

A review of methods for defining population structure in the harbour porpoise (*Phocoena phocoena*)

Christina Lockyer

Danish Institute for Fisheries Research, Charlottenlund Slot, DK 2920 Charlottenlund, Denmark. Currently of the Age Dynamics, Huldbergs Alle 42, DK 2800 Lyngby, Denmark.

ABSTRACT

Wide-ranging methods that have been used to determine population structure, including distribution, life history, biology, ecological factors such as diet and contaminant loads, morphology and genetics, are reviewed. The importance of determining population sub-structure of harbour porpoise throughout the North Atlantic, especially in regions affected by incidental take in fisheries, is discussed in relation to management measures. Some practical proposals are made for integrating diverse information about populations, using the phylogeographic approach, for the purpose of evaluating the need to manage putative subpopulations separately. Examples focusing on the North and Baltic seas areas are used in this discussion, with some reference to other areas. It is concluded that the existing IWC proposal for 13 populations in the North Atlantic is generally supported, but with some refinement and modification; in particular, allowing sub-divisions in the area through the North Sea to the Baltic.

Lockyer, C. 2003. A review of methods for defining population structure in the harbour porpoise (*Phocoena phocoena*). *NAMMCO Sci. Publ.* 5:41-70.

INTRODUCTION

The rationale for studies on the population structure of the harbour porpoise, *Phocoena phocoena*, is primarily based on the need to provide advice on conservation and management issues concerning this species. The need for advice has been triggered by recent international recognition of threats to the species (IWC 1994, 1997, 2000, ASCOBANS 1992, 1994, 1997, 2000, ICES 1997, NAMMCO 2001, Stenson 2002, Vinther 1999) focusing mainly on incidental catches in North Atlantic fisheries operations, notably bottom-set gill-nets. Such threats exist throughout the North Atlantic but are of particular concern to the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS) within its leg-

islative geographical region, which includes the North Sea, Kattegat-Skagerrak and inner Danish waters and the Baltic, to the North Atlantic Marine Mammal Commission (NAMMCO) in the region of the Northeast Atlantic, and to the International Whaling Commission (IWC) Scientific Committee's sub-committee on small cetaceans throughout the entire distributional range of the species. By combining information on numbers of bycaught animals with distribution and abundance obtained, for example, from the Small Cetacean Abundance in the North Sea (SCANS) surveys of June-August 1994 (Hammond *et al.* 2002) throughout the Celtic Shelf, North Sea, Kattegat-Skagerrak and inner Danish waters, it is theoretically possible to estimate bycatch rates in these areas. However, the question for management is whether or not the

areas are populated by a single panmictic group. The alternative is a basic group infra-structure with sub-populations either with discrete boundaries or overlapping boundaries where mixing and interbreeding are taking place. Such factors have grave implications for survival of the harbour porpoise if the rate of removals exceeds the replacement rate of a discrete group within a defined geographical area. Such a population will not necessarily be replaced by immigrants from outside. The main practical purpose of defining a population is therefore, "to direct management efforts to taxon levels below that of the species to ensure that populations that are uniquely adapted to given areas are not irreversibly reduced by harvest or habitat destruction" (Dizon et al, 1992). It is from this standpoint that the following review is written.

The first matter for consideration is the function of the terms "population", "subpopulation" and "stock". All these terms have been used loosely to describe groups of animals distinguishable as such within a species. Donovan (1991) noted, with respect to the IWC, "... definition of stock depends very much on the purpose for which separation is required (Allen 1980). In simple terms one can consider two general 'stock' types: *biological stocks* based on genetic separation; and *management stocks* which can be thought of as population units that can be successfully managed". In fact, although *biological stocks* may be defined primarily on genetic separation, other important biological factors, e.g. feeding habits, migration patterns, and contaminant loads, may also be used as valid criteria. The term 'population' will be used as equivalent to 'stock' which defined at the molecular level is the *Evolutionarily Significant Unit* or ESU (Ryder 1986, Bernatchez 1995, Moritz 1994a, b) which is a natural biological population distinguishable by its evolutionary uniqueness and significance (Dizon et al. 1992). In order to satisfy ESU categorisation, there must firstly be substantial reproductive isolation between the putative population and others, and secondly, the population unit must represent an important component of the species' evolutionary legacy. In practice this is a difficult definition to apply. Moritz, (1994a, b) has discussed this issue and defined the *Management*

Unit or MU which is generally regarded as a better criterion for defining biological populations. The MU is defined by significant divergence in allele frequencies at nuclear or mitochondrial (mt) DNA loci, regardless of the phylogenetic distinctiveness of the alleles, because allele frequencies will respond to population isolation more rapidly than the phylogeographic patterns.

There are several additional confounding factors when considering population structure, such as segregation within a population itself by age, sex and reproductive maturity, and even the extent of mobility of individuals. Segregation may exist seasonally, and in relation to environmental factors such as availability of food resources, sea temperature or ice cover, and biological factors like breeding and calving. Therefore, it is important to consider these factors when collecting and analysing samples from a putative population in order to avert biases. This is one important argument for attempting to integrate a variety of information, e.g. genetic, phenotypic, phylogeographic and environmental, because animals may move around and mix widely but only breed in certain specific areas. Thus genetic information from mt DNA might divulge a lot about maternal population structure, whereas satellite tagging may inform about the movements of individuals perhaps genetically unrelated. Both may provide information about seasonal changes in distribution. Nuclear DNA (e.g. microsatellites) may clarify genetic relatedness in an area and between areas, while fatty acid profiles in blubber, along with contaminant levels and parasites, may reveal recent feeding strategies and distribution, and distributional patterns of different populations in the same region. The situation may therefore be highly complex and difficult to interpret.

Gaskin (1984) proposed a total of 14 stocks or subpopulations, which will be hereafter referred to as populations in this review, of harbour porpoise throughout the North Atlantic region (see also Rosel 1997), and more recently the IWC (1996) revised this to 13 (see Fig.1). Gaskin admitted that much of the original classification was likely to be speculative. Putative populations of concern to ASCOBANS number

eight, including 1) Faroe Islands and Faroe Bank (stock 6 in Fig.1); 2) southwest Ireland and southwest England to north Scotland (stock 11 in Fig.1); 3) English Channel (no IWC designation, but defined separately with Biscay by Gaskin 1984); 4) east coast of England and Scotland (stock 8 - central North Sea in Fig.1); 5) mainland coast of Europe from Dover Strait, UK to Skagen, Denmark (stock 8 - southern North Sea in Fig.1); 6) Skagerrak, Kattegat and Danish island shelves to Gulf of Riga and Gulf of Finland (stock 9, and stock 10 - Baltic Sea in Fig.1); 7) Gulf of Bothnia (stock 10 - Baltic Sea in Fig.1) and 8) southern Norway from Skagerrak to Vest Fjord (stock 8 - northern North Sea in Fig.1). These represent a breakdown or modification of 6 of Gaskin's putative populations in this region, with additional subdivisions within the North and Baltic seas. In March 1999, a joint IWC-ASCOBANS working group addressed the porpoise population structure issue again, and recognised extra subdivisions within the North Sea, Kattegat and Skagerrak (IWC 1999). Since then there have been further proposals for subdivisions (Andersen *et al.* 2001) within the North Sea.

A special meeting was held by the US National

Marine Fisheries Service in Woods Hole, in February 1994, when four hypotheses were discussed concerning population structure within the North Atlantic:

- H_0 : 14 discrete populations;
- H_1 : some number of populations (14 or less) with small amounts of mixing among them;
- H_2 : some number of populations with large amounts of mixing between them;
- H_3 : complete panmixia across the entire North Atlantic.

However, H_0 and H_3 were ruled out by then currently available data. The methods listed in Table 1 were then evaluated regarding strengths and weaknesses in testing these hypotheses, and are expanded from the original.

An assessment was also made at that time of the availability of material and/or data for such analyses, the extent of analytical requirements and the stage of development of suitable techniques. At that time most were classified at a low stage of development, although many of these techniques, notably genetic techniques,

Fig. 1. Revision of Gaskin's (1984) harbour porpoise population divisions - after IWC (1996).

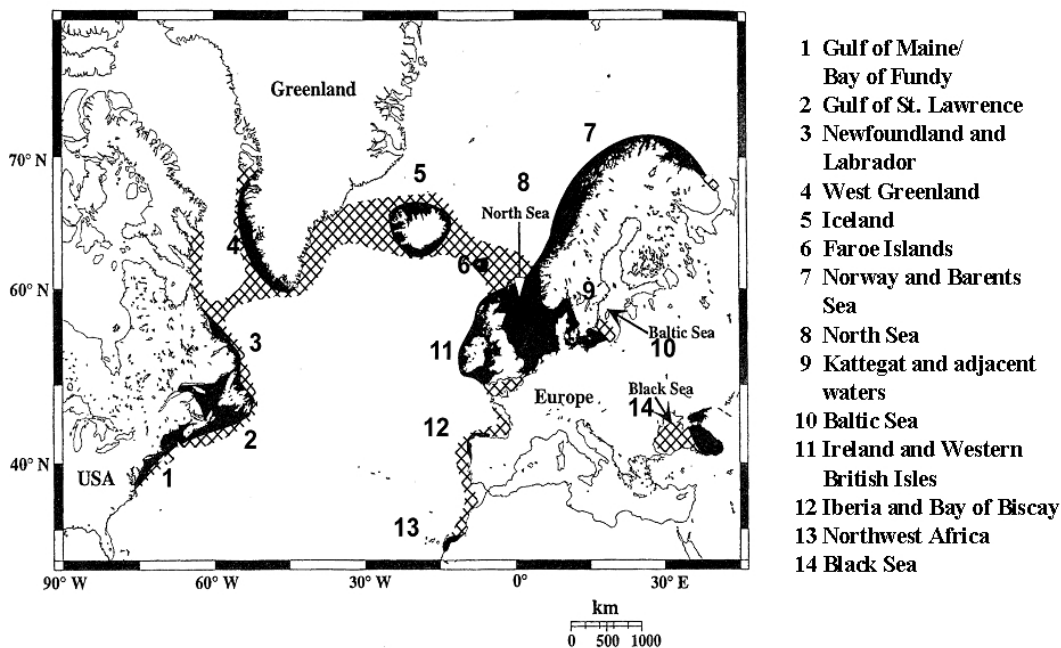


Table 1. Methods for testing hypotheses regarding putative populations, with relative importance and limitations.

Method	1H0 False	2H1	3H2	4H3 False	Relative importance	Limitation
Tagging for movements	5X	X	X		Medium/Low	Needs much effort; informs about individuals; does not tell about reproductive (genetic) mixing.
Biological parameters					Medium/High	Generally stable information, but may be affected by the environment: food supply; pollutants, exploitation which can lead to trends over time; seasonal variations; informs about populations; can be labour intensive.
Timing of breeding		X	X	X		
Life history parameters		X	X	X		
Parasite load and disease		X	X	X		
Tooth ultrastructure			X	X		
Chemical signals and diet					Medium	Can provide clear-cut definitions for populations, but may change over time – years for pollutants, but maybe only months for fatty acid signatures; does not tell about reproduction; labour intensive.
Organochlorine load		X	X			
Heavy metal load		X	X			
Isotope load		X	X			
Fatty acid signatures		X	X			
Morphology					Medium/High	Persistent in individuals; reflects genotype but may be affected by environment and ecology; informs about individuals and populations.
Non-metric skull characters	X	X		X		
Morphometrics of skeleton	X	X		X		
Tooth ultrastructure	X	X		X		
Genetics					High	Persistent; informs about individuals and populations; mt DNA is sex-linked; micro-sats represent nuclear DNA; allozymes are phenotypic expression of genotype; all methods together are very powerful tool
mt DNA sequencing	X	X	X?			
DNA micro-satellites	X	X	X?	X		
mt DNA RFLP	X?	?	?	X		
Allozyme electrophoresis	X	X	X?	X		
1H0 : 14 discrete populations						
2H1 : some number of populations (14 or less) with small amounts of mixing among them						
3H2 : some number of populations with large amounts of mixing between them						
4H3 : complete panmixia across the entire North Atlantic						
5X : method good for testing hypothesis; X? or ? indicates possibly useful; no comment indicates not useful						

chemical techniques and tagging have progressed. Much of the above was presented to the IWC (IWC 1995), ASCOBANS and ICES in 1994 (Palka *et al.* MS 1994) in a research proposal to investigate the population structure of the harbour porpoise, and was endorsed and encouraged by all 3 organisations.

Since then, there has been progress in the development of the different methods, and in particular, in exchanging data and material for genetic studies (Tolley *et al.* 1999, 2001). Researchers have been active within the ASCOBANS area, and some progress has been made (IWC 2000).

In this paper, I attempt to summarise facts known and recent progress, draw some conclusions on what we know of population structure of North Atlantic harbour porpoises to date, and explore ways that this information could be used in a management context.

A REVIEW OF FINDINGS FROM DIFFERENT METHODS

The following is a review of various findings that have relevance to population structure, and considers each of the 5 methods listed in Table 1. The nature of the methods ranks them dif-

ferently in their ability to differentiate between populations. The genetic approach is clearly able to discriminate between populations on an absolute basis if the time scale of separation and divergence is long enough. However it may fail if separation is very recent. However, other methods, particularly biological parameters, chemical signals and to some extent morphological characteristics, incorporate environmental and ecological influences to greater or lesser extents and can identify separation on a recent time scale even if genetic divergence has not yet occurred. The focus is on the eastern North Atlantic, although reference is also made, when pertinent, to central and western North Atlantic areas which have already been covered by Palka *et al.* (1996) and Rosel (1997).

TAGGING

Recently there have been several experimental programmes to tag porpoises with satellite telemetric devices that record not only position but also dive depth and time (Fig. 2). Notably these have been conducted off the western coast of Sweden in 1996 when one animal was tagged in the Skagerrak where it remained for a total of 41 days (Berggren *et al.* MS 1996). Nine porpoises have been satellite-tagged successfully



Fig. 2. A harbour porpoise with a satellite-linked radio transmitter mounted on its dorsal fin. Such applications provide information about local movements and seasonal migrations, and about habitat use. Photo: J. Teilmann.

with time-depth recorders off the eastern Canadian coast, Grand Manan Island at the mouth of the Bay of Fundy in 1994 and 1995 (Read and Westgate 1997, Westgate *et al.* 1995, (MS) 1998a), of which 5 moved out of the Bay of Fundy area into the Gulf of Maine. A rehabilitated female porpoise, tagged and released off the east coast of the USA southeast of New Jersey moved widely and as far north as Cape Cod during a period of 50 days (Westgate *et al.* 1998b). More recently, between April 1997 and July 1999, there have been 17 successful attempts with deployment of satellite tags in Danish waters, which have remained on the animals for 14 to 255 days (Teilmann 2000). Most results were for spring and summer but one animal was monitored all winter. Movements were often extensive and extended from southeast Norway in the Skagerrak (approx. 59° N 10° E), through the Kattegat and Danish belt seas through to Øland (approx. 56° N 17° E), off Sweden in the Baltic. None of the animals moved into the North Sea during the study. However, there has since been one animal that did relocate a short distance into the North Sea. (J. Teilmann, National Environmental Research Institute, Dept of Arctic Environment, Postboks 358, DK-4000 Roskilde, Denmark, pers. comm.). There appeared to be considerable individual variation, but movements were greater in spring and autumn (20 to 30 km per day) and least in summer and winter (5 to 10 km per day). The immature animals showed the greatest dispersion from the tagging site. The conclusion from this study indicated that for management purposes, the porpoises within the area of north Skagerrak through to the western Baltic might be considered as one continuous population. We may assume that this methodology is now not only feasible but directly informative, and will increase in application.

BIOLOGICAL PARAMETERS

There have been several studies of biological parameters of porpoises throughout the North Atlantic in recent years. These cover a range of aspects from age parameters, size at birth and sexual maturity, adult size, to longevity and growth coefficients, and features of reproduction. Information on biological parameters and reproduction from recent times are reviewed in

Lockyer (2003), and are available for Canada and east coast USA (Gaskin *et al.* 1984, Read 1990a, b, Read and Gaskin 1990, Read and Hohn 1995, Read and Tolley 1997, Richardson 1992), Netherlands (Addink *et al.* MS 1995, Addink *et al.* 1995), British Isles (Lockyer 1995a, b, c), Germany (Bandomir-Krischak 1996, Benke *et al.* 1998), Denmark (Sørensen and Kinze MS 1990, Sørensen and Kinze 1994, Lockyer and Kinze 2003), and Norway (Bjørge *et al.* 1991, Kaarstad 1993). In addition there is information from West Greenland (Lockyer *et al.* 2001, 2003), Iceland (Ólafsdóttir *et al.* 2003) and other regions already mentioned.

Studies off the Dutch coast (Addink *et al.* MS 1995, Addink *et al.* 1995) suggest that there may be a separate subpopulation there, based on a protracted breeding season compared with elsewhere in the North Atlantic, and also apparent changes in reproductive parameters over time compared with adjacent areas. However, the latter could be an environmentally driven trend. The West Greenlandic porpoises appear to be consistently smaller at age than both the eastern and western North Atlantic porpoises, and in addition are consistently heavier for length and have a higher proportion of fat in their body composition (Lockyer *et al.* 2003). Age at sexual maturation is generally between 3 to 4 years for all areas studied, and size parameters vary only slightly (Lockyer 2003). However, animals from the eastern North Atlantic appear to attain the greatest lengths recorded anywhere (Gaskin *et al.* 1984, Lockyer 1995b, 2003, Sequiera 1996, Smeenk *et al.* 1992) at up to about 190 cm. However, comparison of extreme outliers may sometimes be misleading, because their occurrence is usually closely related to sample size.

The age distribution of both Canadian and West Greenland porpoises indicates a maximum age of between 13 and 17 years (Read 1990a, Lockyer *et al.* 2001, 2003), whereas the porpoises recorded off the British Isles are not unusually 24 years old (Lockyer 1995a). However there is often an admixture of bycatch, directed take and strandings in many samples, thus rendering such comparisons of questionable reliability. In many areas where there is a history of bycatches (Canada) or directed take

(West Greenland), porpoises tend to show reduced longevity compared with regions where the majority of sampled animals originate as strandings (e.g. British Isles). The majority of published studies from all areas, however, indicate a similar age at first sexual maturation of >3 years in males and females. However, off West Greenland the age is less, about 2 years for males (Lockyer *et al.* 2001, 2003), reflecting a number of early-maturing animals. Therefore, observed differences in biological parameters may be useful, especially when consistent with observations from other methods; but it is important to be aware of potential artificially introduced biases from sample origin, which might affect the parameters. It is also possible that growth and age at sexual maturation may change when animals are subjected to external pressures, such as exploitation in the Bay of Fundy (Read and Gaskin 1990, Lockyer 2003).

Parasite infections can be used as indicators of stock identity (Balbuena *et al.* 1995). Investigation of parasite loads in the harbour porpoise has shown differences in gut parasite species occurrence between east coast Canadian Bay of Fundy and British Isles specimens (Fernandez *et al.* 1993). Herreras *et al.* (1997) reported on the incidence of helminthic parasites in porpoises from Danish waters and compared findings with other porpoise communities. They concluded that differences were directly related to local fauna (other mammals as well as dietary items) and conditions. The incidence of parasites in the ear sinuses, stomach, lungs and liver differed between Denmark and West Greenland, especially with a higher incidence of ear worms and stomach worms in West Greenlandic animals (Kinze 1989). Examination of porpoises from the Faroe Islands recovered 2 species of lungworms in a mixed infection, not previously recorded from porpoises from elsewhere (Larsen 1995). However, a lungworm species, *Torynurus convolutus*, recorded widely from Denmark and other regions of both the eastern and western North Atlantic, was not found in the Faroese animals. Lick (1991) reported that the nematode *Pseudoterranova* was found in the North Sea but not in Baltic porpoises.

One factor to be aware of here is that parasite

loads may vary seasonally within a population, and may depend on changes in food preference and also external factors such as water temperature. In Danish waters, for example, lung worm infestations, normally high, varied with season (unpublished data) in all age groups.

Other health-related factors such as disease and pathology in porpoises also vary between different regions, and might be used as population discriminators. Wunschmann *et al.* (2001) were able to establish that, apart from some differences in types of parasite infections, there was a much greater inflammatory response to parasites and certain bacterial infections in Danish and Baltic porpoises compared to West Greenlandic porpoises, which appeared generally healthier. However, they also determined a degree of morbillivirus (CMV)-specific antibodies in both Danish and West Greenland porpoises indicating some circulation of the virus in both populations. Müller *et al.* (2000) reported that there was a high incidence of PMV-specific antibodies throughout all age groups of porpoises in both the North and German Baltic seas, linking these populations.

In conclusion, it would seem that on the basis of biological parameters there are grounds for considering porpoises from the regions of east coast Canada and USA, West Greenland, Iceland and the eastern North Atlantic as separate for management purposes. In the eastern North Atlantic there are also indications of some separation between parts of the North Sea, Skagerrak-Kattegat-Inner Danish waters, and Baltic, which would suggest that separate management is a prudent option. However, parasite infections may vary over time even in the same population, and that some biological parameters may be sensitive to environmental pressures such as exploitation. Thus population discriminators should be based on comparison of data sets from similar time series.

CHEMICAL SIGNALS AND DIET

The use of organochlorine pollutants in the discrimination of marine mammal populations has been reviewed and assessed by Aguilar (1987). These pollutants are potentially useful, both in

terms of loads and ratios, but care needs to be exercised in interpretation because factors such as sex, age, reproductive state, nutritional status, diet, proximity to coastal waters, sampling time period and the actual conditions of tissue storage must be considered. Current research on organochlorine-type contaminant loads in harbour porpoises (Aguilar and Borrell 1995) has not attempted to separate specimens from different regions of the North Atlantic. On the basis of this paper therefore, no conclusions can be made regarding contaminant load variation between areas. However, Westgate and Tolley (1999) undertook an investigation of organochlorine contaminant levels in porpoises from several coastal areas of the Northwest Atlantic. They reported differences among a total sample of 188 bycaught porpoises sufficient to distinguish between Gulf of St Lawrence, Bay of Fundy/Gulf of Maine and Newfoundland as 3 subpopulations. Otterlind (MS 1976) noted higher levels of tDDT and less PCB in Baltic porpoises compared with porpoises from other areas, but the result might have been an artifact due to the relatively small sample size from the Baltic. Clausen *et al.* (1974) reported very low levels of tDDT contamination in West Greenlandic porpoises compared with the rest of the North Atlantic. Similarly, Granby and Kinze (1991) reported low levels off West Greenland compared with Denmark. Bruhn *et al.* (1999) indicated that, using samples from more recent years, levels of certain chlorinated biphenyls and chlorinated pesticides were significantly higher (by an order of magnitude) in North Sea and Baltic porpoises compared to West Greenland. However, the highest levels of α -HCH were found in West Greenland and p,p' -DDT was detected only in West Greenland. Larsen (1995) has shown that the time period of investigation is critical in contaminant analysis because more recent levels of DDTs and PCBs from inner Danish waters have decreased. Berggren *et al.* (1995) compared levels of DDTs, PCBs, non-ortho-PCBs and PCDD/Fs in porpoise blubber from the Baltic Sea, Kattegat-Skagerrak and western Norway. A significantly different contaminant pattern was evident for Norway, and while differences were noted between the Baltic and the Kattegat-Skagerrak region, these were not conclusive. Smyth *et al.* (2000) reported that

levels of polychlorinated biphenyls and organochlorines determined in porpoises from Irish coastal waters were generally similar to those reported from Scotland but lower than those from Scandinavia (Norway and Denmark - Kleivane *et al.* 1995). A new analytical approach investigating retinol concentrations in lipophilic tissues, *e.g.* blubber, of porpoises off West Greenland, as an indirect indicator of organochlorine levels - the retinol levels gauge the general immune health of the animals - may be a useful technique for distinguishing populations (Borrell *et al.* 1999). However, the authors stressed that knowledge of the age structure of the sampled animals is critical in the interpretation of results using the technique.

Studies of toxic, non-essential and essential metals in harbour porpoises off the Polish Baltic coast (Szefer *et al.* 1995, 2002) indicated levels comparable to those found in porpoises from British, German and Danish waters. However the levels of hepatic and renal cadmium were an order of magnitude less than off West Greenland, suggesting low exposure to this metal in northwestern European waters, especially the Baltic. The explanation offered was a difference in food preferences in the regions. Earlier studies by Paludan-Møller *et al.* (1993) also indicated elevated levels of cadmium in West Greenlandic porpoises with levels 10 times higher than in the North Sea and British northwest coast, although mercury levels were similar. Strand *et al.* (submitted) recently showed that both levels of butyltin and mercury were higher in Danish than West Greenland porpoises. They commented that the substances appeared to be correlated and both increased with age and size of animal - an overriding complication in the interpretation of all contaminant analyses. Koschinski (2002) has recently reviewed the levels of contaminants, both organochlorine and heavy metal, in the Baltic Sea and adjacent area, and has shown that levels have fallen over the time period of the mid-1970s to mid-1990s. Therefore any population structure study depending on contaminant levels should be careful to compare appropriate time series.

A recent study (Long *et al.* 1996, Berrow *et al.* 1998) of radionuclide levels in porpoises from the Irish Sea, while not indicating hazardous

levels, nevertheless found that the relatively higher levels of cesium-137 could indicate a resident population in the Irish Sea. Watson *et al.* (1999), in an investigation of tissues from marine mammals including porpoise, reported a correlation of radiocesium and plutonium concentrations and distance from the British nuclear power plant at Sellafield, which would be a good indicator of the origin of animals. Tolley and Heldal (2002) also undertook an investigation of radioactive cesium in axial muscle tissue of porpoises from 5 different locations along the Norwegian coast ranging from the North Sea northwards into the Barents Sea and found that there was a decline in levels northwards, consistent with the known pattern of radioactive outfall from the United Kingdom and the Baltic. They concluded that this suggested limited north-south movements between porpoises along the coast.

A technique examining fatty acid signatures in blubber and body fats (Iverson *et al.* 1997) influenced by dietary intake, could prove to be helpful in population differentiation on an ecological basis. This method is intimately tied in with differences in feeding habit. Recently, Møller (1999) and Møller *et al.* (in press) investigated possible population differences between West Greenland and Denmark, and within West Greenland waters using fatty acid signatures in porpoise blubber. These analyses showed significant differences between all areas studied, and these could be related to dietary differences.

The transfer of contaminants and the origin of exogenous fatty acid signatures in blubber are clearly through diet and prey choice. These in turn are influenced in some instances by sex and age. It would thus seem relevant to mention some dietary studies in this connection. Szefer *et al.* (2002) have already concluded that high cadmium levels in West Greenland porpoises relative to their Baltic cousins is probably due to the occurrence of squid in the diet (Lockyer *et al.* (2003) reported 37% porpoise stomachs contained squid off Maniitsoq), whereas those from Baltic and Danish waters do not consume cephalopods (Aarefjord *et al.* 1995). The link between contaminants and area in population definition can only be made if there is an understanding of both porpoise and prey migra-

tions/movements. The choice of pelagic or demersal fish is also important in certain contaminant transfers.

Aarefjord *et al.* (1995) investigated the diet of porpoises throughout the coast of North Norway, the Norwegian Sea, Southwest Norway, North Sea, Skagerrak, Kattegat and Baltic, and reported the importance of herring (*Clupea harengus*) in all areas. Capelin (*Mallotus villosus*) was characteristic for the northerly regions whilst plaice (*Pleuronectes platessa*) and flatfish were characteristic for the southerly regions. Cod (*Gadus morhua*) and herring occurred everywhere. They reported that porpoises off Norway took mainly pelagic fish whilst those in the North Sea and inner Danish waters consumed mainly benthic items. Lockyer and Andreasen (in press) recently reported that gadoid fish, and bottom-living gobies (*Gobiidae*), blennies (*Blenniidae*) and sand eels (*Ammodytidae*) were all important in the diet of North Sea and Inner Danish waters porpoises. Herring were not as important. Börjesson *et al.* (2003) reported the predominance of *Gobiidae*, herring-types and whiting (*Merlangius merlangus*) in porpoise stomachs from the Kattegat-Skagerrak area of Sweden, and seasonal changes in the diets of females perhaps associated with change in location. Lick (1991) reported differences and variety in dietary items of porpoises between the German North Sea and the Baltic, with up to 14 fish species (predominantly flatfish and gobies) in the North Sea but only 8 species from the Baltic (almost exclusively gobies). Berrow and Rogan (1996) reported mainly herring-type and gadoids in the stomachs of porpoises off Ireland, similar to other southerly North Atlantic regions. Off West Greenland, in the western North Atlantic, capelin is the main dietary item (Lockyer *et al.* 2003), as is the case off of Iceland (Vikingsson *et al.* 2003). However the actual proportion of other prey varies greatly between Greenlandic regions, and different items such as squids and crustaceans feature significantly in these different areas (Lockyer *et al.* 2003). Considerable seasonal and geographical variation was also found in the diet of harbour porpoises in Icelandic waters (Vikingsson *et al.* 2003). Fontaine *et al.* (1994) also reported capelin as the main prey species in the Gulf of St Lawrence, western North Atlantic, although

herring and redfish (*Sebastes marinus*) were also important. In another western North Atlantic area of Bay of Fundy however, herring was observed to contribute up to 98% of the energy intake (Recchia and Read 1988) while silver hake (*Merluccius bilinearis*) and cod were the other important prey. Earlier studies (Smith and Gaskin 1973) similarly reported the importance of herring, but found more variety in other prey. Reasons for this were presented as different sample sets on account of depth of bycatch, time period and age and sex composition of porpoises. However, the main finding was that herring was the main dietary species, unlike in the eastern North Atlantic and also West Greenland and Iceland. It is important to reflect that age and sex differences in prey selection may exist, such as between reproductively active females and other adults (Smith and Gaskin 1983, Yasui and Gaskin 1986, Víkingsson *et al.* 2003), and also in the young calves (Smith and Read, 1992) which consume mainly euphausiids rather than fish in the Bay of Fundy. These differences in turn will affect fatty acid signatures and possibly contaminant levels as discussed below.

The important fact to be remembered, therefore, in all analyses relying on chemical composition and diet, is that the situation is dynamic and can be significantly influenced by season, age and sex of an individual as well as by reproductive status. Some heavy metal contaminants may be persistent in the body, but organochlorine pollutants may decrease in concentration with age in reproductively active females via placental transfer to the foetus and milk production, although as yet we do not know the lifetime and turnover rate of certain fatty acid signatures from dietary items in the blubber. Certain fatty fish, particularly clupeid fish like herring and sprat, are especially likely to be a reservoir of organochlorine pollutants in contaminated areas. However, even if certain contaminants may diminish over time in individuals, some pathological effects caused by contaminants during the developmental stage, *e.g.* mineral resorption and deformities in bone or teeth, and reproductive organ deformities, might certainly persist, as observed in Baltic seals (Bergman and Olsson 1986, Bergman *et al.* MS 1986, Helle *et al.* 1976, Olsson 1978; Olsson *et al.* 1975, Reijnders 1986, Stede and

Stede 1990, Zakharov and Yablokov 1990). Although not investigated, it is thus possible that mineral resorption and structural disruption observed in porpoise teeth from some areas (Lockyer 1999) may be linked to certain heavy metal or other contaminants and diet.

In conclusion, one may be able to use findings on contaminant levels and other chemical signals to differentiate between populations, but there are many confounding factors to be considered in interpreting results. It would appear nonetheless that the western North Atlantic populations can be discriminated from the eastern North Atlantic ones, but that there is some differentiation possible between east coast Canadian populations and also between the Baltic, North Sea and West Greenland.

MORPHOLOGY

A study investigating metric and non-metric characters of the porpoise skull from 3 geographical regions (northern North Sea, Baltic Sea and Dutch coast) (Kinze 1985) indicated significant separation of Baltic and Dutch animals from the North Sea. Kinze proposed seasonal migratory habits for the Baltic and southern North Sea animals that would keep the animals apart, although a winter mixing of Baltic with northern North Sea animals was suggested. Furthermore, a study of morphometric and meristic characters of porpoise skulls from the western and eastern North Atlantic, the Black Sea and the eastern Pacific Ocean indicated clear separation between the 4 regions (Yurick and Gaskin 1987). Small sample size precluded conclusive results about subpopulations within these major regions. However, there were indications of segregations in the North Sea into Dutch coastal, eastern North Sea and Baltic subpopulations. Kinze (1990a; b) later demonstrated non-metric differences between skulls from porpoises from Dutch and German North Sea specimens, and German and Danish North Sea specimens, and between Swedish Skagerrak and both Danish Skagerrak and Baltic (mainly inner Danish waters) specimens. He concluded that there were 4 separate population units: Dutch coast, German Wadden Sea, northern North Sea through to the Belt region and Swedish

Skagerrak. Börjesson and Berggren (1997) examined porpoise skulls from the Baltic Sea and Kattegat-Skagerrak region, and they investigated seasonal variations to allow for possible migration as suggested by Kinze (1985). Their study showed that regardless of season, females could be distinguished as separate in the 2 areas, whilst males showed no differences. Huggenberger *et al.* (2002) used both metric and non-metric characters in an investigation of 242 porpoises from areas of the German Bight, the central Baltic Sea (Arkona seas and waters of western Sweden) and a transition area in between (Skagerrak, Kattegat, Belt seas, Øresund and Fehmarn Belt Sea). They were able to distinguish the 3 areas by means of discriminant analyses, ANOVA tests and Chi² tests, thus supporting the other studies in this region. A study of 45 metric skull characters among four putative porpoise subpopulations along the coastal western North Atlantic indicated varying differences between regions and also some differences between 4 subregions within the Bay of Fundy (Gao and Gaskin 1996). Considerable overlap existed between them, but overall correct classification of an individual to a particular population by discriminant function was 65.2%. They did not however, report significance levels for the discriminant functions for each group, and correct classification rate was likely inflated because of the large sample from the Bay of Fundy.

A study of tooth ultrastructure and Growth Layer Group (GLG) characteristics (Lockyer 1995b) for porpoise specimens from different geographic regions has shown variation in the incidence of certain mineralisation characteristics. In this study the Danish and British Isles specimens were most similar, and these were different from Norwegian, eastern Canadian and Californian specimens which also differed from each other. More recently, this study was expanded (Lockyer 1999) to include additional specimens from West Greenland, Iceland, Sweden, Poland, and German Baltic as well as sub-areas of the North Sea (British Isles, Netherlands, Germany) and provided some indications that all major "stocks" as originally defined by Gaskin (1984) occurring in this study, probably differ to some extent. These studies on tooth ultrastructure, GLG mineralisation pat-

terns and gross morphology of teeth included a total of nine different characteristics in each specimen. The investigation found that West Greenland was very distinct from the Canadian Bay of Fundy. Furthermore, 3 regions within West Greenland also exhibited some difference, and this appeared greatest between northerly and central/southern groups. Iceland and West Greenland showed few differences, but there were significant differences in the incidence of marker lines and GLG type. A comparison between Iceland and the North Sea/Celtic Shelf region also indicated significant differences. Comparisons within the ASCOBANS area (northern North Sea, central North Sea, southern North Sea, Skagerrak, Inner Danish waters and Kattegat, and Baltic Sea) showed significant differences, thereby indicating that the area is not a homogenous mix of animals. A comparison between northern, central and southern regions within the North Sea indicated some differences, so that while the regions are linked geographically with perhaps much mixing between them, there are still some local traits. Comparison between Skagerrak, Inner Danish waters/Kattegat and the Baltic Sea also indicated differences, but for quite different characters from the 2 noted in the North Sea area. Clearly this area is not a continuum of the same animals, even if there is mixing at certain times and places.

Thus, based on morphological features, the indications are that there is separation between western and eastern North Atlantic porpoises. Furthermore, there are differences between eastern Canada and West Greenland, and even some local differences within West Greenland between northerly and central/southerly areas, based on tooth ultrastructure. The relative similarity between Iceland and West Greenland may be coincidental, and does not mean that the animals in the 2 regions are necessarily from the same stock. There is also a clear difference between the eastern North Atlantic and eastern/central North Atlantic. The Faroes region, where information is currently lacking, could be important to investigate for links. Within the ASCOBANS area there are clearly several possibilities for a mixture of subpopulations, and potential substructure within the North Sea and also within the Skagerrak to Baltic regions.

GENETICS

The techniques used most frequently have involved mt DNA sequencing and more recently DNA microsatellites, as well as some earlier work on isozyme electrophoresis. The mt DNA is maternally inherited while allozymes are phenotypic expressions of an underlying nuclear genetic inheritance. DNA micro-satellites are segments of 2, 3 or 4 nucleotide repeats in the nuclear DNA, and can be identified using specific primers. Therefore there are three different complimentary genetic approaches, each able to provide information on a slightly different aspect of inheritance.

One study has focused on the waters around the British Isles, therefore encompassing both the western Irish waters and Celtic Shelf, northerly Scottish waters, North Sea through to the Dutch coast and the southernmost English Channel (Walton 1997). This study used mt DNA and concluded that generally females were likely to remain more resident and males were more likely to disperse throughout the region. Walton reported that the most common haplotype was recorded in 63% of all samples and was found in all his study areas. Thus he concluded that generally there was a historical inter-connection between these areas. However, his studies also indicated significant differences between northern and southern North Sea animals, and between northern North Sea and the Celtic Shelf/Irish Sea area. These differences were predominantly due to variation in the females. Another study using mt DNA markers (Tiedemann *et al.* 1996) reported on the separation of Baltic Sea (including German coastal waters south of Denmark) and southern North Sea animals based on the fact that all Baltic animals showed one type of haplotype whereas this type only occurred in 45% of North Sea animals. They found nucleotide and haplotype diversity to be much lower in the Baltic and suggested a population separation several thousand years ago, with only limited genetic exchange since then. Wang and Berggren (1997) also used mt DNA RFLP (restriction fragment length polymorphism) to compare porpoises from the Baltic Sea, Kattegat-Skagerrak region and the west coast of Norway, *i.e.* northern North Sea and Norwegian Sea. They concluded that the

frequency of haplotypes in the three areas indicated genetic separation, and that furthermore, the Baltic and Kattegat-Skagerrak seas showed much lower haplotype and nucleotide diversities than the Norwegian animals. Their conclusion was that these former areas might be depleted because of the observed reduced gene pool.

Andersen (1993) investigated the population structure of porpoises from the inner Danish waters (part of the Baltic, Kattegat-Skagerrak) and North Sea using isozyme electrophoresis. She observed a significant difference in genotypic distribution between the summer inner Danish waters and summer North Sea specimens, based on 2 loci. Furthermore she examined samples from the Dutch coast, West Greenland and Canadian Gulf of St Lawrence. Andersen (1993) found significant differences between the Canadian samples and those from the eastern North Atlantic. However, she found that the West Greenland sample differed from both the Canadian and Dutch samples but not from the inner Danish waters. She interpreted this as pure coincidence for the particular alleles chosen. More recently this allozyme investigation has been supplemented with micro-satellite analyses using markers, looking at 2 further loci. Three areas were analysed from West Greenland, North Sea and inner Danish waters (Andersen *et al.* 1995). In this instance, the West Greenland sample was shown to be distinct, while those from North Sea and inner Danish waters could not be differentiated. However, the North Sea sample indicated an excess of homozygotes, and this they interpreted as the mixing of several sub-populations or non-random matings because of males straying from different breeding areas within the North Sea. A more recent study (Andersen *et al.* 1997) combined both isozyme analysis and DNA micro-satellite techniques on porpoises from West Greenland, the North Sea and from inner Danish waters, and examined a total of 5 loci including the 4 earlier ones. The analyses concluded that the 3 regions represented 3 geographically and genetically differentiated populations, even though connected through a degree of gene flow. In concert with Walton (1997), they indicated that there was a tendency for females to remain more stationary than males.

Tolley *et al.* (1999) analysed porpoise samples from the Norwegian (northern) North Sea, Barents Sea and British Isles North Sea, using mt DNA, and found differentiation between the Barents Sea and the British North Sea (Walton's 1997 sample). However, differences between Norwegian and British North Sea porpoises were only apparent after the Shetland Isles were excluded. Thus, based on haplotype frequencies, there may be some population structure within the North Sea - perhaps on a north/south stratification basis. Tolley *et al.* (1999) also reported philopatry in females. In a more recent study, Tolley *et al.* (2001) examined mt DNA from 370 porpoises from 6 locations in the western, central and eastern North Atlantic. The findings revealed some fine structuring but with western samples from West Greenland, Gulf of St Lawrence, Newfoundland and Gulf of Maine being more similar to central North Atlantic samples (Iceland). There was a discontinuity between Norway to the east and Iceland, and Norway therefore appeared distinct from all these 5 areas. They recommended that management be based on a regional basis, and that the Icelandic porpoises be treated as a separate population.

Most recently, Andersen *et al.* (2001) presented information on population structure in the central and eastern North Atlantic through to the western Baltic Sea based on a total of 807 porpoises examined in these areas. Using 12 polymorphic DNA microsatellite loci, and multilocus analyses for allele frequency differences, assignment tests, population structure estimates (FST) and genetic distance measures, they were able to demonstrate 6 genetically differentiated populations/subpopulations off West Greenland, the Norwegian west coast, Ireland, British (western) North Sea, Danish (eastern) North Sea and inner Danish waters. Porpoises off the Dutch coast in the southern North Sea appeared to be a mixture probably derived from migrants from both British and Danish sectors of the North Sea. The chief factors influencing population differentiation were genetic drift and gene flow mediated by male dispersal and counterbalanced by female philopatry. This study supported the general hypotheses originally proposed by Gaskin (1984) in the central and eastern North Atlantic, and more recently modified by the IWC (1996) with 2 additions: an east/west

divide within the North Sea, and a connection between the Skagerrak and North Sea rather than with inner Danish waters. Furthermore, their findings also supported findings of other researchers using different methods, with the exception of a proposed north/south divide in the North Sea by Walton (1997) and Lockyer (1999).

Rosel *et al.* (1999) were able to show, using both mt DNA and micro-satellite analyses on western North Atlantic porpoise samples from the Gulf of Maine, eastern Newfoundland, Gulf of St Lawrence and West Greenland, that there were 3 summer breeding stocks in this region, which admix into winter aggregations along the US east coast. They also indicated that females were more philopatric, based on a high degree of genetic differentiation in this sex alone, whilst the males probably maintained the genetic flow between the areas. This also tended to support Gaskin's proposed population structure in the western North Atlantic.

THE PHYLOGEOGRAPHIC APPROACH

The review of different methods of defining population structure indicates that each approach has limitations. Table 1 summarises the different methods and also lists their limitations as well as indicating their relative importance for stock discrimination. In all approaches, sample size is often critical, and should be appropriate for the method being used. The absolute power of any method to define population structure is the ability to re-assign any individual taken at random to a particular group. Of course this is unrealistic in most situations. Some techniques are inherently less or more reliable in differentiating populations, and thus a relative "weighting" of the method is important. Table 1 attempts to give some guidelines here.

Genetics provide an absolute definition of an individual in a population, whereas population parameters and morphology are all subject to external influences on the individual, being phenotypic expressions. Chemical and ecological markers are defined by the external environment that the animals live in, and like popula-

tion parameters, are also dynamic. They are dynamic both in terms of time and space – but often in the short term, so that they may only be useful and valid over a fixed period. Tagging methods may record both the movements of individuals, and reflect their responses to environmental factors such as food distribution, climate variation, water currents, underwater topography and manmade perturbations. Thus, what may appear as the normal distribution and movement patterns may suddenly change because of external influences from environmental change.

The various techniques presented in the review, and their application comprise a complex summary of findings on population structure of harbour porpoises to date. The strengths of individual results are confirmed when combined with others derived using different techniques. When all investigations point to the same conclusion then it is easy to be confident in determining that this area should be defined as a separate subpopulation. However, it is less easy when there are some similarities and some differences. At what level of difference should the putative populations be regarded as separate? Taylor (1997) has defined “population” in terms of meeting management objectives. Here she uses some level of dispersal between adjacent populations to determine whether or not they should be regarded as separate or not from the management viewpoint. This approach is clearly important and relies heavily on genetic input, and also direct information about movements.

One practical approach at identifying populations by integrating different methods, was presented by Dizon *et al.* (1992). This followed the phylogeographic approach (Awise *et al.* 1987) but has not been used extensively and may have been regarded as too simplistic because it did not focus on evolutionary links, genetic “bottle-necks” and genetic distance. Instead it combined genetic, phenotypic and distributional information and considered the current ecological closeness and biological possibilities. There have been several studies using the phylogeographic approach (Awise 1998, Awise and Ball 1990, Behnke 1992, Bernatchez and Dodson 1991, Bowen *et al.* 1998, Dutton *et al.* 1999, Moritz and Faith 1998, Riddell 1993), but few

specifically on marine mammals (Curry and Smith 1997, Loughlin 1997).

The phylogeographic approach is used as a framework here as a possible way forward in assessing population structure in a qualitative and practical way. The method (Dizon *et al.* 1992) attempts to identify a scientific and biological basis for drawing precise geographical boundaries around stocks. To summarise this approach, the investigator starts with the observation of allopatry or geographic isolation in comparing 2 populations, that could imply reproductive isolation, *e.g.* Californian versus North Sea porpoises. Other observations are made on differential life history events, *e.g.* different breeding times or areas of breeding, differential life history responses that could also indicate reproductive isolation, and morphological differentiation that could indicate drift or genetic evolution under different selective regimes; or differentiation of neutral genetic characters quantifying the degree of isolation and the time since an ancestor was shared. These can be categorised as (a) distributional, (b) population response, (c) phenotypic, and (d) genotypic.

In determining distributional isolation, geographic barriers can be considered, as well as “barren” areas or troughs of extremely low or nil density, areas of upwelling and current, and temperature fronts. Population responses include such parameters as age and size at maturation, fecundity, breeding season, and social behaviour, which could also be indicators of differing pollutant or parasite load and foraging habits. Phenotypic characters would include skeletal meristics, morphometry, pigmentation patterns, shape and size. Genotypic characters would clearly include all genetic approaches using DNA, but also isozyme electrophoresis, although this represents a direct phenotypic expression of genotype.

Once all the evidence for putative populations has been assembled, a population can be compared to another for relative discreteness, based on an initial categorisation into one of 4 population types. These categories are derived from a structure developed by Awise *et al.* (1987) and Awise (1989) based on genetic distance. However in the present approach the genetic

distance has been replaced by character differences that express the locally adapted genome - a phylogeographic categorisation. There are 4 categories of population:

- Category I populations are allopatric and demonstrate clear genetic differences. They are usually separated geographically and have no possibility to mix. These are treated as distinct management units;
- Category II populations have discontinuous genetic diversity between groups of closely related genome groups, and exist either sympatrically or parapatrically, *i.e.* there is weak or little geographic partitioning;
- Category III populations have continuous genetic divergence but have little genetic differentiation. They are separated although there are no actual geographical barriers, but intermingling or interbreeding at the margins is feasible (*i.e.* they are parapatric);
- A category IV population has extensive gene interchange and has no geographical barriers, and can be described as panmictic.

In order to help define the putative population, descriptive criteria that draw on biological information under the coded headings of *a*. distribution, *b*. population parameters, *c*. morphology, and *d*. genetics are assembled. The information is normally applied by comparing 2 or more putative populations and drawing on evidence for separation under each heading. If there is evidence for separation, for example under every heading, the information is represented as */abcd* with the codes to the right of the separator - "splitting". However, if there is no evi-

dence for separation, the information is represented as *abcd/* to the left of the separator - "lumping". In many instances there will be a mixture of positive and negative evidence that may result in there being codes both to left and right. In a few instances, there may be no information available, in which case the relevant code will not appear. Clearly the more codes placed on the right, the stronger the case for a distinct population. However, even in cases where there is little evidence for separation, caution may be used to treat such examples as discrete management units. The process can best be described using comparisons of putative populations, using examples mainly from the eastern North Atlantic. The process is described visually in Fig. 3, using a hypothetical example of a category III population with biological information available.

Example 1 - Inner Danish waters vs West Greenland

The inner Danish waters and West Greenland would qualify as Category I populations, because of geographic separation. The qualifiers would indicate *I/abcd*, where there is geographic separation unlikely to be breached */a*, only slight evidence for differences in population parameters (Lockyer *et al.* 2003), yet heavy metal analysis (Szefer *et al.*, 1995, 2002) indicates significant differences */b*, morphological evidence suggests differences in body size (Lockyer *et al.* 2003) and tooth characters (Lockyer. 1999) */c*, and there is genetic microsatellite evidence (Andersen *et al.* 1997, 2001) that they are distinct */d*. The evidence is therefore strong for population discreteness. How-

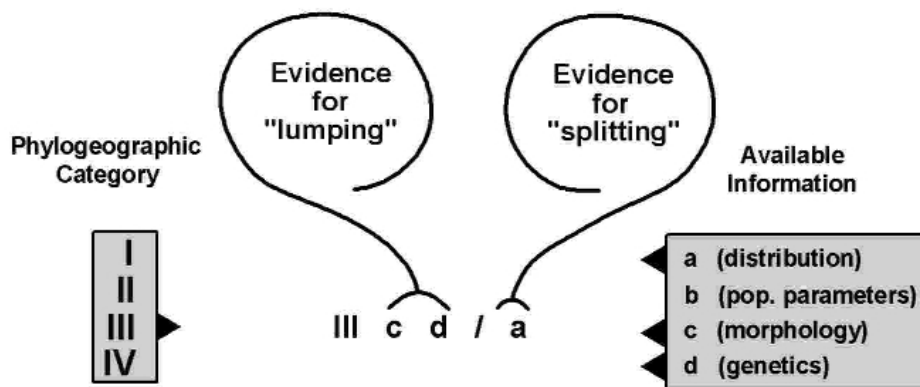


Fig. 3. A shorthand method for qualifying stock type using phylogeographic categories and information regarding the criteria used to make such qualifications (after Dizon *et al.* 1992).

Table 2. Some proposed regional / putative population boundaries within the North Atlantic, with reference to ICES areas, and Gaskin (1984) as revised by IWC (1996).

Eastern North Atlantic and adjacent waters	
North Norway	North Norway and Barents Sea (ICES IIa) (IWC 7)
Northern North Sea	Northern North Sea + southern Norway (ICES IVa) + N.W.Scotland (ICES VIa) (IWC 8)
¹ Central North Sea	Central North Sea (ICES IVb) (IWC 8)
Southern North Sea	Southern North Sea + Netherlands (ICES IVc) (IWC 8)
English Channel	English Channel + S.Cornwall + S.Devon (ICES VIId,e)
Celtic Shelf, S.W.Ireland + S.W.British Isles	Celtic Shelf + Irish Sea + S.Wales + S.W.Ireland (ICES VIIa,g,h,j) (IWC 11)
² Skagerrak	Skagerrak including adjacent Swedish and Norwegian coasts (ICES IIIan) (IWC 8-9)
Kattegat	Kattegat (ICES IIIas) (IWC 9)
Inner Danish waters (IDW)	Inner Danish waters (Belts) (ICES IIIc) + Øresund (ICES IIIb) (IWC 9)
Baltic	Baltic including all bordering coasts (ICES IIId) (IWC 10)
³ <i>Eastern-Central North Atlantic</i>	
S.E.Iceland	S.E.Iceland (ICES Va east) (IWC 5)
S.W.Iceland	S.W.Iceland (ICES Va west) (IWC 5)
<i>Western North Atlantic</i>	
W.Greenland north	W.Greenland Maniitsoq (north) (NAFO 1C) (IWC 4)
W.Greenland central	W.Greenland Nuuk (central) (NAFO 1D) (IWC 4)
W.Greenland south	W.Greenland Paamiut (south) (NAFO 1E) (IWC 4)
Canada-Bay of Fundy	E.Canada, Gulf of Maine / Bay of Fundy (NAFO 4X, 5Y, 5Z, 6A, 6B, 6C) (IWC 1)
Canada-Gulf of St Lawrence	E.Canada, Gulf of St Lawrence (NAFO 3P, 4R, 4S, 4T, 4V, 4W) (IWC 2)
Canada-Newfoundland	E.Canada, Newfoundland and Labrador (NAFO 2G, 2H, 2J, 3K, 3L)(IWC 3)
¹ This area may also be considered divided into east (British North Sea) and west (Danish North Sea) on the genetic evidence of Andersen et al (2001)	
² Skagerrak may be better linked with the Danish North Sea rather than Kattegat, if it is managed together with adjacent areas based on the genetic evidence of Andersen et al (2001).	
³ Based on preliminary evidence of tooth ultrastructure (Lockyer, 1999)	

ever, this is probably a hypothetical comparison, as these populations are unlikely ever to be considered as a single management unit.

Example 2 - North Sea vs Irish Sea

These would qualify as category III populations where there is geographic separation in terms of distance and land mass, yet mixing is possible but probably limited. The qualifiers might define the population as III bc/abd , where there is some geographic containment $/a$, there is no evidence for population parameter differences $b/$, yet isotope analysis suggests that the Irish Sea may house a resident population (Berrow *et al.* 1998) $/b$. Thus there is both negative and positive evidence b/b . There is no clear morphological difference $c/$, yet micro-satellite studies (Andersen *et al.* 2001) and mt DNA studies (Walton 1997) indicate some genetic separation from the western British North Sea and northern North Sea respectively $/d$. The Irish Sea porpoises might thus be regarded as a separate unit for management in any policy that covers the British Isles area.

Example 3 - Baltic vs inner Danish waters

These would qualify as category II populations because while there is some weak geographic separation (they occur within an environment changing from one extreme of saltwater to brackish/fresh at the other with an accompanying diverse ecology), there is no reason to separate them and they represent a continuum. They might be qualified as follows: II ab/bcd . They are continuous geographically, and Teilmann (2000) has now demonstrated that porpoises can move into the western Baltic from the inner Danish waters, even if temporarily $a/$. There are several morphological distinctions $/c$ from skull studies (Berggren *et al.* (MS) 1998, Börjesson and Berggren 1997, Huggenberger *et al.* 2002, Kinze 1985, 1990a; b) and tooth characters (Lockyer 1999); b is placed on both sides (b/b) because while there is no real evidence either way as yet on population parameters, there is clear evidence that Cd (cadmium) levels in the two regions show differences (Szefer *et al.* 2002), and there is some evidence for genetic separation $/d$ (Berggren *et al.* (MS) 1998, Tiedemann *et al.* 1996, Wang and Berggren 1997). From the management perspective, it is clear that from a cautionary standpoint it would

be prudent to regard the Baltic as a distinct population in view of the currently greatly reduced numbers of porpoises in the Baltic (IWC 2000, Koschinski 2002). At present it is unclear exactly where the border exists between these adjacent populations. High densities of porpoises exist in the southwestern-most area between Baltic and inner Danish waters where a natural geographic separation might be drawn. However, it is uncertain whether these are animals of Baltic or inner Danish waters origin. In the future it will be important to define the precise geographic location of any new information and such concerns have been expressed by ASCOBANS (2002).

Example 4 - Northern North Sea vs southern North Sea

These would qualify as category IV populations because there is clearly the possibility for mixing and no barriers, indicating a possibly panmictic population. However, there might be qualifying information that could help decide if these two areas should be managed separately. The outcome might be represented as IV a/bcd where there is no distributional hiatus $a/$, distribution being continuous through the central North Sea (Hammond *et al.* 2002). There is some evidence for reproductive differences *e.g.* Dutch data vs British Isles $/b$ (Addink *et al.* MS 1995, Addink *et al.* 1995), some difference of tooth characteristics and skull morphometrics and meristics $/c$ (Kinze 1985, 1990a; b), and there is some evidence from mt DNA (Walton 1997) suggesting separation $/d$. However, Andersen *et al.* (2001) suggested that the Dutch animals may be a mixture of porpoises from both the western British and eastern Danish North Sea, which would tend not to suggest a separate population *per se*. If the northern North Sea includes a Norwegian component (Tolley *et al.* 2002), then there is a stronger case for separate management. There is evidence therefore for distinction between these two areas, indicating that it would be prudent to recognise a degree of separation, even though there is clearly the possibility for a high degree of mixing. The difficulty arises as to where distinction is made geographically between the regions as both border a "buffer" zone in the central North Sea where there is some evidence for an east/west division. One could define the boundary in terms of ICES

areas IVa and IVc (Table 2), but in reality, the distinction must refer to something tangible such as a distributional hiatus or area of fishery effort and bycatch.

Example 5 - Central North Sea vs southern North Sea

These would again qualify as category IV populations because of proximity and mixing. The categorisation might be IV acd/b where there is no distributional hiatus $a/$ (Hammond *et al.* 2002), no distinct morphological difference $c/$, and no genetic difference $d/$. However, there is some evidence for reproductive differences *e.g.* Dutch data vs British Isles $/b$ (Addink *et al.* MS 1995, Addink *et al.* 1995). The evidence overall is for rather little difference between the 2 regions, and no compelling need for separate management. There may be possible east/west differences *e.g.* east coast British Isles and west coast Denmark (Andersen *et al.* 2001), which have not been considered here (but see Example 7 below). Clearly there is the likelihood of regular mixing, panmixia, between animals in the 2 regions. Discrete management might depend more on fishery practices and overall goals, as discussed above in Example 4, because movements here between areas might be anticipated to be relatively high, even if there is little genetic exchange.

Example 6 - Skagerrak Sea vs inner Danish waters

These are adjacent areas, and as such qualify as category IV populations. The categorisation might be IV a/bcd . There is no obvious distributional hiatus, although topographically, the northernmost Skagerrak has a tongue of water deeper than the inner Danish waters, yet satellite telemetry supports free movement between the areas (Teilmann 2000). There is no clearcut genetic distinction because many genetic studies have combined Skagerrak with Kattegat and inner Danish waters, although Andersen *et al.* (2001) indicate a definite link between Skagerrak and the North Sea, distinct from inner Danish waters. We might therefore classify the population as $/d$. Contaminant loads indicate some differences $/b$ (Berggren *et al.* 1995), and skull (Börjesson and Berggren 1997, Kinze 1985, 1990a; b) and tooth characteristics (Lockyer 1999) also show differences $/c$. Thus

there is some indication of weak population separation. The question is perhaps one of possible links between the northern North Sea and Skagerrak, somewhat like an overflow from the north into the latter at the southeastern margin of the northern North Sea close to Norway. The topographical nature of the Skagerrak, which is a relatively small open-ended strip of water bordered by 3 nations, linking major areas of the North and the Baltic seas, makes it a difficult area to manage. Clearly, many animals are also moving in and out of this region regularly as shown by Teilmann (2000).

Example 7 – Western North Sea (England) vs Eastern North Sea (Denmark)

These are another example of adjacent areas, and as such qualify as putative category IV populations. The categorisation might be IV abc/d . There is no obvious distributional hiatus, the biological parameters and other characteristics known are similar, and the only reason to consider possible separation from a management point of view is that bycatch is mainly Danish to the east and British to the west. However, an apparent genetic difference has been reported (Andersen *et al.* 2001), which is surely a strong reason for examining the management strategy carefully. This also highlights the grey area of genetic distance and rates of mixing. Some genetic traits may reflect distinctly separate populations, whilst others may discriminate family-related groupings that mix only on very rare occasions. The question is how strict should management be in defining management units.

DISCUSSION AND CONCLUSIONS

Putative populations could be compared in many ways; the most difficult to assess being the category II, and also category IV. One may assume extremes of population definition from I $abcd$ where the separation is absolute to IV $abcd/$ where there is no evidence that can be used to distinguish the putative populations. Anything in between these categories should be regarded with varying degrees of caution, especially where existing distributions of porpoise are known to be depleted and/or there is an existing management problem in a localised area, *e.g.* bycatches. As Donovan (1991) stated,

“...there was a utilitarian approach towards stock boundaries prevalent in IWC discussions - interest in stock identity questions very often disappeared with the closing of fisheries”. In other words, the quest for knowledge is need driven, and often only arises once there is a crisis.

It is important for managers to recognise that environmental factors may also contribute to population declines, even when exploitation appears to be adequately controlled. It is important to allow for these risks with a measure of safety. I therefore advocate a cautious approach to management by considering the smallest possible stock unit practicable, bearing in mind the geographic boundaries. A potential list of putative population boundaries for management is offered in Table 2, and combines a practical definition of regions in terms of IWC definition, ICES definition, and geographic and national location. They are the result of integrating all the above definitions with scientific and biological evidence.

It would seem that there is a clear distinction between the biological and management definitions of population/subpopulation/stock, although the 2 are not mutually exclusive; they merely approach the issue differently although the goals may be similar, *i.e.* to maintain the population at optimum level. The biological definition should guide the management decision, but management can still operate with incomplete knowledge of biology as long as effort data and catch records are maintained correctly. Mostly management will be focused on a particular geographical area or season, regardless of which population(s) happens to be there at the time, whilst biology is concerned about the integrity of a particular population even if it migrates elsewhere or mixes with other populations temporarily.

Information relevant to all the proposed putative populations listed in Table 2 has been reviewed in this paper and examples using the technique of Dizon *et al.* (1992) have been developed. For these populations, there appears to be a remarkable coincidence with the IWC-modified categories of Gaskin (1984). However, there are some additional putative sub-divisions, such

as possible stratification east / west and also north / south within the North Sea; separation of Skagerrak, Kattegat and inner Danish waters; and sub-divisions east and west around southern Iceland, and within West Greenland. Some of these may be brought into question, but are listed separately on the basis of caution. There are also areas for which no useful information has been reviewed here. These include the Faroe Islands (IWC 6), Iberia and Bay of Biscay (IWC 12), and Northwest Africa (IWC 13). There is little to contribute here except to advise that treating these areas as separate management units would be prudent until new information becomes available. The Black Sea (Fig. 1) has not been discussed here. It is not part of the North Atlantic, and in addition, it has been amply demonstrated that a possible sub-species exists here (Rosel *et al.* 1995), which should obviously be managed separately. The few porpoises observed within the western Mediterranean in recent times are believed to derive from the Atlantic (Gaskin 1984, Rosel 1997) but almost nothing is known about them. It seems therefore, that with some additional sub-categories, the existing populations proposed in Fig. 1 have some scientific credibility. The only advantage offered by Table 2 is the fitting of ICES and NAFO areas to these populations in order to provide some geographic boundary which might be meaningful in fisheries.

The intention of this paper was not to solve any population structure issues, but to present 1) a review of current knowledge derived from a variety of methods; and 2) suggest a way of integrating a wide variety of information, that might indicate possible population sub-structure. It is hoped that this has been achieved at least in part, and has provided food for thought.

ACKNOWLEDGMENTS

The author wishes to thank Liselotte Wesley-Andersen, Carl Kinze, Michael Walton and Greg Donovan for their comments on the early draft of the paper. Additional constructive comments from independent reviewers and advice from Gísli Víkingsson have been very helpful.

REFERENCES

- Aarefjord, H., Bjørge, A.J., Kinze, C.C. and Lindstet, I. 1995. Diet of the harbour porpoise (*Phocoena phocoena*) in Scandinavian waters. *Rep. int. Whal. Commn* (Special Issue 16):231-242.
- Addink, M.J., Garcia Hartmann, M. and Smeenk, C. (MS) 1995a. The harbour porpoise in Dutch waters: life history, pathology and historical records. Abstract, 11th Biennial Conference on the Biology of Marine Mammals, 14-18 December 1995, Orlando, Florida, p.1.
- Addink, M.J., Sørensen, T.B. and Garcia Hartmann, M. 1995b. Aspects of reproduction and seasonality in the harbour porpoise from Dutch waters. In: Blix, A.S., Walløe, L. and Ulltang, Ø. (eds.); *Whales, seals, fish and man*. Elsevier Science B.V., Amsterdam, 459-465.
- Aguilar, A. 1987. Using organochlorine pollutants to discriminate marine mammal populations: a review and critique of the methods. *Mar. Mam. Sci.* 3:242-262.
- Aguilar, A. and Borrell, A. 1995. Pollution and harbour porpoises in the eastern North Atlantic: a review. *Rep. int. Whal. Commn* (Special Issue 16):231-242.
- Allen, K.R. 1980. *Conservation and management of whales*. University of Washington Press, Seattle, and Butterworth and Co., London, 110pp.
- Andersen, L.W. 1993. The population structure of the harbour porpoise, *Phocoena phocoena*, in Danish waters and part of the North Atlantic. *Mar. Biol.* 116:1-7.
- Andersen, L.W., Holm, L.-E., Clausen, B. and Kinze, C.C. 1995. Preliminary results of a DNA-micro-satellite study of the population and social structure of the harbour porpoise. In: Blix, A.S., Walløe, L. and Ulltang, Ø. (eds.); *Whales, seals, fish and man*. Elsevier Science B.V., Amsterdam, 119-127.
- Andersen, L.W., Holm, L.-E., Siegismund, H.R., Clausen, B., Kinze, C.C. and Loeschcke, V. 1997. A combined DNA-micro-satellite and isozyme analysis of the population structure of the harbour porpoise in Danish waters and West Greenland. *Heredity* 78:270-276.
- Andersen, L.W., Ruzzante, D.E., Walton, M., Berggren, P., Bjørge, A. and C.Lockyer. 2001. Conservation genetics of harbour porpoises, *Phocoena phocoena*, in eastern and central North Atlantic. *Conservation Genetics* 2:309-324.
- [ASCOBANS] Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas. 1992. *Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas*, text + Annex. United Nations, 9pp.
- [ASCOBANS] Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas. 1994. Report from the First Meeting of Parties. Stockholm, 26-28 September 1994.
- [ASCOBANS] Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas. 1997. Report of the Second Meeting of Parties to ASCOBANS. Bonn, 17-19 November, 1997.
- [ASCOBANS] 2001. Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas. Report of the Third Meeting of Parties to ASCOBANS. Bristol, 26.28 July, 2000.

- [ASCOBANS] 2002. Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas. Report of the Ninth meeting of the Advisory Committee, Doc. 7 Draft Recovery plan for Baltic harbour porpoises. Hindås, Sweden, 10-12th June 2002.
- Avise, J.C. 1989. Gene trees and organismal histories: a phylogenetic approach to population biology. *Evolution* 43:1192-1208.
- Avise, J.C. 1998. Conservation genetics in the marine realm. *J. Heredity* 89:377-382.
- Avise, J.C. and Ball, R.M. 1990. Principles of genealogical concordance in species concepts and biological taxonomy. *Oxford Surv. Evol. Biol.* 7:45-67.
- Avise, J.C., Arnold, J., Ball, R.M., Bermingham, E., Lamb, T., Neigel, J.E., Reeb, C.A. and Saunders, N.C. 1987. Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Ann. Rev. Ecol. Syst.* 18:489-522.
- Balbuena, J.A., Aznar, F.J., Fernandez, M. and Raga, J.A. 1995. Parasites as indicators of social structure and stock identity of marine mammals. In: Blix, A.S., Walløe, L. and Ulltang, Ø. (eds.); *Whales, seals, fish and man*. Elsevier Science B.V., Amsterdam, 133-139.
- Bandomir-Krischak, B. 1996. Preliminary results on reproduction of harbour porpoises in German coastal waters. *European Research on Cetaceans* 9:212-214.
- Behnke, R.J. 1992. Native trout of western North America. *Am. Fish. Soc. Monogr.* 6.
- Benke, H., Siebert, U., Lick, R., Bandomir, B. and Weiss, R. 1998. The current status of harbour porpoises (*Phocoena phocoena*) in German waters. *Arch. Fish. Mar. Res.* 46:97-123.
- Berggren, P., Zebühr, Y., Ishaq, R., Naf, C., Bandh, C. and Broman, D. 1995. Geographical, temporal and age variation of chlorinated aromatic contaminants (DDTs, PCBs, non-ortho PCBs and PCDD/Fs) in male harbour porpoises from the Baltic Sea, the Kattegat-Skagerrak seas and off the west coast of Norway. In: Berggren, P. *Stocks, status and survival of harbour porpoises in Swedish waters*. Ph.D. thesis, Stockholm University, 23pp.
- Berggren, P., Börjesson, P., Carlstrom, J., Kull, M., Westgate, A.J., Koopman, H.N. and Read, A.J. (MS) 1996. Satellite tracking of a harbour porpoise in the Skagerrak Sea. ASCOBANS document ASCOBANS/ADV.COM./3/DOC 16.
- Berggren, P., Börjesson, P. and Wang, J.Y. (MS) 1998. Investigating stock structure for proper management of marine mammals: is one method good enough? *The World Marine Mammal Science Conference - Abstracts*:13-14, January 1998, Monaco.
- Bergman, A. and M. Olsson 1986. Pathology of Baltic grey seal and ringed seal females with special reference to adrenocortical hyperplasia: is environmental pollution the cause of a widely distributed disease syndrome? *Finnish Game Res.*44:47-62.
- Bergman, A., Olsson, M. and Reiland, S. (MS) 1986. High frequency of skeletal deformities in skulls of the Baltic grey seal. ICES Marine Mammal Committee C.M. 1986/N:15, 7pp.
- Bernatchez, L. 1995. A role for molecular systematics in defining significant units in fishes. *Am. Fish. Soc. Symp.* 17:114-132.

- Bernatchez, L. and Dodson, J.J. 1991. Phylogeographic structure in mitochondrial DNA of the lake whitefish (*Coregonus clupeaformis*) and its relation to Pleistocene glaciations. *Evolution* 45:1016-1035.
- Berrow, S. and Rogan, E. 1996. Stomach contents of harbour porpoises and dolphins in Irish waters. *European Research on Cetaceans* 9:179-181.
- Berrow, S.D., Long, S.C., McGarry, A.T., Pollard, D., Rogan, E. and Lockyer, C. 1998. Radionuclides (Cs-137 and K-40) in harbour porpoises *Phocoena phocoena*, from British and Irish coastal waters. *Mar. Poll. Bull.* 36:569-576.
- Bowen, B.W., Clark, A.M., Abreu-Grobois, F.A., Chaves, A.Reichart, H.A. and Ferl, R.J. 1998. Global phylogeography of the ridley sea turtles (*Lepidochelys spp.*) as inferred from mitochondrial DNA sequences. *Genetica* 101:179-189.
- Bjørge, A., Aarefjord, H., Kaarstad, S., Kleivane, L. and Øien, N. 1991. Harbour porpoise *Phocoena phocoena* in Norwegian waters. ICES document CM N:16, 24pp.
- Borrell, A., Cantos, G., Aguilar, A., Lockyer, C., Brouwer, A., Heide-Jørgensen, M.P., Jensen, J. and Spenkelink, B. 1999. Patterns of variability of retinol levels in a harbour porpoise population from an unpolluted environment. *Mar. Ecol. Prog. Ser.* 185:85-92.
- Bruhn, R., Kannan, N., Patrick, G., Schulz-Bull, D.E. and Duinker, J. 1999. Persistent chlorinated organic contaminants in harbour porpoises from the North Sea and Arctic waters. *The Science of the Total Environment* 237/238:351-361.
- Börjesson, P. and Berggren, P. 1997. Morphometric comparisons of skulls of harbour porpoises (*Phocoena phocoena*) from the Baltic, Kattegat and Skagerrak seas. *Can. J. Fish. Aquat. Sci.* 75:280-287.
- Börjesson, P., Berggren, P. and Ganning, B. 2003. Diet of harbor porpoises in the Kattegat and Skagerrak seas: accounting for individual variation and sample size. *Mar. Mamm. Sci.* 19:38-58.
- Clausen, J., Braestrup, L. and Berg, O. 1974. The content of polychlorinated hydrocarbons in Arctic mammals. *Bull. Environ. Contam. Toxicol.* 23:728-732.
- Curry B.E. and Smith, J. 1997. Phylogeographic structure of the bottlenose dolphin (*Tursiops truncatus*): stock identification and implications for management. In: Dizon, A.E., Chivers, S.J. and Perrin, W.F. (eds) *Molecular Genetics of Marine Mammals*, The Society for Marine Mammalogy, Special Publication Number 3, pp.209-226.
- Dizon, A., Lockyer, C., Perrin, W.F., DeMaster, D.P. and Sisson, J. 1992. Rethinking the stock concept: a phylogeographic approach. *Conservation Biol.* 6:24-36.
- Donovan, G.P. 1991. A review of IWC stock boundaries. *Rep .int. Whal. Commn* (Special Issue 3):39-68.
- Dutton, P.H, Bowen, B.W., Owens, D.W., Barragan, A. and Davis, S.K. 1999. Global phylogeography of the leatherback turtle (*Dermodochelys coriacea*). *J. Zool., Lond.* 248:397-409.

- Fernandez, M., Herreras, V., Aznar, F.J., Balbuena, J.A., Lockyer, C. and Raga, J.A. 1993. Preliminary data on the helminth fauna of harbour porpoise in British waters. *European Research on Cetaceans* 7:187.
- Fontaine, P.-M., Hammill, M.O., Barrette, C. and Kingsley, M.C. 1994. Summer diet of the harbour porpoise (*Phocoena phocoena*) in the estuary and the northern Gulf of St Lawrence. *Can. J. Fish. Aquat. Sci.* 51:172-178.
- Gaskin, D.E. 1984. The harbour porpoise, *Phocoena phocoena*, (L.): regional populations, status, and information on direct and indirect catches. *Rep. int. Whal. Commn* 34:569-586.
- Gaskin, D.E., Smith, G.J.D., Watson, A.P., Yasui, W.Y. and Yurick, D.B. 1984. Reproduction in the porpoises (Phocoenidae): implications for management. *Rep. int. Whal. Commn* (Special Issue 6):135-148.
- Gao, A. and Gaskin, D.E. 1996. Geographic variation in metric skull characters among proposed subpopulations and stocks of harbor porpoise, *Phocoena phocoena*, in the western North Atlantic. *Mar. Mammal Sci.* 12:516-527.
- Granby, K. and Kinze, C.C. 1991. Organochlorines in Danish and West Greenland harbour porpoises. *Mar. Poll. Bull.* 22:458-462.
- Hammond, P.S., Benke, H., Berggren, P., Borchers, D.L., Collet, A., Heide-Jørgensen, M.P., Heimlich, S., Hiby, A.R., Leopold, M.F. and Øien, N. 2002. Abundance of the harbour porpoise and other cetaceans in the North Sea and adjacent waters. *J. Applied Ecol.* 39:361-376.
- Helle, E., Olsson, M. and Jensen, S. 1976. PCB levels correlated with pathological changes in seal uteri. *Ambio* 5:261-263.
- Herreras, M.V., Kaarstad, S.E., Balbuena, J.A., Kinze, C.C. and Raga, J.A. 1997. Helminth parasites of the digestive tract of the harbour porpoise *Phocoena phocoena* in Danish waters: a comparative geographical analysis. *Diseases of Aquatic Organisms* 28:163-167.
- Huggenberger, S., Benke, H. and Kinze, C.C. 2002. Geographical variations in harbour porpoise (*Phocoena phocoena*) skulls: support for a separate non-migratory population in the Baltic proper. *Ophelia* 56:1-12.
- [ICES] International Council for the Exploration of the Sea. 1997. Report of the working group on seals and small cetaceans in European seas, Stockholm, April 1-4, 1997. ICES 1997/N:1, 18pp.
- Iverson, S.J., Frost, K.J. and Lowry, L.F. 1997. Fatty acid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. *Mar. Ecol. Progr. Ser.* 151:255-271.
- [IWC] International Whaling Commission. 1994. Chairman's Report of the Forty-Fifth Annual Meeting. Appendix 11: Resolution on harbour porpoise in the North Atlantic and the Baltic Sea. *Rep. int. Whal. Commn* 44:34-35.
- [IWC] International Whaling Commission. 1995. Report of the Scientific Committee. Annex G, Appendix 3: Harbour porpoises in the North Atlantic. *Rep. int. Whal. Commn* 45:185-186.

- [IWC] International Whaling Commission. 1996. Report of the Scientific Committee. *Rep. int. Whal. Commn* 46:51-236.
- [IWC] International Whaling Commission. 1997. Chairman's Report of the Forty-Eighth Annual Meeting. Appendix 4: Resolution on small cetaceans 1996-4. *Rep. int. Whal. Commn* 47:49-50.
- [IWC] International Whaling Commission. 2000. Report of the Scientific Committee, Annex O: Report of the IWC-ASCOBANS Working Group on Harbour Porpoises. *J. Cetacean Res. Manage.* 2 (suppl.):297-305.
- Kaarstad, S.E. 1993. Vekst og reproduksjon hos nise (*Phocoena phocoena*) i norske og i svenske farvann. (Growth and reproduction in harbour porpoises in Norwegian and Swedish waters) Cand. Scient. Thesis, University of Oslo, 65pp. In Norwegian.
- Kinze, C.C. 1985. Intraspecific variation in Baltic and North Sea harbour porpoises (*Phocoena phocoena*, (L.1758)) *Vidensk. Meddr dansk naturh. Foren* 146:63-74.
- Kinze, C.C. 1989. On the reproduction, diet and parasitic burden of the harbour porpoise *Phocoena phocoena* in West Greenland waters. *European Research on Cetaceans* 3:91-95.
- Kinze, C.C. (MS) 1990a. Non-metric analysis of harbour porpoises (*Phocoena phocoena*) from the North and Baltic seas: implications for stock identity. IWC document SC/42/SM35.
- Kinze, C.C. 1990b. The harbour porpoise (*Phocoena phocoena*, (L., 1758)) stock identification and migration patterns in Danish and adjacent waters. PhD thesis, University of Copenhagen.
- Kleivane, L., Skaare, J.U., Bjørge, A., de Ruiter, E. and Reijnders, P.J.H. 1995. Organochlorines pesticide residue and PCBs in harbour porpoise (*Phocoena phocoena*) incidentally caught in Scandinavian waters. *Environ. Poll.* 89:137-146.
- Koschinski, S. 2002. Current knowledge on harbour porpoise (*Phocoena phocoena*) in the Baltic Sea. *Ophelia* 55:167-197.
- Larsen, B.H. 1995. Parasites and pollutants in seven harbour porpoises (*Phocoena phocoena* L. 1758) around the Faroe Islands. *Rep. int. Whal. Commn* (Special Issue 16):223-230.
- Lick, R. 1991. *Untersuchungen zu Lebenszyklus (Krebse, Fische, marine Säuger) und Gefrierresistenz anisakider Nematoden in Nord- und Ostsee.* (Investigations on the life cycle (crustaceans, fish, marine mammals) and freezing resistance of anisakide nematodes in the north and Baltic Sea.) Ph.D. dissertation, Institut für Meereskunde, Universität Kiel, 195pp.
- Lockyer, C. 1995a. Investigations of aspects of the life history of the harbour porpoise, *Phocoena phocoena*, in British waters. *Rep. int. Whal. Commn* (Special Issue 16):189-197.
- Lockyer, C. 1995b. A review of factors involved in zonation in odontocete teeth, and an investigation of the likely impact of environmental factors and major life events on harbour porpoise tooth structure. *Rep. int. Whal. Commn* (Special Issue 16):511-529.

- Lockyer, C. 1995c. Aspects of the biology of the harbour porpoise, *Phocoena phocoena*, from British waters. In: Blix, A.S., Walløe, L. and Ulltang, Ø. (eds); *Whales, seals, fish and man*, Elsevier Science, Amsterdam, 443-457.
- Lockyer, C. 1999. Application of a new method to investigate population structure in the harbour porpoise, *Phocoena phocoena*, with special reference to the North and Baltic seas. *J. Cetacean Res. Manage.* 1:297-304.
- Lockyer, C. 2003. Harbour porpoises (*Phocoena phocoena*) in the North Atlantic: Biological parameters. *NAMMCO Sci. Publ.* 5:71-90.
- Lockyer, C. and Andreassen, H. In press. Diet of harbour porpoise (*Phocoena phocoena*) in Danish waters. *European Research on Cetaceans* 15.
- Lockyer, C. and Kinze, C. 2003. Status, ecology and life history of harbour porpoise (*Phocoena phocoena*) in Danish waters. *NAMMCO Sci. Publ.* 5:143-176.
- Lockyer, C., Heide-Jørgensen, M.P., Jensen, J., Kinze, C.C. and Buus Sørensen, T. 2001. The biology of harbour porpoises (*phocoena phocoena*, L.) from West Greenland - age, length and reproductive parameters. *ICES J. Mar. Sci.* 58:154-162.
- Lockyer, C., Heide-Jørgensen, M.P., Jensen, J. and Walton, M.J. 2003. Life history and ecology of harbour porpoises (*Phocoena phocoena*) from West Greenland. *NAMMCO Sci. Publ.* 5:177-194.
- Long, S., McGarry, A., Pollard, D., Rogan, E. and Berrow, S. 1996. Cs-137 and K-40 in harbour porpoise (*Phocoena phocoena*) originating in Irish and British coastal waters. Abstract in *European Research on Cetaceans* 9:281-282.
- Loughlin, T.R. 1997. Using the phylogeographic method to identify Steller sea lion stocks. In: Dizon, A.E., Chivers, S.J. and Perrin, W.F. (eds), *Molecular Genetics of Marine Mammals*, The Society for Marine Mammalogy, Special Publication Number 3, pp.159-171.
- Moritz, C. 1994a. Defining "Evolutionarily significant Units" for conservation. *Trends in Ecology and Evolution* 9:373-375.
- Moritz, C. 1994b. Applications of mitochondrial DNA analysis in conservation: a critical review. *Molec. Ecol.* 3:401-411.
- Moritz, C. and Faith, D.P. 1998. Comparative phylogeography and the identification of genetically divergent areas for conservation. *Mol. Ecol.* 7:419-429.
- Møller, P. 1999. Distinguishing between foraging patterns and sexual maturity of harbour porpoise (*Phocoena phocoena*) utilising blubber fatty acid signature and classification regression analysis. Paper submitted as part fulfilment of a M.Sc. thesis, Århus University, Denmark, March 1999:44-89.
- Møller, P., Lockyer, C., Walton, M., Lund, T., Heide-Jørgensen, M.P. and Jensen, J. in press. Distinguishing between foraging patterns and sexual maturity of harbour porpoise (*Phocoena phocoena*) utilising blubber fatty acid signatures. *J.Cet. Res. Manage.*

- Müller, G., Siebert, U., Wünschmann, A., Artelt, A. and Baumgärtner, W. 2000. Immunohistological and serological investigation of morbillivirus infection in harbour porpoises (*Phocoena phocoena*) from the German Baltic and North Sea. *Vet. Microbiol.* 75:17-25.
- [NAMMCO] North Atlantic Marine Mammal Commission 2001. Report of the Management Committee Working Group on By-catch. In: *NAMMCO Annual Report 2000*, NAMMCO, Tromsø, Norway, pp. 107-114.
- Ólafsdóttir, D., Víkingsson, G.A., Halldórsson, D.S. and Sigurjónsson, J. 2003. Growth and reproduction in harbour porpoises (*Phocoena phocoena*) in Icelandic waters. *NAMMCO Sci. Publ.* 5:195-210.
- Olsson, M. 1978. PCB and reproduction among Baltic seals. Proceedings from the Symposium on the Conservation of Baltic Seals in Haikko, Finland, April 26-28, 1977. *Finnish Game Res.* 37:40-45.
- Olsson, M., Johnels, A.D. and Vaz, R. 1975. DDT and PCB levels in seals from Swedish waters. The occurrence of aborted seal pups. Proceedings from the Symposium on the Seals in the Baltic, June 1974. Lidingö, Sweden, Nat. Swed. Environ. Prot. Bd PM 591.
- Otterlind, G. (MS) 1976. The harbour porpoise (*Phocoena phocoena*) endangered in Swedish waters. ICES document CM N:16:3951-3957.
- Palka, D., Lockyer, C. and Bjørge, A. (MS) 1994. North Atlantic harbor porpoise population structure: a whole ocean collaboration. CMS/ASCOBANS/1/RP.1
- Palka, D.L., Read, A.J., Westgate, A.J. and Johnston, D.W. 1996. Summary of current knowledge of harbour porpoises in US and Canadian Atlantic waters. *Rep. int. Whal. Commn* 46:559-565.
- Paludan-Møller, P., Agger, C.Th., Dietz, R. and Kinze, C.C. 1993. Mercury, cadmium, zinc, copper and selenium in harbour porpoise (*Phocoena phocoena*) from West Greenland. *Polar Biol.* 13:311-320.
- Read, A.J. 1990a. Age of sexual maturity and pregnancy rates of harbour porpoises *Phocoena phocoena* from the Bay of Fundy. *Can J. Fish. Aquat. Sci.* 47:561-565.
- Read, A.J. 1990b. Reproductive seasonality in harbour porpoises, *Phocoena phocoena*, from the Bay of Fundy. *Can. J. Zool.* 68:284-288.
- Read, A.J. and Gaskin, D.E. 1990. Changes in growth and reproduction of harbour porpoises, *Phocoena phocoena*, from the Bay of Fundy. *Can. J. Fish. Aquat. Sci.* 47:2158-2163.
- Read, A.J. and Hohn, A.A. 1995. Life in the fast lane: the life history of harbour porpoises from the Gulf of Maine. *Mar. Mamm. Sci.* 11:423-440.
- Read, A.J. and Tolley, K.A. 1997. Postnatal growth and allometry of harbour porpoises from the Bay of Fundy. *Can. J. Zool.* 75:122-130.
- Read, A.J. and Westgate, A.J. 1997. Monitoring the movements of harbor porpoise (*Phocoena phocoena*) with satellite telemetry. *Mar. Biol.* 130:315-322.

- Recchia, C.A. and Read, A.J. 1989. Stomach contents of harbour porpoises, *Phocoena phocoena* (L.), from the Bay of Fundy. *Can. J. Zool.* 67:2140-2146.
- Richardson, S.F. 1992. Growth and reproduction in the harbor porpoise, *Phocoena phocoena* (L.), from eastern Newfoundland. M.Sc. thesis, Dept of Psychology, Memorial University of Newfoundland, 102pp.
- Riddell, B.E. 1993. Spatial organization of Pacific salmon: what to conserve? In: Cloud, J.G. and Thorgaard, G.H. (eds), *Genetic Conservation of Salmonid Fishes*, Plenum Press, New York, pp.23-42.
- Rosel, P. 1997. A review and assessment of the status of the harbour porpoise (*Phocoena phocoena*) in the North Atlantic. In: Dizon, A.E., Chivers, S.J. and Perrin, W.F. (eds) *Molecular Genetics of Marine Mammals*, The Society for Marine Mammalogy, Special Publication Number 3, pp.209-226.
- Rosel, P.E., Dizon, A.E. and Haygood, M.G. 1995. Variability of the mitochondrial control region in populations of the harbour porpoise, *Phocoena phocoena*, on interoceanic and regional scales. *Can. J. Fish. Aquat. Sci.* 52:1210-1219.
- Rosel, P.E., France, S.C., Wang, Y. and Kocher, T.D. 1999. Genetic structure of harbour porpoise *Phocoena phocoena* populations in the northwest Atlantic based on mitochondrial and nuclear markers. *Molec. Ecol.* 8:41-54.
- Ryder, O.A. 1986. Species conservation and systematics: the dilemma of subspecies. *Trends Ecol. Evol.* 1:9-10.
- Sequiera, M. 1996. Harbour porpoises, *Phocoena phocoena*, in Portuguese waters. *Rep. Int. Whal. Commn* 46:583-586.
- Smeenk, C., Leopold, M.F. and Addink, M.J. 1992. Note on the harbour porpoise (*Phocoena phocoena*) in Mauritania, West Africa. *Lutra* 35:98-104.
- Smith, G.J.D. and Gaskin, D.E. 1974. The diet of harbor porpoises (*Phocoena phocoena* (L.)) in coastal waters of Eastern Canada, with special reference to the Bay of Fundy. *Can. J. Zool.* 52:777-782.
- Smith, G.J.D. and Gaskin, D.E. 1983. An environmental index for habitat utilization by female harbour porpoises with calves near Deer Island, Bay of Fundy. *Ophelia* 22:1-13.
- Smith, R.J. and Read, A.J. 1992. Consumption of euphausiids by harbour porpoise (*Phocoena phocoena*) calves in the Bay of Fundy. *Can. J. Zool.* 70:1629-1632.
- Smyth, M., Berrow, S., Nixon, E. and Rogan, E. 2000. Polychlorinated biphenyls and organochlorines in by-caught harbour porpoises *Phocoena phocoena* and common dolphins *Delphinus delphis* from Irish coastal waters. *Biology and Environment* 100B (2):85-96.
- Stede, G. and Stede, M. 1990. Orientierende untersuchungen von seehundschädeln auf pathologische knochenveränderungen (Orientating investigations on harbour seal skulls regarding pathological bone changes) In, *Zoologische und Ethologische Untersuchungen zum Robbensterben*. Institute für Haustierkunde, Kiel, Germany, pp. 5331-5353. In German.

- Stenson, G. 2003. Harbour porpoises (*Phocoena phocoena*) in the North Atlantic: Abundance, removals and sustainability of removals. *NAMMCO Sci. Publ.* 5:271-302.
- Strand, J., Larsen, M.M. and Lockyer, C. in press. Accumulation of organotin compounds and mercury in harbour porpoises (*Phocoena phocoena*) from the Danish waters and West Greenland. *The Science of the Total Environment*.
- Szefer, P., Malinga, M., Czarnowski, W. and Skora, K. 1995. Toxic, essential and non-essential metals in harbour porpoises of the Polish Baltic Sea. In: Blix, A.S., Walløe, L. and Ulltang, Ø. (eds.); *Whales, seals, fish and man*. Elsevier Science B.V., Amsterdam, 617-622.
- Szefer, P., Zdrojewska, I., Jensen, J., Lockyer, C., Skóra, K., Kuklik, I. and Malinga, M.. 2002. Intercomparison studies on distribution and co-associations of heavy metals in liver, kidney and muscle of harbour porpoise, *Phocoena phocoena*. *Arch. Environ. Contam. Toxicol.* 42:508-522.
- Sørensen, T.B. and Kinze, C.C. (MS) 1990. Reproduction and growth in Danish harbour porpoises (*Phocoena phocoena* (L:)). IWC document SC/42/SM32.
- Sørensen, T.B. and Kinze, C.C. 1993. Reproduction and reproductive seasonality in Danish harbour porpoises, *Phocoena phocoena*. *Ophelia* 39:159-176.
- Taylor, B. L. 1997. Defining “population” to meet management objectives for marine mammals. In: Dizon, A.E., Chivers, S.J. and Perrin W.F. (eds) *Molecular Genetics of Marine Mammals*. Special Publication Number 3, The Society for Marine Mammalogy, pp. 49-65.
- Teilmann, J. 2000. Satellite tracking of harbour porpoises (*Phocoena phocoena*) in Danish waters. Paper submitted as part fulfilment of a Ph.D., University of Southern Denmark, Odense, Denmark, December 2000:61-85.
- Tiedemann, R., Harder, J., Gmeiner, C. and Haase, E. 1996. Mitochondrial DNA sequence patterns of harbour porpoises (*Phocoena phocoena*) from the North and the Baltic Sea. *Z. Säugetierkunde* 61:104-111.
- Tolley, K. and Heldal, H.E. 2002 Inferring ecological separation from regional differences in radioactive caesium in harbour porpoises *Phocoena phocoena*. *Mar. Ecol. Progr. Series* 228:301-309.
- Tolley, K.A., Rosel, P.E., Walton, M., Bjørge, A., and Øien, N. 1999. Genetic population structure of harbour porpoises (*Phocoena phocoena*) in the North Sea and Norwegian waters. *J. Cetacean Res. Manage.* 1:265-274.
- Tolley, K.A., Víkingsson, G. and Rosel, P. 2001. Mitochondrial DNA sequence variation and phylogeographic patterns in harbour porpoises (*Phocoena phocoena*) from the North Atlantic. *Conservation Genetics* 2:349-361.
- Víkingsson, G.A., Ólafsdóttir, D. and Sigurjónsson, J. 2003. Geographical and seasonal variation in the diet of harbour porpoises (*Phocoena phocoena*) in Icelandic coastal waters. *NAMMCO Sci. Publ.* 5:243-270.

- Vinther, M. 1999. By-catch of harbour porpoise (*Phocoena phocoena* L.) in the Danish set-net fisheries. *J. Cetacean Res. Manage* 1:123-135.
- Walton, M.J. 1997. Population structure of harbour porpoises *Phocoena phocoena* in the seas around the UK and adjacent waters. *Proc. R. Soc. Lond. B* 264:89-94.
- Wang, J.Y. and Berggren, P. 1997. Mitochondrial DNA analysis of harbour porpoises (*Phocoena phocoena*) in the Baltic Sea, the Kattegat-Skagerrak Seas and off the west coast of Norway. *Mar. Biol.* 127:531-537.
- Watson, W.S., Sumner, D.J., Baker, J.R., Kennedy, S., Reid, R. and Robinson, I. 1999. Radionuclides in seals and porpoises in the coastal waters around the UK. *The Science of the Total Environment* 234:1-13.
- Westgate, A.J. and Tolley, K.A. 1999. Geographical differences in organochlorine contaminants in harbour porpoises *Phocoena phocoena* from the western North Atlantic. *Mar. Ecol. Progr. Series* 177:255-268.
- Westgate, A.J., Read, A.J., Berggren, P., Koopman, H.N. and Gaskin, D.E. 1995. Diving behaviour of harbour porpoises, *Phocoena phocoena*. *Can. J. Fish. Aquat. Sci.* 52:1064-1073.
- Westgate, A.J., Read, A.J. and Cox, T.M. (MS) 1998a. When you wish upon a satellite: lessons about harbour porpoise conservation from satellite telemetry. *The World Marine Mammal Science Conference - Abstracts*:148, January 1998, Monaco.
- Westgate, A.J., Read, A.J. and Cox, T.M. 1998. Monitoring a rehabilitated harbor porpoise using satellite telemetry. *Mar. Mammal Sci.* 14:599-604.
- Wunschmann, A., Siebert, U., Frese, K., Weiss, R., Lockyer, C., Heide-Jørgensen, M.P., Müller, G. and Baumgärtner, W. 2001. Evidence of infectious diseases in harbour porpoises (*Phocoena phocoena*) hunted in the waters of Greenland and by-caught in the German North Sea and Baltic Sea. *Veterinary Record* 148:715-720.
- Yasui, W.Y. and Gaskin, D.E. 1986. Energy budget of a small cetacean, the harbour porpoise, *Phocoena phocoena* (L.). *Ophelia* 25:183-197.
- Yurick, D.B. 1977. Populations, subpopulations, and zoogeography of the harbour porpoise, *Phocoena phocoena* (L.). M.Sc. Thesis, University of Guelph, 148pp.
- Yurick, D.B. and Gaskin, D.E. 1987. Morphometric and meristic comparisons of skulls of harbour porpoise *Phocoena phocoena* (L.) from the North Atlantic and North Pacific. *Ophelia* 27:53-75.
- Zakharov, V.M. and Yablokov, A.V. 1990. Skull asymmetry in the Baltic grey seal - effects of environmental pollution. *Ambio* 19:266-269.