Application of a new method to investigate population structure in the harbour porpoise, *Phocoena phocoena*, with special reference to the North and Baltic Seas

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ABSTRACT

Tooth ultrastructure in harbour porpoise is examined as a possible tool for differentiating between animals from different geographical regions in the North Atlantic. Nine different characteristics in both dentine and cementum are identified and recorded in the decalcified, sectioned and stained teeth. Significant differences in several characters are found between porpoise tooth samples from the Canadian east coast and West Greenland, between Iceland, the North Sea, and Celtic Shelf, as well as sub-divisions within the North Sea, and between the North Sea, Skagerrak, Kattegat, Inner Danish waters and the Baltic Sea. The method appears promising if used on groups of known geographic origin. However, it is not certain that any one tooth could be assigned to a particular geographic group, when selected randomly.

KEYWORDS: HARBOUR PORPOISE; STOCK IDENTITY; ATLANTIC OCEAN

INTRODUCTION

Any paper on stock structure must consider what its objectives are and hence its working definitions of terms such as 'population', 'sub-population' and 'stock'. Donovan (1991) noted,

> . . . 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.

However, it is not the intention of this paper to provide recommended stock divisions but rather to examine a potential tool to contribute to such discussions. In this context, examination of samples in this paper has been primarily based on geographical location because (1) management interest is often focused on geographical regions and (2) such information is known for the available samples. In order to assist the reader, Tables 1 and 3 also include information on the relationship of the sampling areas to the putative stock boundaries suggested by the International Whaling Commission's Scientific Committee (Donovan and Bjørge, 1995) as well as the ICES (International Council for the Exploration of the Sea) and NAFO (North Atlantic Fisheries Organisation) statistical areas.

Previous studies have indicated that characteristics of incremental layers in the teeth of harbour porpoises had the potential for distinguishing between animals from different areas, based on limited samples from both widely separated regions where differences might have been anticipated to adjacent regions where differences were not so marked (Lockyer, 1995). Teeth are useful indicators of differences because they remain essentially unchanged once formed, although their internal characteristics may be modified throughout time as they grow. They thus provide a permanent phenotypic record for the individual. The importance of whether or not the tooth characters are genetic, phenotypic or environmentally modified in origin is dependent on the context, as will be discussed below. Characters affected by local environmental factors reflect the animals' ecology, and can provide useful information on the recent habitat, diet and habits of the animal. Such information may be dynamic and change rapidly over time, and may thus represent a momentary 'snapshot'. Teeth may also record events in the life history of the animal, such as weaning, sexual maturation, pregnancy and lactation (Klevezal' and Myrick, 1984; Lockyer, 1993), and these in turn may vary according to local environmental conditions. Manzanilla (1989), for example, reported hypocalcified laminae in the teeth of lactating dusky dolphins (*Lagenorhynchus obscurus*) in Peruvian waters during the El Niño years when there were dietary shortages.

Genetic information reveals more about the historic origins, breeding habits and longer term affiliations within populations (e.g. see Tolley *et al.*, 1999). Animals from different areas may interbreed at low levels but with sufficient interchange to preclude genetic data from providing useful information on present stock structure in a management context. Lack of significant genetic differences between putative populations/sub-populations, may therefore be misleading and not adequate for management purposes. Additionally animals may (1) migrate seasonally and/or (2) be geographically and/or temporarily segregated by sex and age; thus knowledge of both the time the samples were collected and the location is important. It is clear therefore, that information from a suite of techniques is ultimately needed to make the best judgment about population discreteness (e.g. Donovan, 1991).

The data presented here extend the work on tooth ultrastructure presented by Lockyer (1995).

MATERIAL AND METHODS

Table 1 lists the geographical regions for which samples were available. For comparative purposes, material from previously analysed teeth from Californian harbour porpoises has also been included (Lockyer, 1995). Ideally, one would examine teeth from approximately 50 or more animals for each region, but this was not possible in every case, especially the Baltic where few samples exist. Sample sizes by region and character are shown in Table 3.

Table 1

Proposed regional / putative population boundaries within the North Atlantic.

EASTERN NORTH ATLANTIC AND ADJACENT WATERS	
North Norway	Norway (ICES IIa) (IWC 7)
Northern North Sea	Northern North Sea + southern Norway (ICES IVa) + N.W.Scotland (ICES VIa) (IWC 8)
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)
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 (Bælts) (ICES IIIc) + Øresund (ICES IIIb) (IWC 9)
Baltic	Baltic including all bordering coasts (ICES IIId) (IWC 10)
EASTERN-CENTRAL NORTH ATLANTIC	
S.E.Iceland	S.E.Iceland (ICES Va east) (IWC 5)
S.W.Iceland	S.W.Iceland (ICES Va west) (IWC 5)
WESTERN NORTH ATLANTIC	
W.Greenland north	W.Greenland Maniitsoq (north) (NAFO 1C)
W.Greenland central	W.Greenland Nuuk (central) (NAFO 1D)
W.Greenland south	W.Greenland Paamiut (south) (NAFO 1E)
Canadian Bay of Fundy	E.Canada, Bay of Fundy / Gulf of Maine (NAFO 4X)
EASTERN NORTH PACIFIC	
California	S.California, USA

Two teeth from each animal were prepared following Lockyer (1995), each cut in different planes, as described in Bjørge *et al.* (1995). For the tooth characters considered here (see Table 2), adult (≥3 years) teeth are potentially most useful, although all animals ≥1 year have been examined. Teeth from neonates and calves (i.e. animals either without a well-formed neonatal line and/or first Growth Layer Group (GLG) boundary layer) have not been examined. The tooth characters examined include five used earlier (Lockyer, 1993; 1995) and an additional four.

Lockyer (1995) found that sex was not a significant factor in tooth character incidence, although larger sample sizes would allow a more complete investigation of this. In the present study, sexes have been combined while maintaining a fairly equal sex ratio throughout to minimise potential or latent biases. Most of the examined samples were collected between 1988 and 1993 to limit possible annual variations in environmental influences on the characters observed.

Comparisons between different regions using original numbers are presented below using Chi-square contingency analysis (Zar, 1984).

RESULTS AND DISCUSSION

The cause and origin is not known for all the characters examined here, but some are known to increase with age and maturation, e.g. *pulp stones* and *marker lines* (Lockyer, 1993; 1995). Thus, it is important to know the age composition of the sample for those characters. Other characters, e.g. *GLG type* and *boundary layer type* do not depend on age once the first GLG has formed. It is likely that some characters are genetic in origin and others, especially

Table 2

Criteria used for classifying anomalies (after Lockyer, 1993; 1995).

Pulp stones	Discrete nodules originating in the pulp cavity, often containing concentric rings, and present in the dentine (Perrin and Myrick, 1980).
Marker lines	Both in dentine and often cementum: discrete laminae which are regular yet noticeably different in appearance from the usual in morphology and affinity for stain; equivalent to the DSLs (densely staining layers) described by Klevezal' and Myrick (1984). They are often coincident with the boundary layer and may be extremely light- or dark-staining. Most frequently they are visible immediately adjacent to the boundary layer in the first or second GLG, or later, adjacent to the start of mineralisation interference.
Mineralisation interference	Irregularities in the lamina formation emanating from differential inhibition/activation of odontoblasts at the mineralisation front (normally, the pulp cavity edge), causing realignment of the dentinal tubules and resulting in wavey lines, squirls and asymmetry, which disrupt usual patterns yet do not prevent continuous lamina formation (Myrick, 1988).
Dentinal resorption	Actual erosion and frequent repair of existing regular laminated dentinal tissue, resulting in an amorphous and/or globular appearance, frequently with holes, cutting across and into regular tissue (Myrick, 1988).
Cemental disturbance	Any anomalous appearance of the usual regular laminated cemental tissue, including mineralisation interference and resorption (Myrick, 1988).
Boundary layer type	The boundary layer is the defining zone between one GLG (Perrin and Myrick, 1980) and the next. The boundary layer may be thin or thick and may be classified as follows: Type 1, (Bay of Fundy type, Bjørge *et al.*, 1995) which has poor affinity for stain (appears light); Type 2, (British type, Bjørge *et al.*, 1995) which has great affinity for stain (appears dark); Type 3 where the tooth may contain a mix of both types at different ages.
GLG type	Overall appearance of the GLG patterns in the sectioned dentine: Type 1, (Bay of Fundy type, Bjørge *et al.*, 1995) is characterised by very distinct GLG differentiation; Type 2, (British type, Bjørge *et al.*, 1995) is characterised by very indistinct GLG differentiation (boundary layers are unclear); Type 3 is a mix of both types present.
Accessory layers	These are additional distinct laminae which appear between the boundary layers within the GLG, and may be light or dark in staining quality (Perrin and Myrick, 1980).
Tooth shape	Any anomalous shape relative to the usual rounded spatulate crown, e.g. cusps or congenitally cleft crown.

marker lines and *dentinal resorption*, may be influenced by environmental factors such as dietary constraints (Manzanilla, 1989) and hormonal stresses (Myrick, 1988) perhaps caused by contaminant loads, or even inherent biological events e.g. weaning or lactation. However, it is not the intention of this paper to speculate on this or to provide an in-depth review of the implications in the broader stock structure context.

Table 3 provides sample sizes and percentage occurrence for most characters (*tooth shape* produced too few incidences) by region and sub-region. Sample size by main region ranges from 41 in the Baltic to 178 for West Greenland. When sub-regions are considered, the smallest sample size is 23 for Paamiut in southern West Greenland.

Fig. 1 shows the mean, minimum and maximum percentage occurrences for each character summed over the total North Atlantic (arranged in order of the range in percent occurrence). The incidence of *dentinal resorption* and *pulp stones* is low (< 15%) in all North Atlantic regions. Interestingly the value for *dentinal resorption* in the Californian sample is considerably higher (25%).

Other characters are considerably more variable, some ranging from less than 5% to over 90% (notably the two *boundary layer* types and the two *GLG* types). In general terms, characters showing greater variability by region are more likely to be of value in considering stock structure.

GLG type and *boundary layer type* reflect biochemical make-up through stainability. *GLG type* 1 has the highest occurrence (> 75%) in the northern North Sea/Norway, northern West Greenland and Canada, and a relatively high (> 60%) incidence in Iceland and the other West Greenland sub-regions. *Boundary layer type* 1 which is light-staining, is also highest (> 75%) in North Sea/Norway, West Greenland, Canada and Iceland, suggesting some correlation between the two characters. In general, the dark-staining *boundary layer type* 2 is most common (> 80%) in the Baltic, central and southern North Sea and Celtic Shelf, with intermediate levels in the Skagerrak.

The incidence of *cemental disturbance* is highest (*ca* 60%) in the Skagerrak and Inner Danish waters (it is also high in California). The lowest levels (< 10%) occur in West Greenland and Iceland. Cementum acts as a physical bond between the tooth and the gum in the jaw, fixing it firmly, and feeding habits and diet may influence this character. Certainly there are known dietary differences between these areas, which might reflect feeding strategies (Aarefjord *et al*., 1995; Víkingsson and Sigurjónsson, 1996; Lockyer and Kinze, 1999; Lockyer *et al*., 1999; Møller, 1999).

The lowest incidences (< 10%) of *mineralisation interference* are found in West Greenland and southwest Iceland. The highest North Atlantic incidence is 24% in the Bay of Fundy, whilst the highest incidence of all, 46.4%

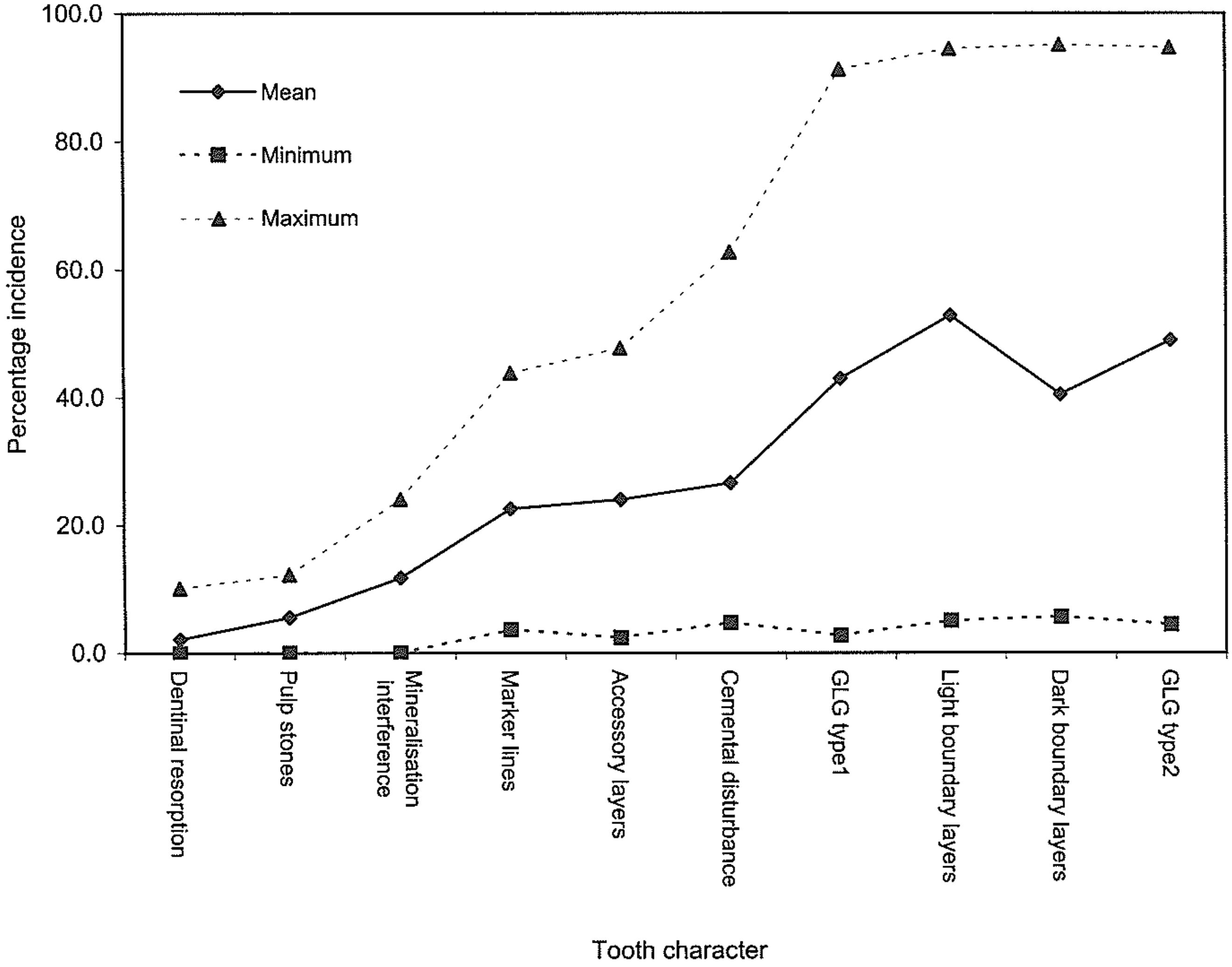

Fig. 1. Mean, minimum and maximum percentage occurrences summed over the total North Atlantic (see text).

Table 3

Percentage incidence of mineralisation anomalies in porpoise teeth by geographic area.

Locality	Putative stock or region IWC	Putative stock or region ICES /NAFO	Sample size	Percent sample<3 yr	Pulp stones	Mineralisation interference	Marker lines	Dentinal resorption	Cemental disturbance	Accessory lines	Light boundary layers	Dark boundary layers	GLG Type 1	GLG Type 2
Baltic	10	IIId	41	61.0	12.2	12.2	12.2	0	24.4	2.4	5.0	95.0	2.7	94.6
Inner Danish waters + Kattegat	9	IIIc; IIIas	59	44.1	6.8	15.3	30.5	6.8	62.7	11.9	15.6	56.3	13.2	81.6
Skagerrak	8-9	IIIan	38	52.6	7.9	15.8	26.3	0	57.9	7.9	60.0	40.0	30.8	69.2
Southern North Sea	8	IVc	69	44.9	5.8	11.6	15.9	10.1	33.3	33.3	6.8	88.1	8.2	80.3
Central North Sea	8	IVb	78	41.0	9.0	14.1	19.2	6.4	34.6	9.0	10.0	80.0	5.9	91.1
Northern North Sea + Norway +NW Scotland	8	IVa; VIa	48	47.0	4.2	20.8	43.8	0	35.4	32.5	82.9	9.8	85.0	10.0
Celtic shelf, S.W.Ireland + S.W.British Isles	11	VIIa,g,h,j	46	50.0	8.7	17.4	17.4	0	28.3	15.6	9.7	90.3	7.9	89.5
S.East Iceland	5	Va	44	36.4	0	11.4	38.6	2.3	6.8	47.7	80.5	5.6	65.0	20.0
S.West Iceland	5	Va	106	61.3	0.9	1.9	23.6	0	4.7	25.5	79.0	18.4	59.2	35.5
West Greenland: Paamiut (south)	4	1E	23	56.5	0	0	4.3	0	13.0	8.7	80.0	20.0	55.6	27.8
West Greenland: Nuuk (central)	4	1D	28	50.0	3.6	0	3.6	0	10.7	31.0	94.4	5.6	57.9	15.8
West Greenland: Maniitsoq (north)	4	1C	127	40.9	3.1	7.9	16.5	0.8	6.3	44.1	87.1	10.1	91.2	4.4
Canada: Bay of Fundy	1	4X	100	36.0	10.0	24.0	41.0	1.0	27.0	42.0	75.0	6.3	75.5	16.3
USA, California	-	-	56	50.0	7.1	46.4	26.8	25.0	48.2	-	-	-	-	-

occurs in California. The lowest incidence (< 10%) of *marker lines* is for southern and central West Greenland. The highest values (> *ca* 40%) are found in Canada, northern North Sea/Norway and eastern Iceland; higher intermediate levels occur in Skagerrak and Kattegat/Inner Danish waters. *Accessory lines* are more numerous in North Sea/Norway, West Greenland, Canada, Iceland and the southern North Sea.

Even from the qualitative analysis above it seems likely that some of the characters examined above are linked, and this possibility is investigated below. Comparisons between regions are analysed initially by conventional chi-square 2-variable contingency tests for presence/absence of each anomaly type, to detect the significance of individual characters in each region relative to other regions.

Regional comparisons by individual anomaly

Regions were compared for each character (presence/absence) or by type for *GLG type* and *boundary layer type*, using chi-square contingency tests, using a standard probability of $p < 0.05$ as statistically significant. Comparisons were made between sampling regions in a progression eastwards across the North Atlantic. Sample sizes were generally those presented in Table 3. However, some character comparisons were hampered by small numbers of observed incidences in specific categories, and differences between regions could not be tested. Regions were grouped logically and progressively to detect differences between adjacent regions and then further afield. Comparisons between geographically distant regions e.g. Bay of Fundy versus North Sea, or Iceland verses Baltic Sea, have not been undertaken because they are sufficiently distant that management issues are unlikely to be linked and would probably be dealt with practically at a more local level.

West Greenland (three localities) vs Canada, Bay of Fundy:

Pulp stones	df = 1, $\chi^2 = 6.47$, $p < 0.025$
Mineralisation interference	df = 1, $\chi^2 = 20.28$, $p < 0.001$
Marker lines	df = 1, $\chi^2 = 28.56$, $p < 0.001$
Dentinal resorption	negligible in both regions
Cemental disturbance	df = 1, $\chi^2 = 18.82$, $p < 0.001$
Accessory lines	df = 1, $\chi^2 = 5.55$, $p < 0.025$
Boundary layer type	df = 2, $\chi^2 = 13.33$, $p < 0.005$
GLG type	no difference, $p > 0.1$

West Greenland - north vs central vs south:

Pulp stones	data sets too small for comparison
Mineralisation interference	df = 1, $\chi^2 = 4.33$, $p < 0.05$ (central and south merged)
Marker lines	df = 1, $\chi^2 = 5.61$, $p < 0.025$ (central and south merged)
Dentinal resorption	data sets too small for comparison
Cemental disturbance	no difference, $p > 0.25$
Accessory lines	df = 2, $\chi^2 = 11.05$, $p < 0.005$
Boundary layer type	no difference, $p > 0.75$
GLG type	df = 4, $\chi^2 = 25.18$, $p < 0.001$

West Greenland (three localities) vs Iceland (east and west):

Pulp stones	data sets too small for comparison
Mineralisation interference	no difference, $p > 0.5$
Marker lines	df = 4, $\chi^2 = 11.70$, $p < 0.001$
Dentinal resorption	data sets too small for comparison
Cemental disturbance	no difference, $p > 0.25$
Accessory lines	no difference, $p > 0.25$
Boundary layer type	no difference, $p > 0.1$
GLG type	df = 2, $\chi^2 = 18.11$, $p < 0.001$

Iceland (east and west) vs North Sea (north, central and south) and Celtic Shelf region:

Pulp stones	df = 1, $\chi^2 = 7.49$, $p < 0.01$
Mineralisation interference	df = 1, $\chi^2 = 10.61$, $p < 0.005$
Marker lines	no difference, $p > 0.1$
Dentinal resorption	df = 1, $\chi^2 = 5.38$, $p < 0.025$
Cemental disturbance	df = 1, $\chi^2 = 41.27$, $p < 0.001$
Accessory lines	df = 1, $\chi^2 = 4.28$, $p < 0.05$
Boundary layer type	df = 2, $\chi^2 = 68.71$, $p < 0.001$
GLG type	df = 2, $\chi^2 = 45.21$, $p < 0.001$

ASCOBANS[1] *area - northern North Sea vs central North Sea vs southern North Sea vs Skagerrak vs Inner Danish waters and Kattegat vs Baltic Sea:*

Pulp stones	data sets too small for comparison
Mineralisation interference	no difference, $p > 0.1$
Marker lines	df = 5, $\chi^2 = 18.23$, $p < 0.01$
Dentinal resorption	df = 5, $\chi^2 = 11.78$, $p < 0.05$
Cemental disturbance	df = 5, $\chi^2 = 24.29$, $p < 0.001$
Accessory lines	d.f = 5, $\chi^2 = 33.17$, $p < 0.001$
Boundary layer type	df = 10, $\chi^2 = 111.05$, $p < 0.001$
GLG type	df = 10, $\chi^2 = 117.05$, $p < 0.001$

Northern North Sea vs central North Sea vs southern North Sea:

Pulp stones	data sets too small for comparison
Mineralisation interference	no difference, $p > 0.1$
Marker lines	df = 2, $\chi^2 = 14.20$, $p < 0.001$
Dentinal resorption	no difference, $p > 0.1$
Cemental disturbance	almost identical incidence-no test
Accessory lines	df = 2, $\chi^2 = 14.37$, $p < 0.001$
Boundary layer type	df = 4, $\chi^2 = 77.88$, $p < 0.001$
GLG type	df = 4, $\chi^2 = 84.06$, $p < 0.001$

Skagerrak vs Inner Danish waters and Kattegat vs Baltic Sea:

Pulp stones	data sets too small for comparison
Mineralisation interference	no difference, $p > 0.5$
Marker lines	no difference, $p > 0.05$
Dentinal resorption	data sets too small for comparison
Cemental disturbance	df = 2, $\chi^2 = 15.52$, $p < 0.001$
Accessory lines	data sets too small for comparison
Boundary layer type	df = 4, $\chi^2 = 16.51$, $p < 0.01$
GLG type	df = 4, $\chi^2 = 9.41$, $p \sim 0.05$

Beginning with the western North Atlantic, it is clear that West Greenland is 'distinct' from the Canadian Bay of Fundy with significant differences for six characters. In

[1] ASCOBANS = Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas, a regional agreement under the Convention on Migratory Species.

Table 4
Sample sizes for different regional data sets, showing presence (+) and absence (-).

Area	Pulp stone		Mineralisation interference		Marker lines		Dentinal resorption		Cemental disturbance		GLG type 1		Boundary layer light-staining		Accessory lines	
	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-
Bay of Fundy	10	90	24	76	41	59	1	99	27	73	37	11	36	12	21	14
W.Greenland	5	173	10	168	23	155	1	177	14	164	125	26	124	20	67	112
Iceland	1	149	7	143	42	108	1	149	8	142	71	42	79	23	48	102
Celtic Shelf	4	42	8	38	8	38	0	46	3	30	3	35	3	28	5	27
N.North Sea	2	46	10	38	21	27	0	48	17	31	34	6	34	7	13	27
C.+S.North Sea	11	136	19	73	26	121	12	135	50	96	7	88	7	82	30	117
Skagerrak	3	35	6	32	10	28	0	38	22	16	4	9	4	6	3	36
Kattegat+IDW	4	55	9	50	18	41	4	55	37	22	5	33	5	27	7	52
Baltic	5	36	5	36	5	36	0	41	10	31	1	36	1	19	1	40

addition, closer inspection of the three regions within West Greenland reveals differences for four characters, which are greatest between north and south. Comparison between Iceland and West Greenland shows only two characters, *marker lines* and *GLG type*, with significant differences in incidence. The comparison between Iceland, the North Sea and Celtic Shelf regions reveals significant differences for seven characters. Comparison between six regions within the ASCOBANS area shows significant differences for six characters, suggesting that the area should not be considered as a single management unit. A smaller scale comparison between the three regions within the North Sea revealed significant differences for four characters. Comparison between Skagerrak, Inner Danish waters/Kattegat and the Baltic Sea shows three significantly different characters, incidentally quite different from the two in the North Sea area. This suggests that this geographical area does not represent a single 'population', although there may be mixing at certain times and places.

The above results are not unexpected in that one would expect the most distantly separated regions to be those exhibiting the most differences. However, it is perhaps more surprising that there are internal differences within West Greenland, and within the North Sea/Skagerrak/Baltic Sea region. The similarities between the Icelandic and West Greenland samples are also interesting. Some of the differences within smaller areas (e.g. West Greenland) may reflect different small-scale local ecology and feeding trends (Lockyer *et al.*, 1999; Møller, 1999). The analyses above suggest that tooth characters are likely to be a useful tool in determining the stock structure of harbour porpoises. However, for their proper interpretation, it is clear that considerable work must be carried out on the nature of the causative factors involved in their occurrence.

Multi-comparisons of incidence of anomaly by region and anomaly

Subsets of the data (Table 4) have been selected for 3-dimensional contingency tests combining all anomaly types for those where a significant difference had already been noted above, to see if presence/absence of an anomaly was dependent on region and other anomaly types. In these analyses, presence or absence of *GLG type* 1 and light-staining *boundary layer type* 1 were used.

The following results were found for the anomalies shown:

West Greenland (three localities) vs Canada, Bay of Fundy:

Pulp stones; Mineralisation interference; Marker lines; Cemental disturbance; Accessory lines and Boundary layer type

df = 16, $\chi^2 > 39.252$, $p < 0.001$

West Greenland (three localities) vs Iceland (east and west):

Marker lines and GLG type

df = 4, $\chi^2 > 18.467$, $p < 0.001$

Iceland (east and west) vs northern North Sea and Celtic Shelf region:

Pulp stones; Mineralisation interference; Cemental disturbance; Accessory lines; Boundary layer type and GLG type

df = 27, $\chi^2 > 55.476$, $p < 0.001$

Northern North Sea vs central and southern North Sea combined:

Marker lines; Accessory lines; Boundary layer type and GLG type df = 12, $\chi^2 > 32.909$, $p < 0.001$

Skagerrak vs Inner Danish waters and Kattegat vs Baltic Sea:

Cemental disturbance; Boundary layer type and GLG type df = 12, $\chi^2 > 32.909$, $p < 0.001$

The results above indicate that presence or absence of the selected characters is dependent on region and the type of other anomalies present. The results all indicate significant differences between regions that might be considered as putative management units.

CONCLUSIONS AND SUMMARY

The aim of this paper was to investigate the suitability of using tooth characteristics (tooth ultrastructure, GLG mineralisation patterns and gross morphology) as one tool in the elucidation of stock structure. The analyses presented here support the value of this approach. Significant differences in several of the considered characters were found between a number of localities. The results are broadly in accord with putative stock boundaries suggested by *inter alia* the IWC.

In particular, the analyses indicated that there may be separation between eastern Canada and West Greenland, with some local differences within West Greenland between north and central/south areas. There is a clear difference between the eastern North Atlantic and eastern/central North Atlantic. In this regard it will be interesting to examine samples from intermediate waters in the region of the Faeroe Islands, where information is currently lacking. Within the ASCOBANS area, the results suggest that there may be several 'sub-populations', within the North Sea and within the Skagerrak to Baltic regions.

As noted in the introduction, a full consideration of appropriate management units requires the integration of results from a variety of techniques. Use of tooth characters alone is clearly not sufficient to allow an individual animal to be assigned to a particular management unit. This will be considered in a future paper. Furthermore, interpretation of any differences in tooth character incidence will require a better understanding of the mechanisms by which such characters occur.

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