But overall, their results were inconclusive due to low sample sizes. Kinze (1985a) suggested the existence of a separate subpopulation in inner Danish waters (Western Baltic, Belt Seas and Kattegat) (fig. 2 a) since animals from these waters were morphologically distinct from the Dutch animals in metric skull characters. A comparison of non-metric characters showed an affinity of animals from inner Danish waters to animals mostly taken in winter from the "northern North Sea" (Schleswig-Holstein, Jutland and Skagerrak areas). This may indicate a migrational movement and a complex mixing of subpopulations in the North Sea during winter. Whether Dutch animals form a distinct subpopulation in the North Sea or whether a cline exists along the Dutch, German and Danish coasts could not be ascertained in that study. In a more sophisticated follow-up study, Kinze (1990) established four different putative subpopulations in Danish and adjacent waters: In the Dutch part of the North Sea, in the Schleswig-Holstein part of the North Sea, along the Swedish coast of Bohuslän and in the waters from west Jutland around the tip of Skagen into the Kattegat, Belt Seas and western Baltic with a cline in some characters (Fig. 2 b).

Unfortunately, specimens from the Baltic Proper were not examined until recently. Børjesson & Berggren (1997) compared skulls of harbour porpoises from the Baltic Proper (from south of the Scanian peninsula to north of Øland) and a winter as well as a summer sample from the Swedish Kattegat and Skagerrak coasts (Fig. 2 c). They found that female harbour porpoises in the Baltic Proper are morphologically distinct from females in the Kattegat and Skagerrak areas. These differences might be due to either lineage-related factors or environmental effects. However, this supposes the existence of two separate subunits. Since there was more conformity between the Baltic and the Kattegat / Skagerrak winter sample (as opposed to the summer sample) the authors concluded that due to migrational movements out of the Baltic Proper into the Kattegat and the Skagerrak a mix of specimens occurs there in the winter. From the similarity of male specimens they concluded that males may move between the areas to a greater extent than females resulting in considerable sampling bias. Unfortunately, a comparison of their work with Kinze's (1985a, 1990) studies is impossible since Kinze examined a mix of animals from the Danish western Baltic, Belt and Kattegat Seas and compared it with samples from the North Sea coasts.

Using a discriminant analysis of cranial characteristics the authors of another recent study (BMBF 1997) point out significant differences between harbour porpoises of both sexes from the German North Sea and from the German Baltic Sea coast. Furthermore, they found differences between the Schleswig-Holstein and the Mecklenburg-Prepomeranian Baltic coasts (Fig. 2 d).

Based on morphometric comparisons, Huggenberger *et al.* (in prep.) presume that two separate subpopulations in the Baltic Sea exist, both different from German North Sea animals. The underwater ridges of Limhamn and Darß delineate these putative sub-units (Fig. 2 e). From their findings it appears that the hypothetical subpopulation off the Schleswig-Holstein Baltic coast postulated by BMBF (1997) might belong to the western Baltic / Belt Sea / Kattegat sub-unit and the Mecklenburg-Prepomeranian specimens to the Baltic Proper subpopulation. Huggenberger and coworkers outline a scenario with strong site fidelity of females during the mating season and migrations occurring, if at all, outside the mating season. This would minimise genetic exchange between subpopulations. They discuss that animals in the Baltic Proper might be remnants of a non-migratory subpopulation. This non-migratory approach is supported by the fact stated above that entrapments of large numbers of harbour porpoises occurred during icy winters (Johansen 1929; Ropelewski 1957; Tomilin 1957).

Population genetics.- Similar to the morphometric study of Børjesson & Berggren (1997), Wang & Berggren (1997) comparing mitochondrial DNA restriction fragments came to the conclusion that two distinct subpopulations with an unknown level of genetic exchange exist in the area of the Swedish Baltic Sea coast. (Fig. 2f). One provisional subpopulation is suggested in the Baltic Proper (south and east coast of Sweden) and another one along the Swedish Kattegat and Skagerrak coast. Both subpopulations are genetically distinct from each other as well as from animals from western Norwegian waters. Interestingly the authors found a very low haplotypic and nucleotide diversity in the Baltic Proper. Compared to western Atlantic subpopulations, genetic diversity was also low in the Kattegat / Skagerrak samples. In these cases, low diversity can either be an indicator for a depleted subpopulation (with a low number of reproducing animals remaining) or may reflect the comparatively late colonisation of the Baltic after the last glaciation (about 8000 years ago) with a limited exchange with reproducing animals from outside the area.

Using mitochondrial DNA sequence patterns, Tiedemann *et al.* (1996) also suggest a limited genetic exchange since the colonisation of the Baltic Sea several thousand years ago, proposing the existence of a distinct subpopulation in the Baltic Sea (Fig. 2g). They explained the observed genetic segregation with philopatry, assuming that at least females (mtDNA is inherited maternally) return to their area of birth for mating. This is consistent with observations of naturally marked females with calves in the same area in subsequent years (Kinze 1990).

Andersen *et al.* (1997) found not only differences between subpopulations based on the maternally inherited mtDNA but also with respect to isoenzymes which are encoded in the nuclear genome and thus are susceptible for gene flow in both sexes. They suggest a subpopulation in inner Danish waters (Kattegat, Belt Sea and western Baltic) that is genetically differentiated from North Sea animals, but connected with them through "a fairly high" degree of gene flow (Fig. 2 h). It can also be concluded from that study that separation of both subpopulations is not only maternal but bi-parental. Although they did not examine any animals from the Baltic Proper, this concept is not in contradiction to the studies of Huggenberger *et al.* (in prep.), Børjesson & Berggren (1997), Wang & Berggren (1997) and Tiedemann *et al.* (1996).

Contaminant profiles.- The patterns of geographical variation in the levels and composition of different contaminants found in harbour porpoises from different regions were examined by several authors. They showed that the proportion of several polychlorinated biphenyl (PCB) congeners in tissue samples can assist in identifying separate subpopulations in the Baltic and North Seas.

Bruhn *et al.* (1999) found clear differences in the spatial distribution of certain PCBs. The PCB mixtures in harbour porpoises from Arctic, German Baltic and German North Sea waters represent separate groups. Spatial differences in PCB composition could occur due to (1) different inputs in the three regions, (2) different diets or (3) different capacities of porpoises to metabolise these compounds in relation to their concentration. Mature male harbour porpoises sampled in the Swedish part of the Baltic Proper had significantly different contamination patterns of PCBs than animals from the Swedish Kattegat and Skagerrak coasts and from western Norway (Berggren *et al.* 1999a). Specimens from the latter two areas showed differences in patterns, but due to low sample sizes and possible sampling bias this result was not conclusive. Baltic Proper animals also had 41 to 254% higher mean levels of polychlorinated dibenzodioxins and -furans (PCDD/Fs) and PCBs than the corresponding sample from the Kattegat and Skagerrak. Concentrations of several individual PCB congeners were shown to differ between their samples.

Tooth ultrastructure.- Yurick & Gaskin (1987) suggest an endogenous control of layering of dentine and cementum in teeth rather than an exogenous control through seasonal food availability. This would qualify the investigation of tooth ultrastructure as a tool for detecting differences between subpopulations. Lockyer (1995, 1999) described different characters in tooth layers which may be genetic in origin or influenced by life history events and other factors. She detected differences between tooth samples from the North Sea, Skagerrak, inner Danish waters and the Baltic Proper (Lockyer 1999). This method seems promising for future investigations in combination with genetic and morphometric studies of the same samples.

Synthesis.- The existence of a Baltic subpopulation seems likely. Two scenarios can be discussed. (1) Considering a certain amount of gene flow between sub-units (e. g., Andersen *et al.* 1997) it can be assumed that a Baltic subpopulation may not be totally separated from a possible North Sea subpopulation. Individuals living in particular habitats might show specific migratory patterns with a certain overlap between neighbouring porpoises but not with porpoises from geographically more remote areas. Therefore it is possible that a cline exists in some characters from the North Sea into the Kattegat, Belt Seas and Baltic Proper, making it difficult to determine a sharp boundary between possible subpopulations. (2) Other studies indicate a very low genetic exchange between the different subpopulations (e. g., Tiedemann *et al.* 1996; Wang & Berggren 1997). The concept of strong site fidelity (cf. Huggenberger *et al.* in prep.) with mating in confined traditional breeding areas appears to be possible in this context. In that case the Baltic Sea harbour porpoise subpopulation could be considered genetically isolated and its status would be as dramatic as that of the critically endangered vaquita (*Phocoena sinus*) in the Gulf of California/Mexico (Vidal 1995). To clarify these uncertainties, a study using samples from all over the Baltic Sea and combining different methods should be conducted. As a precautionary approach the harbour porpoise-working group of the IWC and ASCOBANS agreed that the small stock in the Baltic Proper should be treated as distinct from the stock in the Kattegat, inner Danish waters and German Baltic Sea, where larger numbers of porpoises are present (IWC 2000). It was noted that the Darß and Limhamn ridges delineate a putative subpopulation in the Baltic Proper.

MIGRATION

Historic large scale migrations which occurred during winter and spring can be inferred from the successful catch of harbour porpoises in the Danish straits in the 19th and early 20th century during particular times of the year. However, there is no evidence where the hunted animals had come from. Furthermore, it is unclear whether these historic migration patterns still exist.

Many references can be found (e. g., Dudok van Heel 1962; Wolk 1969) reporting that harbour porpoises followed herring schools into the Baltic in spring and left the inner Baltic waters escaping from sea ice formation in fall and winter. However, the information on this possible migratory pattern is mainly based on anecdotal evidence and traditional knowledge of Danish fishermen who used to hunt harbour porpoises in significant numbers for centuries. In spring (end of March until early May) porpoises used to appear in considerable numbers in Isefjord and in Smålandsfarvandet southeast of the Great Belt area. In early spring annually 300 - 800 porpoises were hunted with nets in Isefjord. Other than the Isefjord catch in spring a drive catch was performed during winter in Gamborg Fjord and adjacent Skærbæk (Little Belt). During one hunting season, which usually lasted from November 11th until February 2nd, 2500 harbour porpoises could be hunted there in the most favourable years (Kinze 1995). A much higher number must have passed through these areas. Andersen (1982) conducted a study in winter 1969/70 in Gamborg Fjord and came to the conclusion that winter migration of harbour porpoises out of the Baltic Sea in late autumn and early winter as reported from catch years "has almost completely ceased". Numbers of apparently migrating animals dropped from far over 1000 per year (which were caught annually in the drive catch) in the 19th century to several hundred animals sighted in 1957/58 (Dudok van Heel 1962) and about 20 animals sighted in 1969/70 (Andersen 1982).

Møhl-Hansen (1954) studied the composition of groups killed during the hunting seasons 1941/42 to 1943/44. He reported that groups travelling northwards at Gamborg Fjord often consisted exclusively (or nearly so) of adult males. "Female" groups were found less frequently. Mixed groups often consisted of adult females and their offspring. He concluded that many adult males travelled apart from females which usually were accompanied by their calves and therefore swam more slowly.

Reports of mass mortality of harbour porpoises in the Baltic Proper during winters with strong sea-ice formation of 1928/29, 1939/40 and 1946/47 (Johansen 1929; Ropelewski 1957; Tomilin 1957) show that at least a number of porpoises remained in the Baltic Proper during winter. In most winters at least some areas stayed ice free in the central Baltic Sea allowing harbour porpoises to survive.

Recent observations suggest complex migration patterns. Several authors suggested that males tend to stray around to a greater extent than females do (Andersen *et al.* 1997; Børjesson & Berggren 1997). This could not be verified by Teilmann (2000); using satellite-linked telemetry he found no differences in daily travelling distance between sexes. Interestingly, he recorded a long directed journey of a satellite-tagged immature female from the Little Belt into Norwegian waters with very little "back-tracking" during summer. However, a number of animals appear to be rather sedentary during the breeding season (Kinze 1990). Kinze presented evidence for a homing or residential behaviour reporting that naturally marked individual females with calves were seen in the same area in subsequent years. Teilmann (2000) recorded a number of immature and adult porpoises staying for prolonged periods in small areas. Four females with calves (captured in the Great Belt region) showed a pattern of swimming back and fourth along the north coast of Sjælland for prolonged periods. This indicates that at least a part of the population is summer resident in certain areas. This is also confirmed by several genetic and morphometric studies suggesting a strong site fidelity at least of adult female porpoises returning to their natal area for mating and calving (Tiedemann *et al.* 1996; Andersen *et al.* 1997; Huggenberger *et al.* in prep.).

Outside the breeding season, movements might occur more frequently. But these are definitely not as distinct as described in older references. From swimming directions observed from ferry lines in the Belt Sea area, Kinze (1985b) suggested a tendency for northward movements in October and November and southward movements from April to May. Further north, in the Kattegat, he assumed a more complex or a more diffuse mode, presumably with a greater proportion of non-migrators. In a more recent study he found no marked migration patterns at all (Kinze 1990). However, during the winter months, porpoises seemed to aggregate in the northern Kattegat. Although in his study there was a high variability of sightings between years the author noted a marked difference between cold and mild winters. In a three-year period of mild winters, a decline in sightings in the northern Kattegat area around Læsø and increased numbers of sightings in the Belt Seas and Western Baltic was recorded, compared to a three year period of cold winters. The similarity in morphometric characters of summer and winter samples from inner Danish waters and the North Sea indicate a rather short migration range if any at all (Kinze 1990).

So far a systematic telemetry study conducted to investigate harbour porpoise movements in the Baltic Sea has not been able to show any definite migratory pattern (Teilmann 2000). Individual animals showed a considerable variability in movement patterns. Unfortunately, most of the 17 animals in this study were tracked during summer. Surprisingly, the only animal tracked through the winter, an immature male tracked between July 28th, 1999 and April 7th, 2000, displayed a behaviour which cannot be explained in terms of the historic view of migration patterns. It left the area north of Fyn (where it was captured in a pound net) into the northern Kattegat, came back in September, swam southward through the Little Belt, where it stayed in an area south of Fyn until late February, and finally went for a 35 day trip far into the Baltic Proper before returning to Fyn. This telemetry study is still underway and a number of interesting tracks are not published yet: during the last two winters, four more porpoises captured in the Kattegat were tracked. Three of these animals area swam around the tip of Skagen into the North Sea while the fourth one swam southward into the western Baltic (Teilmann, pers. comm.). This is consistent with the morphometric and genetic studies of Kinze (1985a) and Andersen *et al.* (1997), indicating a mixing of animals from different areas in the North Sea (e. g., Belt Sea, Kattegat and North Sea animals) in winter.

Unfortunately, most information on possible migration patterns stems from the Kattegat and Belt Seas. Virtually no direct information could be obtained from the Baltic Proper because sightings are so rare. By-catch in the Baltic Proper occurs during all months of the year. Increased numbers taken in spring months in Poland might be explained by increased fishing effort in the salmon fishing season (Skóra 1991a; Berggren 1994) or by immigration of harbour porpoises into the area (cf. Ropelewski 1957). It must be concluded that at least some of the harbour porpoises spend the winter in the Baltic Proper. The same is true for the western Baltic as indicated by by-catch data from the German Baltic Sea coast (Kock & Benke 1996) and by telemetry data (Teilmann 2000). As seen above, for the Baltic Proper, Huggenberger *et al.* (in prep.) even suggest a non-migratory relict subpopulation.

It can only be speculated why the migrating

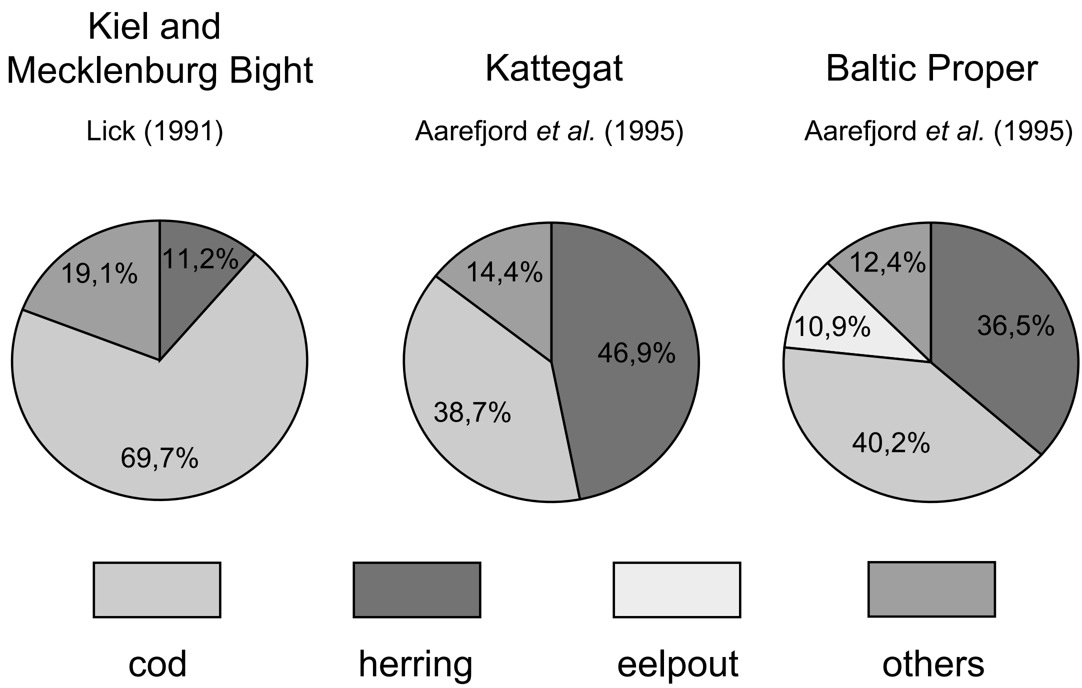

Fig. 3. Relative food consumption of harbour porpoises in the Baltic Sea. Percentages are given by weight. The large amount of "others" in Lick (1991) mainly consist of gobiids.

behaviour of harbour porpoises seems to have changed from the 19th century until present times. Climate change or a different composition of Baltic Sea harbour porpoise stocks might be an explanation. It is also possible that a general migration out of the Baltic Proper never existed, since it is unknown where the animals caught in Gamborg Fjord spent their summers. Unfortunately, until now most animals equipped with satellite transmitters were from the Kattegat and Belt Seas. If there is a separate Baltic Proper population, as indicated by different studies (see above) satellite tracking of harbour porpoises from that area could illuminate this question.

In conclusion, a migratory pattern as described from the old days does not seem to exist at present. Indeed, migratory behaviour is much more complex and diffuse: (1) There seems to be a tendency of animals from the Kattegat to migrate into the North Sea during winter months. (2) A proportion of animals stays in the western Baltic during the winter or even strays around into the Baltic Proper. (3) There might be a difference in migratory tendency between putative subpopulations. (4) Migration patterns might be dependent on winter severity or might have shifted due to climate change. (5) There might be a non-migratory relict subpopulation in the Baltic Proper.

Genetic investigations of the animals equipped with transmitters might provide some of the answers (regarding affiliation of tracked porpoises to putative subpopulations). Future investigations of movement patterns may help to clarify hitherto existing uncertainties.

DIET

During the 1950s, concern was raised that harbour porpoises were the main cause for Baltic salmon (*Salmo salar*) fluctuations. Lindroth (1962) therefore designed a study to assess the impact of harbour porpoises on salmon stocks. However, he did not find any remains of salmon in the stomachs of 50 examined specimens taken from the Swedish salmon drift net fishery. Instead he identified herring (*Clupea harengus*), sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) as the main food species. He also found a large number of transparent gobies (*Aphya minuta*) in some of the specimens and - since there was a strong invasion of that species that year - concluded that harbour porpoises are quite opportunistic with respect to the choice of their prey. Källquist 1974 found gadoids - mainly whiting (*Merlangius merlangus*) to be the most common fish type in a sample taken between 1941 and 1944 by Møhl-Hansen (1954) in the Little Belt area.

In a more recent systematic study of Baltic and North Sea animals (by-caught or stranded in Denmark, Sweden and Norway) a total of 13 fish species were identified in the stomach contents of harbour porpoises from the Baltic Proper, Belt Seas and Kattegat (Aarefjord *et al.* 1995). The most important food species in the Kattegat and Baltic Proper were herring and cod. Stomachs from animals of the Baltic Proper also contained a substantial number of eelpout (*Zoarces viviparus*); see Fig. 3. Harbour porpoises from the western Baltic (Kiel and Mecklenburg Bight) were found to feed mainly on cod (70% by weight), Gobiids (19%) and herring (11%) with a total of eight fish species identified (Lick 1991; Fig. 3). According to BMBF (1997) cod (90% by weight), sprat (5%) and herring (4%) were the most important out of a total of seven identified fish species. The maximum length of food items found in porpoise stomachs (based on otolith data) was 48.5 cm but most of the fish species eaten (74%) had an average length of 25 cm or less (Aarefjord *et al.* 1995). In juvenile harbour porpoises (≤ 1 yr old) *Gobiids* were the most common prey (Aarefjord *et al.* 1995; BMBF 1997). Benke *et al.* (1998) found a high number of gobies in porpoise stomachs of all ages (98% by number; 53% by weight). Taken together, the contrast between studies (even from the same geographical areas) indicates that there is considerable variation in the diet of Baltic Sea harbour porpoises. However, it is not known how "opportunistic" they are in prey selection. This term expresses that a predator feeds on the most abundant prey available, and it cannot be concluded from the studies mentioned above whether this is the case (IWC 1996). It only appears that they preferably take certain species and seemingly can switch to other prey if a preferred species is overfished.

For the Baltic Sea there are no systematic studies of the amount of daily food consumption. Berggren & Petterson (1990) assume a daily requirement of 3 to 5 kg fish. Andersen (1965) reported 4.3 kg for captive harbour porpoises and Sergeant (1969 - cited in Lick 1991) estimates 10.8% of body mass per day. Taking a mean weight of 48 to 57 kg into account (Møhl-Hansen 1957) the latter would result in 5.2 to 6.2 kg fish. For harbour porpoises in the Bay of Fundy (Canada) Yasui and Gaskin (1986) estimated a daily feeding rate of only 3.5% of body mass per day resulting in 1.7 to 2 kg of fish. Kastelein *et al.* (1997), under laboratory conditions, found a considerable variation in daily food intake of 6 specimens from the North Sea. On average the porpoises of various body size consumed between 750 and 3250 g herring and sprat per day, corresponding to 4 - 9.5% of their body mass.

HABITAT UTILISATION

For management purposes it is necessary to identify critical habitat requirements of harbour porpoises in the Baltic Sea. However, it is difficult to assess what - from a porpoise's view - is a suitable habitat. Food availability can be considered one important factor. It has been shown above that porpoises can shift between different prey species. As a result, feeding grounds might vary from year to year. Not many systematic habitat use studies are available for Baltic Sea harbour porpoises. However, some information can be derived from telemetry studies or sightings surveys. For example, one juvenile male equipped with a time-depth recorder, tracked in the Kattegat and in the Øresund spent most of its bottom time (presumably feeding dives) at water depths of 6 m to 53 m. Its preferred dive depth was around 10 -15 m (Teilmann 2000). This corresponds to the actual water depth along its swimming route. From this depth range, a large proportion of the area covered by this animal qualifies for feeding habitat. However, since food availability might change from year to year, it is almost impossible to identify feeding grounds which would qualify as well-defined protected areas.

Probably the most important areas to identify for management purposes are calving and nursing habitats. Calves were widely distributed in the SCANS census area. It is assumed that shallow areas play an important role for this species with respect to calving and nursing (cf. Kinze 1990; Hammond *et al.* 1995). Calving areas have been identified in waters inside the 20 m depth contour, e. g., in the northern part of the Little Belt, Great Belt, Sejrø Bight, waters north of Fyn, the archipelago south of Fyn (Sydfynske Øhav) and Smålandsfarvandet (Kinze 1990). The waters around Læsø (Lockyer & Kinze in prep.) and the shallow waters of the Mecklenburg-Prepomeranian coast (Schulze 1991) might also serve as breeding

Fig. 4. Possible calving areas of harbour porpoises in the Baltic Sea. The arrow indicates movements of a number of females accompanied by calves as described in Teilmann (2000).

areas. All these possible calving grounds are shown in Fig. 4.

As discussed above, some individual females have been shown to use the same nursing areas in subsequent years (Kinze 1990). From the observation of five tagged animals, Teilmann (2000) identified a route which is apparently used by a number of adult females with calves, with regular patrolling movements in the northern part of the Great Belt and along the north coast of Sjælland. It is assumed that these females might show important habitats to the calves.

REPRODUCTION

For the Baltic Sea only a few systematic studies are available. The first systematic analysis of the reproductive cycle of the harbour porpoise was undertaken by Møhl-Hansen (1954). He investigated 695 animals caught in the winters of the years 1941 to 1944 in Gamborg Fjord. Unfortunately his investigation was conducted before an age determination method had been developed (e. g., Nielsen 1972) and the animals investigated were exclusively from the winter catch. Therefore more reliable information can be found in more recent studies (e. g., Sørensen & Kinze 1994; BMBF 1997). Sørensen & Kinze (1994) investigated 365 by-caught or stranded specimens from both Danish coasts between 1985 and 1991 collected year round. In a recently conducted BMBF study (1997) 23 Baltic Sea and 54 North Sea harbour porpoises collected during 1994 and 1995 were investigated. Clausen & Andersen (1988) also provide

Table 2. Demographic information on harbour porpoises from the Baltic Sea from different studies.

Specimen taken from	*Age at sexual maturity*	*Mating season*	*gestation period*	*parturition*	*lactation period*	*pregnancy rate*	*maximum age*
Denmark[1]	2.93 males 3.64 females	late July / early August	10.5 months	30. June	9 months	0.61 (0.73)	
Denmark[2]	3.11 males 3.50 females		-	June	-	0.79	13 years
Little Belt Denmark[3]		July - August	10-11 months	May - June	8 months	0.84	19 years
German waters[4]	4.58 females	July - August				0.78	22 years

[1] Sørensen & Kinze (1994)
[2] Clausen & Andersen (1988), recalculations from Sørensen & Kinze (1994)
[3] Møhl-Hansen (1954)
[4] BMBF (1997)

some data on reproduction although their study was mainly focused on by-catch. Unfortunately, in these three studies animals from the North and Baltic Sea were treated as one sample. A list of the findings of the different authors is given in Table 2.

Age at sexual maturity (ASM).- ASM is generally calculated as the sum of the fraction of immature animals in each age class (DeMaster 1978). With this method, Sørensen & Kinze (1994) determined an ASM for males of 2.93 and for females of 3.64 years. They also used the data from Clausen & Andersen (1988) to calculate an ASM of 3.11 years for males and 3.5 years for females, respectively. Only few females reach sexual maturity between the ages of 2 and 3. Pubertal males were identified in the age class between 2 and 3 years, maturity usually occurs after the third year (Clausen & Andersen 1988; Sørensen & Kinze 1994). According to BMBF (1997) females from the German Baltic and North Sea coasts reach maturity about one year later (ASM = 4.58 yrs). Interpreting peaks in a weight curve as various year-classes Møhl-Hansen (1954) came to the conclusion that harbour porpoises were already sexually mature at the age of 14 months. This finding is in sharp contrast with the more recent studies. Since at the time of the study Møhl-Hansen had no method of ageing the animals his interpretation must be doubted.

Sex ratio.- All three Danish studies mentioned above show a male preponderance. This is most significant in the survey of Møhl-Hansen (1954) with 62% males. The more recent studies found 55% (Sørensen & Kinze 1994) and 52% males (Clausen & Andersen 1988). Here it is important to note that Møhl-Hansen (1954) received his specimens from the winter drive catch at Gamborg Fjord. Since he observed males travelling in large groups (which would have been more attractive to hunt than smaller female groups) there is a potential for serious bias. The sex ratio in foetuses is almost 1:1 (Møhl-Hansen 1954; Sørensen & Kinze 1994). However, Lockyer & Kinze (in prep.) report a foetal sex ratio of 1.1 males to 1 female for harbour porpoises from all Danish waters.

Mating, gestation and parturition.- Using data from his investigation and from other sources, Møhl-Hansen (1954) estimated that mating occurs from July to August. The findings of Sørensen & Kinze (1994) support a reproductive seasonality with a mating season from late July to early August in Danish waters. They calculated that conception should occur during the latter half of July or at the beginning of August. In German waters, the mating season was also reported to occur in July and August (BMBF 1997). The gestation period appears to be approximately 10.5 months (Møhl-Hansen 1954; Sørensen & Kinze 1994). Females give birth from the middle of June to early July. The mean birth date for Danish waters was calculated to be 30 June based on 16 full term foetuses or newborn calves found from May to July (Sørensen & Kinze 1994). However, Møhl-Hansen (1954) reported data that indicates some earlier and later births. Observations from Kinze (1990) of newborn calves from April through October north of the island of Fyn support these findings. The average length at birth is reported to be about 70 to 75 cm with a mass range of 5000 to 6000 g (cf. Møhl-Hansen 1954; Sørensen & Kinze 1994).

Lactation period.- Lactation lasts for 6 to 9 months. Sørensen & Kinze (1994) found both lactating females and calves with milk in their stomach as late as March. In contrast, Møhl-Hansen (1954) reported fish in the stomachs of juveniles as early as November, which coincides with tooth eruption and the first occurrence of parasitic nematodes that are taken in with the porpoises' fish diet.

Life span.- A widely accepted method for the estimation of age in mammals is the determination of annual dental growth layer groups. Especially in mammals from temperate or arctic regions annual layers form distinct 'primary lines' (Langvatn 1995). Bjørge et al. (1995) discussed uncertainties and potential sources for bias in the age determination of harbour porpoises. In their experiment aimed at testing the variability in age readings from incremental lines in dental tissues, results showed little variation between experienced readers in estimating the age of animals less than 5 years old. The reliability of readings was lower for older animals or inexperienced readers. In addition to these methodological effects, age selectivity in sampling is a potential reason for bias because specimens in most systematic investigations are by-caught or stranded animals Therefore, the average and maximum life span of harbour porpoises in the Baltic Sea remains uncertain. It has been suggested that harbour porpoises are relatively short lived compared to other Phocoenids and reach a maximum of 12 to 13 years of age with only a few animals living beyond 8 years of age (cf. Gaskin *et al.* 1984; Read & Gaskin 1990). The oldest animal in the sample of Clausen & Andersen (1988) was 13 years old. More recent investigations show that the maximum age can be somewhat higher. The oldest animals in two samples from the German Baltic Sea coast were shown to be a 16.5 year old male (Benke *et al.* 1998) and a 22 year old female which was still lactating! (BMBF 1997). Sørensen & Kinze (1994), found two females aged 18 and 19 years which they identified as post-reproductive. From a large database for Danish North Sea and Baltic Sea harbour porpoises, Lockyer & Kinze (in prep.) suggest a maximum age in both sexes of 22 to 23 years. They report a high mortality in the first years of age and a proportion of less than 5% of the animals living beyond 12 years. The mean life expectancy, which has to be considered for estimates of the potential for increase of the stocks is therefore somewhere below 12 years of age.

Pregnancy rates and calving intervals.- The most uncertain life history parameter of the Baltic harbour porpoises is the pregnancy rate. This is the ratio of pregnant to mature females. Sørensen & Kinze (1994) calculated this ratio using two indicators for pregnancy: the presence of a corpus luteum or the presence of a foetus. The former results in a rate of 0.61 (taking the entire sample as a basis), the latter yields a rate of 0.73 (taking only the sample collected after implantation into account) for all Danish waters. For German waters (Baltic and North Sea) a pregnancy rate of 0.78 was reported (BMBF 1997). Møhl-Hansen's (1954) data yields an annual pregnancy rate of 0.84 (93 out of 111 presumably mature females). Even when allowing slightly higher values due to the possibility of overlooking very small foetuses shortly after implantation (in samples collected during all seasons as opposed to the winter samples of Møhl-Hansen (1954)) the pregnancy rate is lower in the more recent studies. Reproduction rates in the range of 0.7 to 0.8 show that a large proportion of females produce calves in consecutive seasons.

Gross annual reproductive rate (GARR).- From the pregnancy rate, sex ratio and fraction of mature animals, the GARR can be calculated as follows: *GARR = (proportion of females) x (proportion reproductive) x (annual pregnancy rate)*. This method is described by Perrin *et al.* (1977). Gaskin *et al.* (1984) extracted from Møhl-Hansen's (1954) data a GARR of 0.21 for the Baltic harbour porpoises (assuming an equal proportion of males and females) while for animals from the Bay of Fundy they found a GARR of only 0.10 in the 1950s and 0.06 in the 1970s. Gaskin *et al.* (1984) suggest that during autopsies very small embryos might have been overlooked resulting in a low GARR. This shows that there is a strong potential for bias in these studies making exact calculations of reproductive rates difficult. However, because the potential rate of increase of a population can be calculated from the reproductive rate and natural as well as human-caused mortality, this parameter is crucial for a thorough management of harbour porpoise populations (Woodley & Read 1991; IWC 2000).

HEALTH STATUS

A large number of different lesions and abnormalities have been reported from harbour porpoises in the Baltic Sea. This study can only give a short overview over their health status. For example typical autopsy findings in by-caught harbour porpoises from Danish waters as reported in Andersen (1974) were: heavy attack from parasites in lungs, liver, stomach, intestines and middle-ear cavities, oesophageal abrasions, skin lesions and pneumonia. Siebert *et al.* (1999) add liver fibrosis, arthrosis, abscesses in muscles, lungs and other organs as well as fractions. Clausen & Andersen (1988) found abscesses in the uterus and ovary that had probably developed in association with pregnancy. Kinze (1986) reported six cases (out of 148 Baltic and North Sea specimens), BMBF (1997) 13 light cases (out of 102 skeletons) of *Spondylitis deformans*, a certain pathological deformation of the vertebral column primarily found in old animals (Paterson 1983 - cited in Kinze 1986). However, two of the Danish cases were reported from young animals (< 3 yr old).

Parasites.- Significant infections of Baltic harbour porpoises with various parasites and corresponding pathological changes have been reported. The most affected organs were lungs, ear sinus and liver (e. g., BMBF 1997). Parasitic infection rate was shown to be age dependent (Clausen & Andersen 1988; Lockyer & Kinze in prep.) and higher in the Baltic Sea than in the North Sea with respect to the nematodes *Anisakis simplex, Tonyurus convolutus* and *Stenurus minor* (BMBF 1997). However, Lick (1991) found markedly lower infection rates with *Anisakis simplex* in Baltic Sea animals. The differences probably reflect a certain species composition in the diet of harbour porpoises in different areas and during different times. Only very young animals, which did not have the chance to take up any parasitic larvae or eggs with their food, were free of parasites (Møhl-Hansen 1954; BMBF 1997). The variation in infestation rates between different studies probably also reflects the proportion of young animals (< 1 yr) in the sample. Clausen & Andersen (1988) for example found infestation rates of 30.9% in animals less than 1 year old and 96.8% in older animals (both from Baltic and North Sea). A high proportion of young animals (e. g. in a by-catch study; cf. Kinze 1994) therefore reduces the overall infestation rate in the sample (as opposed to a sample from the direct catch; cf. Møhl-Hansen 1954).

Two thirds of stranded and by-caught animals were affected by lung-worms, almost half of the animals were infected by parasites in the alimentary system and one third had trematodes in the liver (Siebert *et al.* 1999). Clausen and Andersen (1988) reported a slightly higher prevalence of parasitic infections in the respiratory system (72%) and the liver (48%) and a markedly lower infection rate in the digestive system (17%). Differences might be due to a different proportion of younger animals and a different proportion of Baltic animals in the mixed samples (Baltic and North Sea).

Different species of nematodes were found in the studies mentioned above: *Anisakis simplex, Halocercus invaginatus, Pseudalisus inflexus, Stenurus minor*, and *Tonyurus convolutus*. Trematodes were represented by *Pholeter gastrophilus* in stomachs and the liver fluke *Campula oblonga*. Lockyer & Kinze (in prep) add *Crassicauda sp.* to this list. Infestations by ear nematodes *Stenurus minor* were found in 87% of mature Baltic Sea animals in maximum numbers of 5404 per animal. This was similar to the infection load in a representative sample shot in Greenland (BMBF 1997). In animals caught in the Little Belt in the 1940s, an infestation rate of 82.9% with *Stenurus minor* is reported (Lockyer & Kinze in prep.). Clausen & Andersen (1988) suggested that the high parasite loads and the high number of animals harbouring mycoplasma might indicate an unhealthy population. It is interesting to note that in adult animals one third of the lung tissue might have been out of function due to lung worm infection, but the general body condition did not appear to be affected (Clausen & Andersen 1988). Compared to harbour porpoises from Greenland or to reference material from the 1940s, the findings for the Baltic Sea do not seem to be abnormal (e. g., Møhl-Hansen 1954; Clausen & Andersen 1988; BMBF 1997). Therefore it is likely that harbour porpoises in the Baltic experience "normal" parasitic infestations.

Fungal, bacterial and viral infections.- Undetermined fungus species were found producing greyish spots on the skin of harbour porpoises (Andersen 1974; Clausen & Andersen 1988). Furthermore, 42% of the lungs were infected by one of two different types of mycoplasma (Clausen and Andersen 1988). Hemolytic streptococci were identified in abscesses of the reproductive organs of two females (Clausen & Andersen 1988) as well as in putrid tissue in two live stranded animals (Siebert *et al.* 1999). Viral distemper has been shown to be the cause of death in harbour porpoises stranded on the British and Dutch coasts (Kennedy *et al.* 1988) but no evidence was found in animals from the Baltic Sea (BMBF 1997; Benke *et al.* 1998).

THREATS

Harbour porpoises in the Baltic Sea appear to be in a serious long-term decline (ASCOBANS 1997b). Major drops of harbour porpoise numbers in certain parts of the Baltic Sea, mainly in the Western Baltic, Baltic Proper and the north-eastern reaches, after the late 1800s were reported. When the decline of harbour porpoises in these waters started and whether this is a gradual downward trend, as opposed to the consequence of several specific incidents or a mixture of both factors, is subject to speculation. According to different authors, declines of porpoise stocks in the Baltic Sea have occurred during various periods. The increased catch of harbour porpoises in the last half of the 19th century may have led to an overexploitation and initiated the decline (Kinze 1995). Schulze (1996) suggested a decline in porpoise stocks around 1900 and two others in the 1930s and 1940s. He also refers to the directed catch of large numbers of harbour porpoises in the Belt Sea as well as to icy winters and supposes a gradual decrease since the 1940s. Ropelewski (1957) assumed that the decline in porpoise numbers in the Baltic Proper after the 1930s until the 1950s was a temporary effect of icy winters combined with effects of the fishery. But until now, population levels on the Polish coast have not recovered (Skóra 1991a). Otterlind (1976) and Määttänen (1990) state that numbers of harbour porpoises in Swedish and Finnish waters have declined drastically since the 1940s followed by another drop in the late 1960s (Otterlind 1976). The latter is confirmed by Berggren & Arrhenius (1995b), who, based on questionnaires distributed among fishermen, revealed a sharp decline in Swedish waters in the 1960s and 1970s, possibly continuing into the late 1980s and by Kinze (1987), who identified the end of the 1960s as the starting point for a sharp decline.

The causes for these declines are likely to be multi-factorial: It is striking that an increase in fishing effort from the 1950s into the 1970s (probably resulting in higher by-catch numbers) and the uncontrolled use of persistent organochlorine chemicals like PCBs in the 1960s and 1970s coincide with some of these periods of major decline. The catch of harbour porpoises may have been the first coffin nail for the Baltic stock. Mass mortalities caused by ice entrapments could have long-term effects on harbour porpoise populations, but are believed to play a minor role because few winters in the last century had the severity to eliminate major proportions of the stock (Teilmann & Lowry 1996). However mechanisms, which have led to low porpoise abundance in the Baltic Proper and to a narrower distribution range, are not understood yet. Since the events, which possibly are part of the explanation occurred almost simultaneously, and because the time of the declines cannot be exactly determined, it is impossible to correlate the declines to one or another incident. However, it is idle to speculate about the reasons for earlier declines. It is more important for the conservation of harbour porpoises to identify and eliminate the actual threats.

By-catch.- Incidental entanglement and mortality in fishing gear are global problems affecting many species of small cetaceans. These appear to represent the most significant threat to many porpoise populations (e. g., Jefferson & Curry 1994; Teilmann & Lowry 1996). By-catch is known to occur in different types of fisheries in the Baltic Sea, but no reliable estimates are available (IWC 2000).

By-catch in gillnets is not a new phenomenon. It has already been reported from the late 19th and early 20th century. Several authors noted that harbour porpoises were incidentally caught in salmon nets in the eastern Baltic between Gdansk Bay and Estonia each spring (Braun 1906; Japha 1908; Greve 1909) or in Danish waters (cf. Lockyer & Kinze in prep.). In some seasons this by-catch appeared to be quite substantial.

Harbour porpoises should theoretically be able to detect nylon mesh as used in gillnets at sufficiently long ranges to avoid entanglement

(Au 1994). Kastelein *et al.* (2000) calculated 3 to 6 m as a minimum detection distance of nylon nets by harbour porpoises if approached at perpendicular angles under low noise conditions. Why do they become entangled then? Echolocation clicks are emitted in a narrow beam with an angle of 16° from the long axis of the body (Au *et al.* 1999). When searching for food at the bottom, this narrow beam might not point towards the net. This could be one reason for entanglement. This hypothesis is supported by Teilmann (2000), who was able to show that one study animal equipped with a time-depth-recorder was pointing its body > 16° to the bottom during 23% of total bottom time, probably searching for food. Another reason could be the masking effect of ambient noise or echoes from prey which are markedly stronger than the faint echoes from the net mesh (cf. Kastelein *et al.* 2000). However, the reasons for entanglement are not yet fully understood and require further investigation.

The effect of incidental entanglement on harbour porpoise populations is evident - animal numbers are reduced immediately because most animals die when entangled. To assess whether the impact of this interaction is eminent, the numbers of porpoises being killed needs to be put into a biological context. An initial step is to compare the number of animals killed with the size of the population, which first needs to be determined. If the kill rate appears to be significant, it then must be compared to the likely capacity for increase of the population. Berggren *et al.* (1999b) suggested that the by-catch rate must not exceed half the capacity for increase. Potential rates of increase for small cetacean populations have been suggested to be in the range of 4 to 10% per year (e. g., Reilly and Barlow 1986; Woodley & Read 1991; Caswell *et al.* 1998). However, these estimates were based on uncertain data and therefore are not sufficiently accurate for Baltic Sea harbour porpoise subpopulations. Since the combination of relatively short life span and low numbers of annual births limit the net reproductive rate of individual females and prevent populations from achieving high rates of increase it is widely accepted that the maximum rate of increase for harbour porpoise populations is close to the lower end of this range (IWC 2000). This means that harbour porpoise stocks have only limited potential to replace even moderate fishery takes. ASCOBANS (1997a) accordingly considers a by-catch exceeding 2% of the maximum likelihood of abundance of a subpopulation as an "unacceptable interaction". The sub-committee on small cetaceans of the IWC even adopted a figure of 1% of the estimated abundance as a "reasonable and precautionary level beyond which to be concerned about the sustainability of anthropogenic removals" (IWC 1996). To make an assessment in a particular case we need to know: (1) the identity of the affected subpopulations, (2) the number of animals killed each year, (3) the current size of each subpopulation and (4) the possible potential for increase. It was shown above that accurate data for these parameters are still lacking. However, there are reasons to believe that in some areas of the Baltic Sea, by-catch numbers exceed the mortality limit set by ASCOBANS (cf. Berggren *et al.* 1999b).

Danish fishery includes the largest gillnetting fleet within the European Union (Lowry & Teilmann 1994). A systematic assessment of by-catch exists only for the Danish North Sea fleet (Vinther 1999), and estimated an annual by-catch of 6785 animals, mostly taken in bottom-set gillnets for cod and turbot (*Psetta maxima*). For the Baltic Sea no total levels of by-catch have been estimated (e. g., IWC 1996). Therefore, only a minimum number can be taken from reported by-catches. According to Clausen & Andersen (1988) this figure should be 44 for 6 months in the Danish Kattegat and Belt Sea fishery, while Kinze (1994) in a salvage program received only 68 dead specimens in 4 years in the same region. Berggren (1994) considered 150 harbour porpoises per year as a minimum by-catch in Sweden. In the German part of the Baltic, the corresponding figure is about 25 (Benke 1994; BMBF 1997); for Poland annual incidental take is in the order of 5 (Skóra, pers. comm.). The last numbers appear to be low but since the putative subpopulation in the Baltic Proper is depleted, these figures are likely to be unsustainable (Berggren *et al.* 1999b). Therefore there is an urgent need not only for detailed investigations but also for immediate political action (cf. IWC 1996).

The by-catch rate varies considerably between fisheries. The fishing gear responsible for most by-catches is the bottom-set gillnet. In the Baltic Sea, significant by-catch is reported from cod and plaice nets set at the bottom in water depths between 5 and 60 m (Benke 1994; Berggren 1994; Kock & Benke 1996), from the fishery for lumpfish in the Kattegat and Belt Sea (Kinze 1994; Vinther 1999), and from salmon surface driftnets in Poland (Skóra

1991a) and along the East coast of Sweden (Berggren 1994). All the mentioned net types have relatively large mesh sizes between 10 and 27 cm (diagonally). Trawls also produce some harbour porpoise by-catch, but total take appears to be much less than in static gear (Clausen & Andersen 1988; Kinze 1994; Teilmann & Lowry 1996). Catches in pound nets for herring, cod and eel (*Anguilla anguilla*), are also occasionally recorded, but probably represent only a minor part of the by-catch. Furthermore, many animals entrapped in pound nets can be released alive (Lowry & Teilmann 1994; Kock & Benke 1996; Teilmann 2000).

About three quarters of all by-caught harbour porpoises are juveniles of 1 year and less or sub-adults of 1 to 2 years (Kinze 1994; Berggren 1994; Kock & Benke 1996; BMBF 1997; Lockyer & Kinze in prep.). Possible explanations for the high proportion of subadults are that entanglement might be related to experience of the animals and their behaviour around gillnets or due to a greater proportion of exploratory behaviour in young animals. Males and females are by-caught in similar proportions (Clausen & Andersen 1988; Berggren 1994; Kinze 1994). Vinther (1999) found a significant seasonal effect with highest by-catch rates in August - September. Clausen & Andersen (1988) reported a maximum between September and November. In the Swedish Kattegat fishery, largest numbers were taken in April and May (Berggren 1994) and in the German Baltic Sea highest by-catch numbers were observed between August and November (Kock & Benke 1996). This high variability can be explained by variable fishing effort and patchiness in porpoise distribution.

In the Baltic Sea as a whole the cod fishery in the Kattegat, Belt Seas and western Baltic with bottom-set nets appears to be the most important fishery with respect to harbour porpoise by-catch. For example in the Swedish fishery in the Kattegat, between 1973 and 1993 72% of the reported by-caught harbour porpoises (n = 175) were taken in cod nets (Berggren 1994). In the Danish fishery (Baltic and North Sea) between 1986 and 1989 23% of by-catches (n = 94) (Kinze 1994) and between September 1980 and February 1981 even 60% (n = 149) of reported by-catches were from cod nets (Clausen & Andersen 1988). In Germany most by-catches also occur in the cod-fishery (Benke 1994). Mean mesh size used in this fishery in the Baltic Sea is 12.5 cm. Nets used are typically between 1 and 2 m high and 600 m long and can be set in strings reaching lengths of over 4 km (Benke 1994; Vinther 1999)!

In addition the 'caviar' fishery for lumpfish (*Cyclopterus lumpus*), which is performed in spring in the waters north of Sjælland and the Belt Seas, is responsible for substantial by-catch numbers (Lowry & Teilmann 1994). In the Danish Baltic and North Sea (between 1986 and 1989) 36% of harbour porpoise by-catches (n = 94) were caught in this fishery (Kinze 1994). Mean mesh size used in this fishery is 25.6 to 27 cm (diagonal) with a very fine twine. Nets used are up to 2 m high (Vinther 1999).

Vessels from Russia, Finland, Sweden, Denmark, Poland and Germany participate in a large-scale pelagic driftnet fishery for salmon in the Baltic Proper (Christensen 1991). In the Swedish fishery in the Baltic Proper 53.8% of the reported by-caught harbour porpoises between 1973 and 1993 (n=13) were taken in surface salmon driftnets (Berggren 1994). Only three by-catches were reported for the Danish salmon fisheries in the Baltic Proper between 1986 and 1989 (Kinze 1994). The Polish fishery accounts for 4-6 by-caught animals each year (Skóra, pers. comm.), a large proportion of which is from salmon nets (Skóra 1991). From the other participating nations no data is available. Mean mesh size of driftnets used is 16 cm (diagonal), nets are up to 6 m high and strings are 0.8 to 5 km (!) long (cf. Ropelewski 1957; Christensen 1991; Vinther 1999). At first sight, these numbers do not seem to be high, but in earlier years, salmon driftnets appear to have caught more porpoises than today. In the early 1960s Lindroth (1962) obtained 50 specimens from Swedish fishermen for a porpoise prey analysis during one year! Since during that time conservation aspects played no role and harbour porpoises were considered a nuisance competing with salmon fishermen (Lindroth 1962) it can be speculated whether a major by-catch problem was simply overlooked because it seemed worthless to fishermen to report any by-catch. Polish annual by-catch numbers were at a maximum between 20 and 250 in the 1920s when a bounty was paid (Ropelewski 1957; Skóra *et al.* 1988).

In conclusion, it is not possible to quantify the threat by-catches represent to harbour porpoises in the Baltic Sea in the absence of reliable estimates of by-catches and abundance and with the present uncertainty over stock identity (e. g., IWC 1996). However, the existence of by-catch in several fisheries, and the high mortality level caused by it are a serious cause for concern. This warrants immediate action, especially if the stock of the Baltic Proper were, as shown above, isolated.

Environmental contaminants.- Contaminants are discussed as one of the main reasons for the decline in harbour porpoise populations in the Baltic Sea (e. g., Otterlind 1976; Teilmann & Lowry 1996). Contamination of the marine environment by anthropogenic inputs has increased dramatically during the last century. Many of the contaminants, such as certain PCB congeners or pesticides like DDT, which give the greatest cause for concern are relatively poorly metabolised or excreted by animals (e. g. Bruhn *et al.* 1999). As a result species higher up the food chain tend to accumulate higher burdens of these mostly lipidophilic persistent organic pollutants than those lower down (e. g., Busbee *et al.* 1999). As a consequence, the potential effects of environmental contaminants on small cetacean populations are of great concern. In general, lipidophilic pollutant levels increase with age in both sexes until sexual maturity is reached. In males, levels continue to rise after sexual maturation whereas in females they decline because the milk of lactating females takes up a considerable amount of these substances (Granby & Kinze 1991). For example adult harbour porpoise males from German Baltic waters had a PCB concentration eight times higher than adult females (BMBF 1997).

Harbour porpoises from the Baltic Sea carry a significant burden of these contaminants (e. g., Berggren *et al.* 1999a). Not much is known about the biological significance of high loads of many of these substances. It is almost impossible to correlate certain lesions or disorders found in porpoises to one specific pollutant (cf. Siebert *et al.* 1999) since a large number of different contaminants can be found in the food web which contribute to toxicity and which might even interact. Furthermore, several pollutants might contribute to disorders without having been identified yet: new pesticides and other chemicals are permanently being developed and released into the environment, while the understanding of their toxicology typically lags years behind (cf. Lozàn *et al.* 1996).

To date a wide range of high molecular weight organo-halogen compounds have been released into the environment, many of which are highly persistent and toxic. Several of these, in particular PCBs and members of the DDT "family" are ubiquitous contaminants accumulating in fatty tissues. PCBs have been claimed to be responsible for immunological deficiencies or reproductive abnormalities. De Swart *et al.* (1994) reported suppression of natural killer cell activity in harbour seals (*Phoca vitulina*). Uterine occlusions or stenosis were found in ringed seals (*Pusa hispida*) from the northern Gulf of Bothnia and grey seals (*Halichoerus grypus*) from the Baltic Proper (Helle *et al.* 1976b). Helle *et al.* (1976a) and Reijnders (1986) found less obvious signs of reduced fertility of seals due to PCB contamination. These were expressed in abortion or resorption of implanted ova. For a more detailed review of impacts see Busbee *et al.* (1999). Although similar PCB related disorders have not been reported for Baltic Sea harbour porpoises in conspicuous numbers, many workers seem to agree that they could have been overlooked (e. g., Otterlind 1976; Kinze pers. comm.) because no systematic analysis on reproduction of harbour porpoises from the Baltic Sea is available from the 1960s and 1970s, when these chemicals were used almost uncontrolled. In later studies, due to decreasing concentrations (cf. Kannan *et al.* 1993; Teilmann & Lowry 1996; Berggren *et al.* 1999a), contamination related effects can be assumed to be more diffuse. Neither Clausen & Andersen (1988) nor Sørensen & Kinze (1994) found evidence of reproduction failure of harbour porpoises caused by PCB contamination. However, the specimens in their studies were collected much later and a large proportion of the specimens were collected in the North Sea. A smaller part stemmed from the Kattegat, Belt Sea and western Baltic. No animals were from the Baltic Proper, where other studies found the highest concentrations (Table 3). Whether the reduced pregnancy rate of harbour porpoises in a sample from 1985-91 (Sørensen & Kinze 1994) compared to earlier studies or the finding of Clausen & Andersen (1988) of a 53 months old reproductively inactive female with ovaries developed like those found in juveniles might have been an effect of contaminants can only be a matter of speculation. However, it is possible that in the 1960s and 1970s contaminant concentrations in harbour porpoises reached levels that had a serious impact on their health and reproduction. Otterlind (1976) measured PCB concentrations in blubber from Baltic harbour porpoises by-caught

Table 3. Mean concentrations of some selected organochlorine compounds in harbour porpoise blubber samples. All values given in mg kg-1, except for sum PCDD/F [ng kg-1]. (m = male, f= female, mat. = mature, immat. = immature). For a better comparison, concentrations given per wet weight were transferred to approximate concentrations per lipid weight using a conversion factor of 1.25 (cf. Christie 1982).

sampling area reference	sampling and measuring details	sum PCB (range)	CB 153	DDE	DDT (range)	gamma-HCH	sum PCDD/F
German Baltic Sea Bruhn *et al.* (1999)	1993-96,m+f, immat., per lipid weight	14.9 (5.6-38.5)	2.9	4.8	<0.0015	0.6	1.3
Danish Baltic Sea Otterlind (1976)	1974-75, m+f?, immat., per lipid weight	142 (68-210)					
Danish Baltic Sea Granby & Kinze (1991)	1986-88,m+f, immat., per wet weight, transf. to lipid wt	18.4 (1.9-60.5)	6.2	8.6	6.5	0.5	
Danish North and Baltic Sea Clausen & Andersen (1988)	1980-81, m+f mat. + immat. per wet weight, transf. to lipid wt	82.4 (3.7-340)			23.5 (1.4-180)		
Swedish Kattegat / Skagerrak Otterlind (1976)	1972-76, m+f?, immat., per lipid weight	159.4 (36.4-260)					
Swedish Kattegat / Skagerrak Berggren *et al.* (1999a)	1978-81,m, mat., per lipid weight	40 (17-67)	19		46		19
Swedish Kattegat / Skagerrak Berggren *et al.* (1999a)	1989-90,m, immat., per lipid weight	11 (2.2-20)	4.8		6.4		9.2
Swedish Kattegat / Skagerrak Berggren *et al.* (1999a)	1988-90,m, mat., per lipid weight	13 (6.7-22)	5.7		10		6
Baltic Proper (Sweden) Otterlind (1976)	1970-75, m+f, 6 immat., 2 mat., per lipid weight	93.4 (28-190)					
Baltic Proper (Sweden) Berggren *et al.* (1999a)	1985-93,m, immat., per lipid weight	16 (2.9-32)	6.6		7.1		13
Baltic Proper (Sweden) Berggren *et al.* (1999a)	1988-89,m, mat., per lipid weight	46 (14-78)	20		49		36
Baltic Proper (Poland) Falandysz *et al.* (1994)	1989-90,f, 2 immat., 1 mat., per wet weight, transf. to lipid wt	39.1 (36.3-52.5)	9.9				

between 1970 and 1975. As shown in Table 3 he found mean concentrations of PCB congeners ranging from 93 mg kg^{-1} lipid weight (n=8) on the Swedish east coast to 159.4 mg kg^{-1} lipid weight (n=6) on the west coast in mostly immature animals. These concentrations were similar to those found in the seal study of Helle *et al.* (1976a) who found mean values of 110 mg kg^{-1} in extractable fat of females with uterine occlusions (n=40). Levels of PCBs in the 1990s from the Swedish west coast (Berggren *et al.* 1999a) correspond well with levels from Danish (Granby & Kinze 1991) or German waters (Bruhn *et al.* 1999). Concentrations found in the Baltic Proper were up to three times higher (Falandysz *et al.* 1994; Berggren *et al.* 1999a). Although there were some differences in age distribution between samples, these figures show a clear trend.

During the last decades, pollutant levels recorded for Baltic Sea harbour porpoises declined (cf. Kannan *et al.* 1993). Table 3 shows markedly lower concentrations of PCBs in samples from 1986-90 (Granby & Kinze 1991; Berggren *et al.* 1999a) compared to samples from 1978-81 (Clausen & Andersen 1988; Berggren *et al.* 1999a). These latter values were already lower than concentrations in animals sampled in the 1970s (Otterlind 1976; Andersen & Rebsdorff 1976 - cited in Granby & Kinze 1991). But still, the contaminant levels recorded for organochlorine components are a serious cause for concern.

Whereas older studies on PCB concentrations only determined the sum of PCB congeners new multidimensional gas chromatography techniques made it possible to investigate congener specific data (Duinker *et al.* 1988a,b). Specific congener distribution patterns help in identifying harbour porpoise population structure (see above) and allow conclusions on metabolism of single compounds (cf. Bruhn *et al.* 1995). In all studies conducted to date, PCB concentrations showed great individual variation. In recent years, polybrominated compounds have been used to replace PCBs. The biological effects of these compounds are not fully understood yet and as a consequence their concentrations in the marine food web should be monitored carefully.

Table 3 also shows concentrations of some other selected organochlorine contaminants. DDT levels found in the Baltic Proper were up to ten times higher than levels found on the Swedish west coast (Falandysz *et al.* 1994; Berggren *et al.* 1999a). Similar to the downward trend in PCBs the more recent studies show a decline in DDT concentrations as compared to the older studies.

Animals from the Baltic Proper had a higher mean level of polychlorinated dibenzodioxins and -furans (PCDD/F) than the corresponding sample from the Kattegat and Skagerrak area (Berggren *et al.* 1999a). Bruhn *et al.* (1999) suggest that due to the toxic equivalents of certain congener concentrations they found in harbour porpoises, PCDD/F are ecotoxicologically less important than PCBs. The major contributors to PCB concentrations are CB 153 and CB 138 (Granby & Kinze 1991; Berggren *et al.* 1999a; Bruhn *et al.* 1999), both non-metabolisable chemicals (Bruhn *et al.* 1995).

Other pesticides identified in Baltic harbour porpoises include hexachlorocyclohexane (HCH) isomers including lindane (gamma-HCH), and hexachlorobenzene (HCB) (Granby & Kinze 1991; Kannan *et al.* 1993; Hummert *et al.* 1995; Bruhn *et al.* 1999). In harbour porpoises from the Polish coast, relatively high concentrations of the pesticides aldrin, dieldrin and chlordane were identified. Furthermore mirex, heptachlor and heptachlor epoxide were found in their blubber (Kannan *et al.* 1993; Strandberg *et al.* 1998). Strandberg *et al.* (1998) found highest biomagnification factors in harbour porpoises in relation to herring for chlordanes (accumulated with a factor of up to 25), dieldrin, PCBs and DDTs, followed by HCB and HCH. Polychlorinated naphtalenes (PCNs) were studied by Falandysz & Rappe (1996) in a pelagic food web in the southern Baltic Sea. CN 66 and 67 were identified as congeners with a high bioaccumulative potential. Possible sources of PCNs are chlorine production, waste incineration or the use of dielectric fluids, flame-retardants and fungicides. Not much is known about the possible effects of PCNs on cetaceans. In birds, PCNs have been shown to be embryotoxic. In the blubber of two male and two female harbour porpoises sampled along the Polish coast considerable amounts of PCNs were detected (Falandysz & Rappe 1996).

Non-essential metals are those that have no recorded biological function in a species, including heavy metals such as mercury, lead and cadmium. Concentrations of these metals in the Baltic Sea are recognised as relatively low (Clausen & Andersen 1988; Teilmann & Lowry 1996). However, some heavy metals are often toxic even at relatively low levels (Bowles 1999). Mercury shows biomagnification at all levels of the food chain and concentrations in cetacean species show a positive correlation with age (Siebert *et al.* 1999). Mercury mainly accumulates in the liver (Szefer *et al.* 1994, 1995) and is known for its high toxicity, long biological half-life and lipophilicity (Bowles 1999). Especially its organic form, methylmercury is known to cause serious disorders in liver, kidney and brain, and may have immunosuppressive effects (Bowles 1999). A tolerance level of 100 - 400 mg kg^{-1} (wet weight) in hepatic tissue was proposed by earlier studies to be a threshold

Table 4. Concentrations of some selected heavy metals in harbour porpoise tissue samples. All values given in mg kg^{-1}. (m = male, f= female, mat. = mature, immat. = immature).

sampling area reference	sampling and measuring details	cadmium in liver (range)	cadmium in kidney (range)	mercury in kidney (range)	mercury in liver (range)
Baltic Proper (Poland) Szefer et al. (1995)	1989-93,m+f, 12 immat., per dry weight	0.29 (0.02-0.7)	1.6 (0.2-3.9)	5.2 (2.1-13.2)	19.6 (2.1-52.3)
German Baltic and North Sea Siebert et al. (1999)	1991-93,m+f, mat. + immat., per dry weight			9.6 (0.5-160)	38.8 (0.6-449)
German Baltic and North Sea Siebert et al. (1999)	1991-93,m+f, mat. + immat., per wet weight			2.3 (0.1-33.5)	12.1 (0.2-130)
Danish Baltic and North Sea Clausen & Andersen (1988)	1980-81,m+f, mat. + immat., per wet weight		0.4 (0.01-1.6)	1.2	

for lesions (see Bowles 1999 for review). Cadmium and lead accumulate best in kidney tissue (Szefer *et al.* 1994, 1995; Bowles 1999). In humans, cadmium causes renal damage above concentrations of 200 - 400 mg kg^{-1} wet weight (Bowles 1999). Lead may cause severe brain damage, kidney damage or anaemia. The major route of lead into the Baltic Sea area used to be via the atmosphere from car exhaust emissions prior to the use of unleaded gasoline (Bowles 1999).

Table 4 shows some heavy metal concentrations of harbour porpoises from the Baltic Sea. Harbour porpoises carry a significant burden of mercury. Liver tissue of porpoises of all age classes from German waters (Baltic and North Sea) had a mean concentration of 38.8 mg kg^{-1} (dry weight) (Siebert *et al.* 1999). Mean concentrations in twelve presumably immature harbour porpoises from the Polish Baltic Sea coast were about half as high (Szefer *et al.* 1995). The higher mean mercury level in German animals is probably due to differences in age structure and higher values of North Sea animals which were included in the calculation of the mean level (Siebert *et al.* 1999). Although some of the specimens in the German study reached the tolerance limit of 100 to 400 mg kg^{-1} (wet weight) (sample range was 0.2 to 130) no signs of acute or chronic toxic effects were detected. According to Siebert *et al.* (1999) "there were significant associations between mercury levels and severity of lesions (mainly caused by helminths) with respective to nutritional state [...] and adjusted for the effects of age and location". Kidney tissue cadmium levels were roughly in the same order in western and eastern Baltic samples. Relatively low mean cadmium levels in the order of 1.6 mg kg^{-1} (dry weight) were reported from Polish immature harbour porpoises. The corresponding level from inner Danish waters was roughly in the same order (0.4 mg kg^{-1} wet weight) (Clausen & Andersen 1988). However, the data from both studies are not directly comparable, due to differences in age structure of samples and analytical methods. Szefer *et al.* (1994) recorded a maximum level of 7.5 mg kg^{-1} (dry weight) lead in kidneys of Polish immature harbour porpoises. Two of the animals from the Polish study had markedly elevated levels of silver in their livers indicating that these individuals were exposed to point sources of pollution (e. g., harbours and industrial plants).

Tributyltin (TBT) has been used extensively in antifouling paints for over 30 years. TBT has been identified as a substance that has hormone-like effects causing sex changes in gastropods (e. g., Bryan *et al.* 1986) or embryotoxic effects in fish (e. g., Fent 1992). Kannan & Falandysz (1997) showed that in the harbour porpoise butyltins are transferred from mother to calf as they found concentrations of 18 and 27 ng g^{-1} (wet weight) in liver tissues of two neonates. From the analysis of fish and seabird concentrations they also suggested a trophic transfer. Due to its hormone-like structure, TBT might cause disorders even in very low concentrations and should be monitored carefully (e. g., Bryan et al. 1986).

Hydrocarbons can be conveniently divided into aliphatic and aromatic compounds. The polycyclic aromatic hydrocarbons (PAHs) are known to be potent carcinogens. The major source of all hydrocarbons in the marine environment is from the extraction, transportation and incineration of fossil fuels. A substantial part also comes from routine ship operation or oil spills. No information was found on the effect of these contaminants on harbour porpoises in the Baltic Sea. Since ship traffic on the Baltic Sea is expected to increase in the future, it can be anticipated that a larger amount of hydrocarbons will be discarded into the Baltic Sea.

Overexploitation.- As discussed earlier, substantial numbers of harbour porpoises were hunted in historical times. Otterlind (1976) suspects an unsustainable use of porpoise stocks during historical catch periods, resulting in a sharp decline of harbour porpoises moving through the Danish straights and low numbers in the Baltic Proper. This is also discussed in papers in combination with other factors like entrapment of large numbers of animals during ice winters (e. g., Schulze 1996). However, since it is unknown from where the hunted animals originated, the impact on any of the putative subpopulations is only a matter of speculation. Declining catches of harbour porpoises in the Little Belt after the period 1834-1892 do not provide conclusive evidence on declined stocks. They were explained by market shifts from harbour porpoise oil products to the cheaper oil of large whales and by increased use of electricity for lighting (Mohr 1935, cited in Schulze 1996).

Overfishing.- The effects of overfishing may be deleterious or advantageous to a particular population, depending on the target species of the fishery. If the stock of a competitor is reduced, this might be positive for harbour porpoises. A negative effect is likely to occur when the fishery and the cetaceans compete for the same target species. It has been suggested that the decline in strandings of harbour porpoises off the Dutch coast during the 1970's may have been caused by a reduction in the herring stocks through overfishing (Reijnders 1992). This is supported by the fact that the recovering of herring stocks in the 1980s was followed by an increase in porpoise sightings off the Dutch coast (Camphuysen 1994). Generally, little is known about the effects of fisheries on cetacean food resources. Reduction in certain food resources may force harbour porpoises to switch prey. As shown above there is considerable variation in prey selection and it appears that porpoises can switch to other prey if a preferred species is lacking. However, if manifold prey species are depleted porpoises could be forced into a suboptimal niche or habitat. This may have effects on distribution and the long-term viability of porpoise stocks (IWC 1996).

Noise.- Sources of noise in the marine environment of the Baltic Sea include ships, power boats and jet skis, aircraft, offshore wind power generators, and a range of other activities. Because of the relative ease of sound propagation in water, sound effects are more pervasive in the marine environment than in air (cf. Richardson et al. 1995). Noise may cause masking of naturally-generated sounds, impairing interspecific communication or negatively affect prey detection (Au 1993). Andersen (1976) assumes that neonate harbour porpoises are not able to gain enough weight for their first winter if heavily disturbed in the nursing areas e.g., by speedboats. In its most extreme form, i. e. during underwater explosions, the possibility of hearing loss and other injuries must be considered (Richardson *et al.* 1995). However, harbour porpoises are often observed in areas with heavy ship or boat traffic, e. g., the Danish straits. One of the highest harbour porpoise densities found in the SCANS survey was in the Great Belt, a busy shipping lane and construction area of a major bridge by the time of the survey (Hammond *et al.* 1995). The distribution and presence in conjunction with large numbers of vessels rather indicate a certain tolerance for marine traffic. However, this depends on the vessel type, traffic density or the individual harbour porpoise (Kinze 1985b, 1990) Especially, fast moving vessels such as speedboats deter harbour porpoises (e. g., Amundin & Amundin 1974; Kinze 1990). Hence, it can be speculated that fast ferries, which are increasing in numbers on the Baltic Sea now, also have a negative impact. At the moment, plans for major offshore wind power plants in the Baltic Sea are being assessed (Federal Maritime and Hydrographic Agency of Germany, pers. comm.). Because a recent study showed that harbour porpoises will avoid the underwater sound of a wind power generator (Koschinski & Culik, unpublished data), the aspect of noise during construction and operation must be considered.

IMPLICATIONS FOR MANAGEMENT

The status of the harbour porpoise in the Baltic Sea is a subject of concern. This has been concluded from substantial incidental catches in bottom set gillnets, from indications of declines in several parts of the Baltic and from the possibility that contaminants can affect the long-term viability of the stock.

As shown here, the gillnet fishery is one of the most threatening activity for Baltic Sea harbour porpoises. For an impact assessment, different types of information are required: (1) mortality induced by each identified fishery, (2) distributional limits and the size of the subpopulations affected, (3) the carrying capacity and (4) the potential for increase of subpopulations.

The monitoring of these different variables is very important to assess the success of fishery related conservation measures (e. g., Clarke *et al.* 1997; IWC 2000). To date neither mortality, abundance nor population structure are known for Baltic Sea harbour porpoises. Possible density dependent changes in the ASM and survival rates make it difficult to model trends in abundance using simulation trials (cf. IWC 2000). Therefore the initial state of the population cannot be determined exactly. As a consequence, the recovery time for populations to reach the ASCOBANS conservation objectives - to restore populations to a level of 80% of the carrying capacity (ASCOBANS 1997a) - cannot be estimated. Although no time frame is defined in ASCOBANS within which these conservation objectives are to be achieved, immediate political action is required.

The importance of using independent observers to collect by-catch data and recording total fishing effort in each region has been recognised (e. g., IWC 1994, 1995, 1996, 1997) but until now almost no such information has become available. Since most data on take numbers are based on fishermen's reports, these must be regarded as the absolute minimum. Most likely they are much higher because fishermen might not report all animals caught (e. g. Clausen & Andersen 1988; IWC 1994, 1995, 1996, 1997).

Other data from by-caught animals (e. g., sex, age, date, location or genetic information) are extremely valuable for the assessment of the actual rate of increase or decrease and the capacity for increase of each subpopulation. Therefore, the collection of these carcasses for post-mortem analysis should be assured (e. g., IWC 1991, 1995).

From a management perspective, there is sufficient evidence to suggest that at least two sub-units for the harbour porpoises in the Baltic Sea area must be considered, one in the Kattegat and Belt Seas, and the other in the Baltic Proper. In a review of the status of the harbour porpoise in Danish waters, it has been mentioned that the numbers in the former area are quite stable, although reduced (Teilmann & Lowry 1996). In the Baltic Proper, however, harbour porpoises appear to be depleted and concern was raised over the viability of this stock (e. g., Berggren & Arrhenius 1995a,b). The precautionary principle calls for minimising all threatening activities if an adverse impact is suspected or even if there is deficient information to prove an adverse effect. Thus, by-catch in gillnets, disturbance to areas of apparent importance, emission or discard of contaminants, and over-fishing must be phased out.

Many studies relevant to most topics mentioned above were conducted during the past decades and contributed to the knowledge about Baltic Sea harbour porpoises. However, only a small proportion of the needed information has been gathered in sufficient detail. Therefore little is known about some key topics, including population structure, habitat use or migrations of harbour porpoises from the Baltic Proper (e. g., IWC 1991, 1992, 1994, 1997, 1998, 2000).

Research needs.- Consequently further research is needed to enlighten the mysteries about Baltic Sea harbour porpoises. One of the most important areas of research is the determination of the population sub-structure (e. g., IWC 1991, 1992, 1995, 1996, 1998) using a combination of various methods (population genetics, morphometrics and maybe tooth ultrastructure) on the same samples which ideally stem from all over the Baltic Sea with special reference to the Baltic Proper. To exclude sampling bias by drifting carcasses, only by-caught or fresh stranded animals should be taken. Since it is difficult to assess to what extent migrational movements add to sampling bias, ideally, adult animals by-caught in summer or neonates (<1 yr) should be analysed separately. In the reviewed studies, specimens were assigned to *a priori* defined groups. These were subsequently compared. Unfortunately, it is difficult to discern the distributional barriers for a highly mobile species such as the harbour porpoise. This could result in some bias since animals from different sub-units may be lumped together or individuals from the same sub-unit may be split up.

It is extremely difficult to obtain better estimates of life history parameters than in the studies mentioned above because of the various and often unknown biases in the composition of samples from by-catches or strandings affecting the age, sex or reproductive condition of animals (IWC 1996). However, since this is one of the critical points in simulation models of population dynamics further research is necessary (e. g., IWC 2000).

Furthermore, acoustic methods must be developed to determine harbour porpoise abundance in areas with very low densities (Clarke *et al.* 1997). For abundance estimates, shipboard surveys using line transect sampling have been proven to be effective only when high densities are expected, whereas aerial surveys are suitable when a large area with a lower density has to be covered (Hammond *et al.* 1995; Clarke *et al.* 1997). However, for areas with a very low density, no effective techniques exist. A combination of sightings surveys with acoustic methods using click detectors could be successful here. Click detectors can also be helpful when surveys are undertaken during poor sighting conditions, e. g., in seasons other than summer.

Another important area of research is the investigation of movement patterns of individuals of different subpopulations with a special focus on the Baltic Proper (e. g., IWC 1991, 1995, 1996, 1998). The identification of critical habitat (e. g., for breeding and overwintering) must be prioritised in order to suggest position and size of possible marine protected areas or time closures for certain human activities. Further, the impact of disturbances (e. g., fast moving vessels, noise of windpower plants, construction, etc.) must be assessed (e. g., IWC 1991).

An important conservation measure would be the development of new fishing techniques (e. g., IWC 1992, 1995). More effort should be put into research in this field. The use of acoustic pingers in nets with a high by-catch potential should just be considered as an interim measure. Although there are some indications that active acoustic modifications may eventually result in a reduction in by-catches in some fisheries (e. g., Kraus *et al.* 1997; Larsen 1999) a number of problems still have to be resolved (e. g., IWC 2000). For example the questions of habituation to sound sources (cf. Koschinski & Culik 1997; Teilmann 2000) and displacement from food sources and habitat (cf. Culik *et al.* 2001) have not been sufficiently dealt with.

Political action needs.- Effective management must also include immediate means of mitigating threatening anthropogenic activities. In this respect it is important to (1) establish large marine protected areas within critical habitat of harbour porpoises (2) take measures to phase out by-catch in gillnets, disturbance to critical habitat, disposal of contaminants, and over-fishing, (3) compile appropriate fisheries statistics including fishing effort as opposed to only landings to allow estimates of total annual by-catch for each area, (4) establish mandatory observer programmes in the fisheries, (5) initiate conservation measures like time- and area-closures and other restrictions on fishing activity if the by-catch of certain fisheries is likely to be unsustainable (e. g., IWC 1995, 1998, 2000). It should also be considered to phase out fishing methods requiring a large gillnetting effort for a relatively low yield (e. g., the salmon drift net fishery).

Acknowledgements.- This study was made possible by a grant of IFAW Germany. Harald Benke, Stefan Huggenberger, Carl Kinze, Karl-Hermann Kock, Finn Larsen, Christina Lockyer, Kai Mattsson, Valdis Pilats, Gerhard Schulze, Krzysztof Skóra and Jonas Teilmann added bits and pieces of background information. Silke Hansen helped with translation of Swedish and Finnish sources. Two anonymous reviewers improved the manuscript by giving helpful comments.

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