Inferring ecological separation from regional differences in radioactive caesium in harbour porpoises *Phocoena phocoena*

Krystal A. Tolley[1],*, Hilde Elise Heldal[2]

[1]Marine Mammal Division and [2]Marine Chemistry Division, Institute of Marine Research, PO Box 1870 Nordnes,
5817 Bergen, Norway

ABSTRACT: Geographic variation in the level of radioactive caesium-137 (^{137}Cs) was examined from the axial muscle of 36 harbour porpoises *Phocoena phocoena* obtained as bycatch from 5 locations along the coast of Norway, ranging from southern (North Sea) to northern (Barents Sea) Norway. Levels of ^{137}Cs in seawater and sediments have been found to differ along the coast of Norway due to distance from point sources, such as the Sellafield nuclear fuel reprocessing plant in Cumbria, UK (discharging into the Irish Sea) and outflow from the Baltic Sea, which contains significant amounts of ^{137}Cs that originated in Chernobyl. Radioactive caesium is accumulated in muscle in a manner related to ambient levels in the environment through exposure and/or ingestion of contaminated prey items. Hence, we hypothesised that if harbour porpoises are philopatric, their muscle tissue would reflect concentrations of ^{137}Cs in their area of residence. The levels found in harbour porpoise muscle were consistent with that found in the area from which they were caught. Porpoises from the Barents Sea had significantly lower levels of ^{137}Cs than porpoises from the west and south coasts of Norway, reflecting the concentration patterns of ^{137}Cs in the waters of those areas. This suggests ecological separation of harbour porpoises in these regions, and that porpoises are limited in their movements along the coast of Norway.

KEY WORDS: Population structure · Harbour porpoise · Caesium-137

INTRODUCTION

Elucidating population structure for species threatened by human activities is critical for formulating conservation and management plans. However, it is often difficult to create *a priori* hypotheses regarding population structure, especially for species whose distribution is not delimited by obvious natural zoogeographic barriers. Furthermore, many marine species have the potential for high dispersal and gene flow, making population structure difficult to detect (Palumbi 1994, Hoelzel 1998, Waples 1998) even if hypotheses on their

structure can be formulated. Despite such homogenising qualities, marine species inhabiting geographically different areas can be evolutionarily and/or demographically independent and, depending upon management objectives, may require separate management plans (Taylor & Dizon 1999). Consequently, information on population structure is essential to manage such species effectively and to ensure that no one population sustains disproportionately high anthropogenic impacts.

There appears to be no universally held definition of a 'population' (sometimes called a 'biological stock'), but generally a population can be characterised as a group of interbreeding individuals living in a limited geographic area (Carvalho & Hauser 1994, Hartl & Clark 1997). If gene flow between populations is minimal, individual populations will be on separate

*Present address: Zoology Department, University of Stellenbosch, Private Bag X1, 7602 Matieland, South Africa
E-mail: tolley@sun.ac.za

demographic and evolutionary tracks (Waples 1998). Eventually, such populations will become genetically distinct, and genetic markers could be useful to identify population structure. However, genetic markers may fail to detect population structure when separation is too recent for genetic differences to have accumulated between the populations, or if gene flow is high enough to prevent detectable differences from accumulating (Slatkin 1987, Waples 1998). In such instances, ecological markers may be useful for making inferences regarding contemporary population structure. However, caution in the interpretation of ecological separation must be used. Such markers are acquired rather than inherited, and therefore do not necessarily indicate the presence of populations, but instead suggest where an individual has spent a portion of its lifetime (Avise 1994). Hence, such information reflects contemporary spatial distribution of the individuals. Nevertheless, ecological markers can be used to assist in creating hypotheses regarding population structure when genetic markers fail to detect differences.

The harbour porpoise *Phocoena phocoena* suffers heavy mortality as bycatch in commercial gillnet fisheries. In some regions, it has been suggested that bycatch rates are higher than intrinsic rates of population growth (Jefferson & Curry 1994, Tregenza et al. 1997, Anonymous 2000a,b), the effect of which would be declining populations. In many other areas, bycatch is known to exist, but has not been quantified (International Whaling Commission [IWC] 1996); hence the effects of bycatch in these areas are virtually unknown. Although conservation actions are needed for this species, bycatch mitigation plans are unlikely to be effective without a full understanding of the population structure, because such measures may not be applied to units that are biologically meaningful. For harbour porpoises, the difficulty in identifying such units lies in the spatial distribution of this species and its high potential for dispersal. Harbour porpoises are found in the coastal waters of the North Pacific, North Atlantic, and the Black Sea. In the North Atlantic, they are distributed in patches of varying density from Senegal in West Africa northward into European waters and westward to Iceland, Greenland, and North America as far south as North Carolina. Their distribution is concentrated around land masses and islands, but they are occasionally observed in the deep oceanic expanses dividing these land masses (Donovan & Bjørge 1995). Hence, there is a potential for these concentrations of porpoises to form distinct populations but to remain connected by corridors through which gene flow may occur.

In the North Atlantic, harbour porpoises have been divided into 13 putative populations by the IWC (1996).

The designations were based on the distribution and abundance of porpoises plus oceanographic features that could potentially restrict gene flow (Donovan & Bjørge 1995). Recently, ecological and genetic markers have been used to gain insight into the structuring of the North Atlantic populations. These studies have supported some of the IWC designations, especially in the western North Atlantic (Wang et al. 1996, Read & Westgate 1997, Rosel et al. 1999, Westgate & Tolley 1999, Tolley et al. 2001). Conversely, morphometric, genetic, and ecological data have lent support to the presence of fine-scale population structure in the eastern North Atlantic that is not captured by the IWC definitions (e.g. Andersen 1993, Kleivane et al. 1995, Tiedemann et al. 1996, Börjesson & Berggren 1997, Walton 1997, Wang & Berggren 1997, Berrow et al. 1998, Tolley et al. 1999).

Radionuclides can be useful biomarkers for indicating ecological separation in high trophic-level marine species. Radioactive caesium-137 (^{137}Cs) is useful in this respect, because this contaminant accumulates in muscle tissue due to its chemical similarity to potassium (Dahlgaard et al. 1994). ^{137}Cs (half-life = 30 yr) is a fission product and an important component of radioactive wastes discharged into coastal waters of northwest Europe. The main sources are the nuclear reprocessing plants at Sellafield (UK), which has discharged into the Irish Sea since 1952, and La Hague (France), which has discharged into the English Channel since 1966 (Kershaw & Baxter 1995, Kershaw et al. 1999). These discharges are transported from their sources into the North Sea, where they mix with waters from the Baltic Sea containing significant amounts of ^{137}Cs originating from fallout of the Chernobyl nuclear reactor accident (Herrmann et al. 1995, Kershaw & Baxter 1995, Føyn & Sværen 1997, Kershaw et al. 1997). The contamination is transported further northwards in the Norwegian Coastal Current, which splits into 2 branches off northern Norway: the North Cape Current, which enters the Barents Sea to the east, and the West Spitsbergen Current, which enters the Fram Strait to the west (Kershaw & Baxter 1995). Other potential sources for radioactivity in Norwegian and adjacent seas are global fallout, dumping of radioactive material in the Barents and Kara Seas off northern Russia, fallout from nuclear weapons testing near Novaya Zemlya by the former Soviet Union, and discharge into Russian rivers draining into the Barents and Kara Seas (Aarkrog 1998).

Radioactive caesium in the water column is useful for labelling water masses (Herrmann et al. 1995) as its concentration varies depending on distance from the source and the oceanographic forces that spread the contamination. In Norway, the southern coastal waters have the highest levels of contamination due to the

nearby locations of point sources for ^{137}Cs (Kershaw et al. 1997). The west coast of Norway is less contaminated because the distance from these sources is greater, while the northern coast of Norway has low levels of contamination because of its great distance from Sellafield and the Baltic Sea (Føyn & Sværen 1997, Kershaw et al. 1997). Sources in northern Russia do not appear to have a large effect on contamination levels along the coast of northern Norway because of the eastward-flowing current systems transporting contamination away from northern Norway.

In this study, we hypothesised that the level of ^{137}Cs in the muscle tissue of harbour porpoises should reflect the ambient concentration in the local region from which they were sampled, if porpoises are philopatric. The elimination rate of ^{137}Cs from muscle is species-dependent, and has not been investigated in marine mammals. However, elimination proceeds at a slower rate with increasing body size, and when at steady state with ambient levels of ^{137}Cs for both poikilotherms (Mailhot et al. 1989, Rowan & Rasmussen 1995) and homeotherms (Mailhot et al. 1989). Given this general pattern, we assumed that elimination does not proceed rapidly for harbour porpoises, because of their large body size and their potential for chronic exposure from the environment. Given the distribution of ^{137}Cs in the water column, we expected porpoises from the southernmost regions of Norway to have the highest levels of ^{137}Cs, those from western Norway to have intermediate levels, and those from the Barents Sea to have the lowest levels. Alternatively, if harbour porpoise movements are not restricted along the coast of Norway, levels of ^{137}Cs in muscle should not show a high correspondence to geographic location.

MATERIALS AND METHODS

Samples were collected opportunistically from porpoises caught incidentally by commercial bottom-set gillnet fisheries along the Norwegian coast between April–June 1999 and April 2000. Thirty-six porpoises were collected (13 females, 23 males) from 5 different counties in Norway (Vest-Agder: n = 3; Rogaland: n = 5; Hordaland: n = 2; Nordland: n = 7; Finnmark: n = 19) spanning a distance of ca. 2200 km (Fig. 1). Large quantities of muscle tissue are required for the analysis, therefore approximately 500 to 750 g of epaxial muscle were obtained from each individual and frozen at –20°C. The samples were subsequently ground, freeze-dried, homogenized, and filled into polyethylene counting boxes of appropriate size prior to analysis. The gamma-counting for ^{137}Cs was performed on a Canberra HPGe detector with 30% efficiency, an electric cryostat cooling system, and 10 cm lead shielding.

Three regional groupings were used to compare geographic variation of ^{137}Cs levels in porpoise tissue. Because of small sample sizes in some of the regions, the 3 most geographically close counties (Vest-Agder, Rogaland, and Hordaland) were grouped together (n = 10), and are hereafter referred to as the 'Southwest' group. Porpoises collected from the counties of Nordland (n = 7) and Finnmark (n = 19) were grouped separately.

The levels in tissues for some classes of contaminants have been shown to vary with age, sex, body size, and diet (Aguilar et al. 1999). Data on ages of individuals were not available for these samples, so the relationship of the level of ^{137}Cs (Bq kg^{-1} wet wt) with body size was investigated by regression against standard length separately for each region. Although length is not a flawless proxy for age, length and age are positively related up to at least 5 yr of age in male harbour porpoises and 7 yr of age in females (Lockyer 1995, Read & Tolley 1997). Because sample sizes were small, regressions were stratified according to region only and not by sex.

To investigate the possible implications of combining both sexes within each region, a Mann-Whitney *U*-test was conducted between the sexes for the Finnmark sample. The comparison was limited to a single region so as not to introduce any bias due to regional differ-
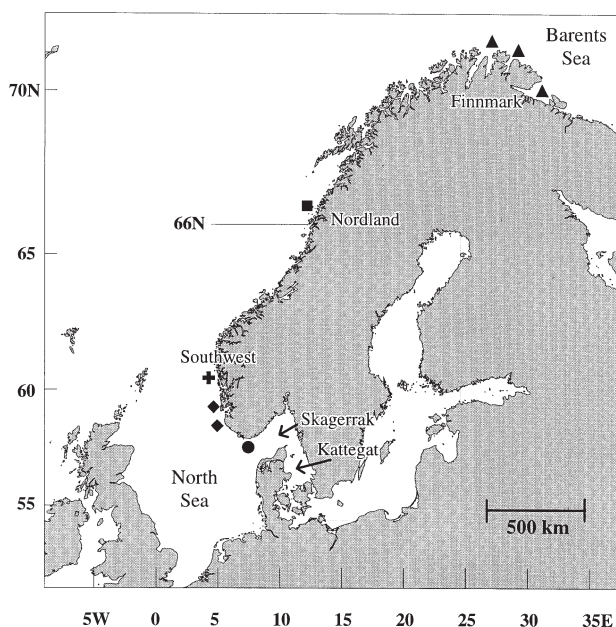

Fig. 1. *Phocoena phocoena*. Sampling locations of porpoises on the coast of Norway. (●) Vest-Agder; (◆) Rogaland, (✚) Hordaland; (■) Nordland; (▲) Finmark. Line (at 66°N) dividing the North Sea and the North Norway/Barents Sea putative populations defined by the International Whaling Commission is shown

Table 1. *Phocoena phocoena.* Sampling locations and levels of ^{137}Cs (Bq kg^{-1} wet wt) in skeletal muscle of porpoises collected along the coast of Norway. Counting error for each measurement (Error) and concentration factor (CF) are also given. M: male; F: female

Location ID no.	Sex	Bq kg^{-1}	Error	CF
Vest-Agder				
N9922	M	3.83	0.05	191
N9925	M	2.46	0.02	123
30-03-00	F	1.18	0.01	59
Rogaland				
N9908	F	0.60	0.01	50
N9905	M	0.39	0.01	33
N9906	M	0.53	0.01	44
N9907	M	0.50	0.02	42
N9921	M	1.11	0.03	93
Hordaland				
N9901	F	0.88	0.01	74
N9902	F	1.07	0.02	89
Nordland				
N9932	F	0.80	0.02	100
N9918	M	1.22	0.02	152
N9919	M	0.78	0.01	98
N9920	M	0.92	0.02	115
N9929	M	0.65	0.01	81
N9930	M	0.53	0.01	66
N9931	M	1.49	0.03	186
Finnmark				
N9904	F	0.40	0.01	99
N9909	F	0.51	0.01	127
N9910	F	0.41	0.01	103
N9911	F	0.58	0.02	146
N9913	F	0.30	0.01	75
N9914	F	0.68	0.01	170
N9916	F	0.68	0.01	169
VF06	F	0.53	0.01	134
N9903	M	0.58	0.02	145
N9912	M	0.43	0.01	109
N9915	M	0.56	0.01	139
N9917	M	0.49	0.01	124
N9923	M	0.36	0.01	89
N9924	M	0.52	0.01	130
N9926	M	0.35	0.01	87
N9927	M	0.39	0.01	96
N9928	M	0.57	0.01	142
VF03	M	0.49	0.02	122
VF04	M	0.58	0.01	145

ences in the level of ^{137}Cs. This comparison was run only for the Finnmark group because its sample size was largest (8 females, 11 males).

For the regional comparisons of ^{137}Cs levels in porpoises, raw and log-transformed data showed heterogeneity of variances among groups (Levene's test of equality of variance). Hence, a non-parametric test was used to compare the levels of ^{137}Cs among the 3 regions (Kruskal-Wallis test), and pairwise comparisons were made using a Mann-Whitney *U*-test.

The concentration factor (CF) for each porpoise was calculated by dividing the level of ^{137}Cs in each porpoise by the ^{137}Cs concentrations in seawater from the region where the porpoise was caught. The ^{137}Cs concentrations used were median values of those available in the literature (Brungot et al. 1997, Kershaw et al. 1997, Grøttheim 1998, Brungot et al. 1999). Values used were 0.020 Bq l^{-1} (Vest-Agder), 0.012 Bq l^{-1} (Rogaland), 0.012 Bq l^{-1} (Hordaland), 0.008 Bq l^{-1} (Nordland) and 0.004 Bq l^{-1} (Finnmark).

RESULTS

The levels of ^{137}Cs in porpoises from the Norwegian coast ranged from 0.30 to 3.83 Bq kg^{-1} wet wt (Table 1). Overall, there was a trend of decreasing ^{137}Cs level with increasing standard length, but this was due to the high levels found in the tissue of porpoises from Vest-Agder (Fig. 2). Within each region, there was no significant relationship between the standard length of porpoises and levels of ^{137}Cs (Southwest: $r^2 = 0.15$, p = 0.24; Nordland: $r^2 = 0.36$, p = 0.21; Finnmark: $r^2 = 0.04$, p = 0.42; Fig. 2).

There was no significant difference between the sexes within the Finnmark region (Mann-Whitney *U*-test, p = 0.457). Among the 3 geographic regions, there was a significant difference in ^{137}Cs level in the muscle of porpoises (Kruskal-Wallis test, p = 0.001; Table 2). Pairwise comparisons indicated that porpoises from Finnmark had significantly lower levels than those from the Southwest region (p = 0.002), and those from Nordland (p = 0.001). There was no significant difference in ^{137}Cs levels between porpoises from the Southwest and Nordland (p = 0.961). To investigate whether the high levels observed in several of the porpoises from Vest-Agder (Fig. 3) could have biased the results
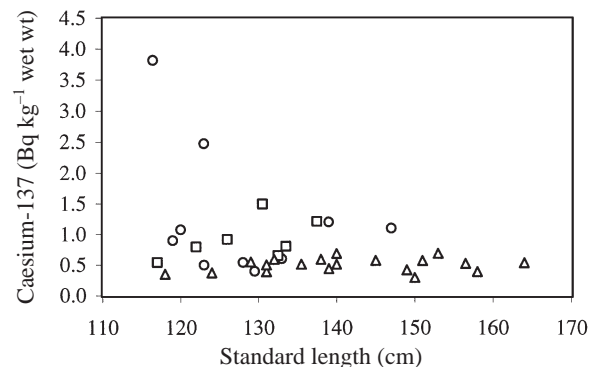
Fig. 2. *Phocoena phocoena.* Standard lengths and levels of ^{137}Cs in Harbour porpoises from 3 regions in Norway. (O) Southwest; (□) Nordland; (△) Finnmark (Southwest = Vest Agder, Rogaland and Hordaland)

Table 2. *Phocoena phocoena.* Sample size (n), means and standard deviations (SD) for levels of ^{137}Cs (Bq kg^{-1} wet wt) in harbour porpoises from 3 regions (Southwest = Vest-Agder, Rogaland and Hordaland) Sig. diff.: significant differences between groups

Region	n	Mean	SD	Sig. diff.
Southwest	10	1.26	1.082	Finnmark
Nordland	7	0.91	0.334	Finnmark
Finnmark	19	0.49	0.109	Southwest, Nordland

of the regional comparison, an additional comparison was run with all Vest-Agder porpoises excluded from the Southwest group. Pairwise comparisons showed the same regional differences even when these Vest-Agder porpoises were excluded (Mann-Whitney *U*-test; Finnmark vs Southwest, p = 0.029; Nordland vs Southwest, p = 0.302).

Fine-scale regional differences for all 5 counties were investigated by comparing the mean level of ^{137}Cs in porpoises from each county with the ambient concentrations of ^{137}Cs in seawater (Fig. 3). The levels of ^{137}Cs in porpoises generally decreased from south to north (highest in Vest-Agder and lowest in Finnmark), which mirrored the concentrations found in seawater (Fig. 3). The exception was that the seawater concentration off Nordland was lower than some of the other locations in western Norway, yet the porpoises from this region did not show a corresponding lower concentration of ^{137}Cs (Fig. 3). Concentration factors ranged from 33 to 191, with a mean of 110. The average is consistent with that reported for other cetaceans, although the range is wider (Calmet et al. 1992, Berrow et al. 1998, Watson et al. 1999).

DISCUSSION

The levels of ^{137}Cs in porpoises collected from the 5 geographic regions along the coast of Norway generally reflected ambient water concentrations in the same regions. Levels were highest in porpoises from southern Norway, intermediate in those from the west coast, and lowest in those from northern Norway. The exception was for Nordland, where seawater concentrations of ^{137}Cs were lower than in other west-coast regions (Kershaw et al. 1997), but the ^{137}Cs concentrations in porpoise tissue were not lower (Fig. 3). However, because seawater concentrations from this region were only available from measurements taken at sea and not in the inshore waters that the porpoises inhabit, there is a potential for bias in the results. In Nordland, a substantial amount of ^{137}Cs enters the coastal waters as run-off from the northern fjords, as

this region received high levels of Chernobyl fall-out (Dahlgaard et al. 1994). Furthermore, this is a region where porpoises inhabit near-coastal waters because the continental shelf that they prefer is very narrow. Therefore, they could receive higher doses than expected due to their being restricted to more contaminated coastal waters. Although the level of ^{137}Cs has not yet been quantified in these near-coastal waters, the level of ^{137}Cs in seaweed and sediments from the Nordland region has also been found to be slightly higher than in other regions along the west coast (Brungot et al. 1997). This suggests that higher concentrations than predicted (based on the available seawater concentrations) may be expected in porpoises from this region.

The International Whaling Commission has proposed that there are 3 populations of harbour porpoises along the Norwegian coast: (1) in the Kattegat and adjacent waters, (2) in the North Sea, and (3) in North Norway and the Barents Sea (Fig. 1). The putative division between the North Sea population and the North Norway/Barents Sea population is located on the west coast of Norway at 66°N (present Fig. 1, and Donovan & Bjørge 1995). Of the 5 collection areas in the present study, 3 fall into the North Sea population (Vest-Agder, Rogaland, Hordaland), 2 into the North Norway/Barents Sea population (Finnmark, Nordland), and none into the Kattegat and adjacent waters. The differing levels of ^{137}Cs in porpoises from the Norwegian coast provide some information on the biological significance of the populations proposed by the IWC. Given the difference in ^{137}Cs concentrations between Finnmark and Nordland, a single North Norway/Barents Sea population is not supported. Nordland porpoises showed significantly higher levels of ^{137}Cs than those from the Barents Sea, suggesting that there is little movement of porpoises between the northwest coast (Nordland) and the Barents Sea (Finn-
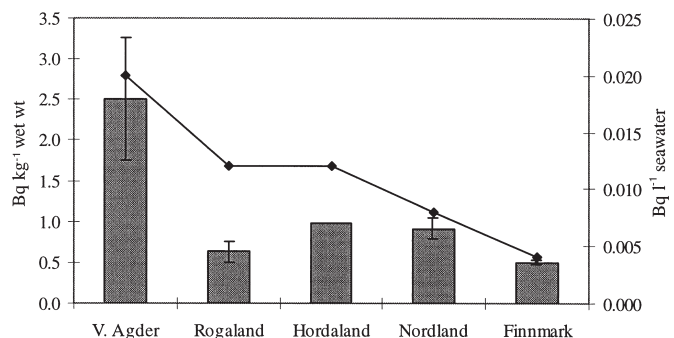

Fig. 3. *Phocoena phocoena.* Mean levels (±SE) of ^{137}Cs porpoises from 5 locations in Norway (histograms). Continuous line: median concentrations of ^{137}Cs in seawater within each area (Southwest = Vest-Agder, Rogaland and Hordaland)

mark). Hence, the IWC's North Norway/Barents Sea population may encompass a region that is too broad to reflect population structure on an ecological scale; combining porpoises from the Barents Sea with those south to 66° N may be inappropriate.

There was no significant difference detected between the Southwest region (Vest-Agder, Rogaland, Hordaland) and Nordland. However, ambient ^{137}Cs concentrations in seawater from these regions are similar, which limits the ability of this technique to detect differences between these regions. Within the Southwest group, porpoises from Vest-Agder averaged higher levels of ^{137}Cs than the other regions (Fig. 3), but sample sizes in that region were too small to treat Vest-Agder as a separate group. The higher levels for Vest-Agder porpoises possibly suggest that they are part of a Kattegat population to the east, an area which is more heavily contaminated with ^{137}Cs than both the North Sea and the west coast of Norway (Brungot et al. 1999).

Porpoises from Rogaland had somewhat lower levels than those in Hordaland and Nordland (Fig. 3). Near Rogaland, the Norwegian Coastal Current (NCC), which transports ^{137}Cs northwards, is relatively narrow (Sætre & Ljøen 1971). Porpoises off southwest Norway (i.e. Rogaland) could be moving outside the narrow NCC and into more saline North Sea or Atlantic waters, as they are known to utilise the relatively shallow offshore waters of the North Sea (Hammond et al. 1995). As a result, they may spend a substantial amount of time in less-contaminated waters, resulting in lower levels of ^{137}Cs in their tissue. At higher latitudes, the NCC undergoes mixing with Atlantic water (Sætre & Ljøen 1971), and the zone of ^{137}Cs contamination tends to extend westwards (Casso & Livingston 1984). Thus, variability associated with the NCC will be less of a factor in northern regions.

As contaminants are acquired by the individual rather than inherited, these data measure population structure on an ecological time scale, and are suggestive of ecological separation. This differs from the time scale at which genetic data measures population structure. For groups that have become isolated, it may take hundreds or thousands of generations for genetic differences to accumulate, even when highly sensitive markers such as mitochondrial DNA or microsatellites are used to quantify this variation (Palumbi et al. 1991). In a study of the sequence variation in the mitochondrial DNA control region, harbour porpoises from the Barents Sea and southwestern coast of Norway could not be differentiated, suggesting that porpoises in these 2 regions are genetically similar (Tolley et al. 1999). These genetic data stand in contrast to the differences found for ^{137}Cs levels in porpoises from these 2 regions. One explanation for genetic similarity may

be a recent recolonisation of the Barents Sea by harbour porpoises since the end of the last Pleistocene glaciation, ca. 10 000 yr BP (Tolley et al. 1999, Tolley et al. 2001). The genetic similarity of southern and northern porpoises could be the result of the short time span since recolonisation, perhaps coupled with some contemporary gene flow. However, the differences in ^{137}Cs indicate that ecological separation does exist, despite the absence of genetic differentiation.

Fine-scale population structure in the eastern North Atlantic has been suggested previously, and porpoises from the Kattegat-Skagerrak Seas have been found to be genetically different to those from the west coast of Norway (Wang & Berggren 1997). Furthermore, geographic variation in organochlorine levels has been detected in male harbour porpoises from the Barents Sea and the west coast of Norway (Kleivane et al. 1995), which suggests that porpoises do not regularly move throughout the coast of Norway but may be restricted to relatively limited geographic regions. Further support comes from monitoring the movements of individual porpoises in the eastern North Atlantic. Satellite telemetry data from Denmark indicates that porpoises do not regularly move out of the Kattegat-Skagerrak region (Teilmann 2000). In Teilman's study, 17 porpoises were satellite-tagged off the coast of Denmark, and these individuals restricted themselves to the Kattegat throughout the study period, which spanned the breeding season. Only 2 of the 17 porpoises moved northwards toward the Skagerrak Sea early in the breeding season (Teilmann 2000). Although the telemetry data cannot confirm that the Kattegat contains a separate population, it does suggest that there is limited movement between the Kattegat and other regions. The situation may be similar in the Barents Sea, where 7 satellite-tagged porpoises did not move west of 29° E throughout the breeding season (K. A. Tolly unpubl. data). This suggests that there may be limited exchange between the Barents Sea and the northwest coast of Norway.

The results of the present study are based on a single tracer, and therefore must be interpreted with some caution. Firstly, elimination rates associated with ^{137}Cs exposure have not been conducted for this species. Although it is not possible to generalise across species, experimental studies of elimination rates from fishes suggest this contaminant could remain present for several years if exposure were chronic, rather than acute, and body size large (Rowan & Rasmussen 1995, Forseth et al. 1998). Furthermore, some types of pollutants are known to be influenced by age, sex, and/or reproductive status (Kleivane et al. 1995, Westgate et al. 1997, Aguilar et al. 1999). Because sample sizes of several of the southern regions were small, it was necessary to combine individuals of all sizes and both

sexes in the analysis, perhaps confounding the results. In the present study, there was no indication of a significant relationship between the level of ^{137}Cs and body size, suggesting that, for these data, patterns of accumulation due to size (as a proxy for age) may not be sufficient to bias the analysis. Similarly, Berrow et al. (1998) found no strong relationship between levels of ^{137}Cs and age, length, or weight in harbour porpoises from British and Irish waters. Furthermore, there was no difference between females and males from Finnmark for ^{137}Cs loads, suggesting that any bias due to differences between the sexes would be limited for this sample.

The movements of prey items should be considered in the interpretation of the results because the uptake of ^{137}Cs could be due to either direct ingestion of seawater or ingestion of contaminated prey items. In the regions investigated, harbour porpoises generally prey on small coastal fishes such as herring *Clupea harengus*, capelin *Mallotus villosus*, pollack *Pollachius pollachius*, cod *Gadus morhua*, saithe *Pollachius virens*, haddock *Melanogrammus aeglefinus*, and whiting *Merlangius merlangus* (Bjørge et al. 1991). Although the data are limited, many of these fishes from the Barents, Norwegian, and North Seas have similar levels of ^{137}Cs in their tissues, generally on the order of 0.2 to 0.5 Bq kg^{-1} wet wt in adult fish, and 0.1 Bq kg^{-1} wet wt or less in juvenile fish (Brungot et al. 1999, H. E. Heldal unpubl. data). The similarities in the levels of ^{137}Cs in fishes from these regions may be due to similar levels of ^{137}Cs in seawater between some of the areas and the movements associated with spawning migrations between regions of varying ambient levels of ^{137}Cs, as individuals moving between regions of varying contamination will have homogeneous levels of ^{137}Cs in their tissues. It is possible that some of the regional similarities in porpoise tissue are due to predation upon these fishes with homogeneous ^{137}Cs levels that have migrated in from another region. Conversely, it is possible that porpoises in southern Norway have preyed upon fishes that had moved out of the more contaminated Baltic Sea. In particular, the Rügen herring spawns in the Baltic Sea but is known to move through the Skagerrak (Knijn et al. 1993), and the levels of ^{137}Cs in both Skagerrak fishes (ca. 1 Bq kg^{-1} wet wt; Brungot et al. 1997) and Baltic fishes (ca. 12 to 22 Bq kg^{-1} wet wt; Holm 1994) are higher than fishes from the other regions. Ingestion of prey fishes containing higher levels of ^{137}Cs, rather than direct exposure from the water, could have caused the elevated levels observed in the Vest-Agder porpoises.

The present results, when taken together with the differences in organochlorine loads among porpoises from the same regions (Kleivane et al. 1995), indicate that there is ecological separation of harbour porpoises

along the coast of Norway. This separation is in contrast to the findings based on mtDNA, where no differences were found between porpoises from southern and northern Norway (Tolley et al. 1999). Although the results from ecological and genetic markers apparently contrast, these methods assess population structure on 2 very different time scales. Presumably, porpoises in the Barents Sea have only recently recolonised that region and have not substantially diverged from porpoises in southern Norway at a level that is detectable using the available genetic markers (Tolley et al. 1999). However, the lack of genetic differences does not necessarily indicate panmixia along the coast of Norway, as ecological separation could indicate that porpoises are philopatric within a region. Hence, there is a need to consider the time scale relevant to management. If the objective of management is to preserve only evolutionarily independent units, management must proceed based solely on genetic differences, yet this criteria is extremely strict. In the present case, it would be precautionary to give credence to the results as shown by ecological markers when making assumptions regarding population structure.

LITERATURE CITED

Aarkrog A (1998) A retrospect of anthropogenic radioactivity in the global marine environment. Radiat Prot Dosim 75: 23−31

Aguilar A, Borrell A, Pastor T (1999) Biological factors affecting variability of persistent pollutant levels in cetaceans. In: Reijnders PJH, Aguilar A, Donovan GP (eds) Chemical pollutants and cetaceans. J Cetacean Res Manag (Spec Issue 1):83−116

Andersen LW (1993) The population structure of the harbour porpoise, *Phocoena phocoena*, in Danish waters and part of the North Atlantic. Mar Biol 116:1−7

Anonymous (2000a) Annual Report to Congress, 1999. Marine Mammal Commission, Bethesda, MD

Anonymous (2000b) A UK conservation strategy for the harbour porpoise (*Phocoena phocoena*). UK Department of the Environment, Transport and the Regions, Wetherby

Avise JC (1994) Conservation genetics. In: Avise JC (ed) Molecular markers, natural history and evolution. Chapman & Hall, New York

Berrow SD, Long SC, McGarry AT, Pollard D, Rogan E, Lockyer C (1998) Radionuclides (^{137}Cs and ^{40}K) in harbour porpoises *Phocoena phocoena* from British and Irish Coastal waters. Mar Pollut Bull 36:569−576

Bjørge A, Aarefjord H, Kaarstad S, Kleivane L, Øien N (1991) Harbour porpoise *Phocoena phocoena* in Norwegian waters. Int Counc Explor Sea Comm Meet Working Paper 1991/N:16

Börjesson P, Berggren P (1997) Morphometric comparisons of skulls of harbour porpoises (*Phocoena phocoena*) from the Baltic, Kattegat, and Skagerrak seas. Can J Zool 75: 280–287

Brungot AL, Sickel MAK, Bergan TD, Bøe B, Hellstrøm T, Strand P (1997) Radioactive contamination in the marine environment. NRPA Report 1997:3, Report no. 2 from the National Surveillance Programme. Norwegian Radiation Protection Authority, Osteraas

Brungot AL, Føyn L, Caroll JL, Kolstad AK, Brown J, Rudjord AL, Bøe B, Hellstrøm T (1999) Radioactive contamination in the marine environment. NRPA Report 1999:6, Report no. 3 from the National Surveillance Programme. Norwegian Radiation Protection Authority, Osteraas

Calmet D, Woodhead D, André JM (1992) ^{210}Pb, ^{137}Cs and ^{40}K in three species of porpoises caught in the Eastern Tropical Pacific Ocean. J Environ Radioact 15:153–169

Carvahlo GR, Hauser L (1994) Molecular genetics and the stock concept in fisheries. Rev Fish Biol Fish 4:326–350

Casso SA, Livingston HD (1984) Radiocaesium and other nuclides in the Norwegian-Greenland Seas 1981–1982. Woods Hole Oceanogr Inst Tech Rep WHOI-84–40

Dahlgaard H, Notter M, Brittain JE, Strand P, Rantavaara A, Holm E (1994) Nordic radioecology 1990–1993. In: Dahlgaard H (ed) Nordic radioecology: the transfer of radionuclides through Nordic ecosystems to man. Elsevier, Amsterdam, p 7–20

Donovan GP, Bjørge A (1995) Harbour porpoises in the North Atlantic: edited extract from the Report of the IWC Scientific Committee, Dublin 1995. Rep Int Whal Comm Spec Issue 16:3–25

Forseth T, Ugedal O, Naesje TF, Jonsson B (1998) Radiocaesium elimination in fish: variation among and within species. J Appl Ecol 35:847–856

Føyn L, Sværen I (1997) Distribution and sedimentation of radionuclides in the Barents Sea. ICES J Mar Sci 54: 333–340

Grøttheim S (1998) A preliminary report on radioactive contamination in the northern marine environment. Studies on distribution of radiocaesium, plutonium and americium in seawater and sediments. MSc thesis, University of Oslo

Hammond PS, Benke H, Berggren P, Borchers DL and 7 others (1995) Distribution and abundance of the harbour porpoise and other small cetaceans in the North Sea and adjacent waters, LIFE 92–2/UK/027. European Commission Directorate General for the Environment, Nuclear Safety and Civil Protection, Brussels

Hartl DL, Clark AG (1997) Principles of population genetics. 3rd edn. Sinauer Associates, Sunderland, MA

Herrmann J, Kershaw PJ, Bailly du Bois P, Guegueniat P (1995) The distribution of artificial radionuclides in the English Channel, southern North Sea, Skagerrak and Kattegat, 1990–1993. J Mar Syst 6:427–456

Holm E (1994) Polonium-210 and radiocaesium in muscle tissue of fish from different Nordic marine areas. In: Dahlgaard H (ed) Nordic radioecology: the transfer of radionuclides through Nordic ecosystems to man. Elsevier, Amsterdam, p 119–126

Hoelzel AR (1998) Genetic structure of cetacean populations in sympatry, parapatry, and mixed assemblages: implications for conservation policy. J Hered 89:451–458

International Whaling Commission (1996) Report of the sub-committee on small cetaceans. Rep int Whal Comm (Annex H) 46:160–179

Jefferson TA, Curry BE (1994) A global review of porpoise (Cetacea: Phocoenidae) mortality in gillnets. Biol Conserv 67:167–183

Kershaw PJ, Baxter A (1995) The transfer of reprocessing wastes from north-west Europe to the Arctic. Deep-Sea Res Part II Top Stud Oceanogr 42:1413–1448

Kershaw PJ, Gurbutt P, Woodhead D, Leonard K, Rees J (1997) Estimates of fluxes of ^{137}Cs in northern waters from recent measurements. Sci Total Environ 202:211–223

Kershaw PJ, McCubbin D, Leonard KS (1999) Continuing contamination of north Atlantic and Arctic waters by Sellafield radionuclides. Sci Total Environ 237/238: 119–132

Kleivane L, Skaare JU, Bjørge A, de Ruiter E, Reijnders P (1995) Organochlorine pesticide residue and PCBs in harbour porpoise (*Phocoena phocoena*) incidentally caught in Scandinavian waters. Environ Pollut 89:137–146

Knijn R, Boon TW, Heessen HJL, Hislop JRG (1993) Atlas of North Sea Fishes. Int Counc Explor Sea Coop Res Rep 194: 1–268

Lockyer C (1995) Investigation of aspects of the life history of the harbour porpoise, *Phocoena phocoea*, in British waters. Rep Int Whal Comm Spec Issue 16:189–197

Mailhot H, Peters RH, Cornett RJ (1989) The biological half-time of radioactive Cs in poikilothermic and homeothermic animals. Heath Phys 56:473–484

Palumbi SR (1994) Genetic divergence, reproductive isolation, and marine speciation. Annu Rev Ecol Syst 25: 547–572

Palumbi SR, Martin AP, Kessing B, McMillan WO (1991) Detecting population structure using mitochondrial DNA. Rep Int Whal Comm Spec Issue 13:271–278

Read AJ, Tolley KA (1997) Postnatal growth and allometry of harbour porpoises from the Bay of Fundy. Can J Zool 75: 122–130

Read AJ, Westgate AJ (1997) Monitoring the movements of harbour porpoises (*Phocoena phocoena*) with satellite telemetry. Mar Biol 130:315–322

Rosel PE, France SF, Wang JY, Kocher TD (1999) Genetic structure of harbour porpoise *Phocoena phocoena* populations in the Northwest Atlantic based on mitochondrial and nuclear markers. Mol Ecol 8: S41-S54

Rowan DJ, Rasmussen JB (1995) The elimination of radiocaesium from fish. J Appl Ecol 32:739–744

Sætre R, Ljøen R (1971) The Norwegian coastal current. In: Proceedings of the first international conference on port and ocean engineering under Arctic conditions, Vol 2. Technical University of Norway, Trondheim, Norway, p 514–535

Slatkin M (1987) Gene flow and the geographic structure of natural populations. Science 236:787–792

Taylor BL, Dizon AE (1999) First policy then science: why a management unit based solely on genetic criteria cannot work. Mol Ecol 8:S11-S16

Teilmann J (2000) The behaviour and sensory abilities of harbour porpoises (*Phocoena phocoena*) in relation to bycatch in gillnet fishery. PhD thesis, Odense University, Denmark

Tiedemann R, Harder J, Gmeiner C, Haase E (1996) Mitochondrial DNA sequence patterns of harbour porpoises (*Phocoena phocoena*) from the North and Baltic Sea. Z Säugetierkd 61:104–111

Tolley KA, Rosel PE, Walton MJ, Bjørge A, Øien N (1999) Genetic population structure of harbour porpoises (*Phocoena phocoena*) in the North Sea and Norwegian waters. J Cetacean Res Manag 1:265–274

Tolley KA, Víkingsson GA, Rosel PE (2001) Mitochondrial

DNA sequence variation and phylogeographic patterns in harbour porpoises *Phocoena phocoena* from the North Atlantic. Conserv Gen 2:349–361

Tregenza NJC, Berrow SD, Hammond PS, Leaper R (1997) Harbour porpoise (*Phocoena phocoena* L.) by-catch in set gillnets in the Celtic Sea. ICES J Mar Sci 54:896–904

Walton MJ (1997) Population structure of harbour porpoises *Phocoena phocoena* in the seas around the UK and adjacent waters. Proc R Soc Lond Ser Biol Sci 264:89–94

Wang JY, 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

Wang JY, Gaskin DE, White BN (1996) Mitochondrial DNA analysis of harbour porpoise, *Phocoena phocoena*, sub-populations in North American waters. Can J Fish Aquat Sci 5:1632–1645

Waples RS (1998) Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. J Hered 89:438–450

Watson WS, Sumner DJ, Baker JR, Kennedy S, Reid R, Robinson I (1999) Radionuclides in seals and porpoises in the coastal waters around the UK. Sci Total Environ 234: 1–13

Westgate AJ, Tolley KA (1999) Regional differences in organochlorine contaminants in harbour porpoises (*Phocoena phocoena*) from the western North Atlantic. Mar Ecol Prog Ser 177:243–254

Westgate AJ, Muir DCG, Gaskin DE, Kingsley MCS (1997) Concentrations and accumulation patterns of organochlorine contaminants in the blubber of harbour porpoises, *Phocoena phocoena*, from the coast of Newfoundland, the Gulf of St. Lawrence and the Bay of Fundy/Gulf of Maine. Environ Pollut 95:105–119