

**PREDICTING KEY HABITAT AND POTENTIAL DISTRIBUTION
OF NORTHERN BOTTLENOSE WHALES (*HYPEROODON
AMPULLATUS*) IN THE NORTHWEST ATLANTIC OCEAN**

by

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Thesis submitted to the University of Plymouth
in partial fulfilment of the requirements for the degree of

MSc Applied Marine Science

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December 2004

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ABSTRACT

The distribution, status and specific habitat requirements of northern bottlenose whales (*Hyperoodon ampullatus*) in the Northwest Atlantic are unknown beyond the well-studied small population that uses the Scotian Shelf. The population in the Labrador Sea is believed to be distinct from that of the Scotian Shelf, with the potential for interchange between the populations unclear. Ecological-Niche Factor Analysis (ENFA), a predictive modelling approach is used to identify areas of key habitat for northern bottlenose whales within the Northwest Atlantic, and establish whether a habitat corridor links the Labrador and Scotian Shelf populations. ENFA models species' distribution in relation to ecogeographical variables (EGVs). A database of 2,103 records was compiled from sightings and catch data and combined with four EGVs: depth, slope, aspect and sea surface temperature. A habitat-suitability (HS) value between 0 (low suitability) and 100 (maximum suitability) was calculated for each grid cell within the study area. Northern bottlenose whale habitat was found to be concentrated in steep, shelf-edge waters, with habitat of at least marginal suitability (HS values 34-66) providing a continuous link between the Scotian Shelf and the Labrador Sea, potentially allowing movement of individuals between these two areas. Mean area-adjusted frequency during jack-knife cross-validation showed the model to be a good fit to the data: $F_t=11.95 \pm 1.884$ for high HS values. The model also highlighted the specialisation of this species in terms of their habitat requirements and the limited potential habitat of this species, with predicted 'core' habitat representing only 2.5% of the study area.

Key words: Northern bottlenose whale, distribution, Northwest Atlantic, ecological-niche factor analysis, habitat suitability.

INTRODUCTION

Detailed knowledge of the habitat requirements and consequent distribution of a species is a central theme within ecology and a key factor in delivering effective conservation and management (Hirzel et al. 2001, Gurnell et al. 2002). This kind of knowledge is very limited for family Ziphiidae (beaked whales) due to their oceanic nature, cryptic behaviour and long dive durations (Hooker et al. 2002, Reeves et al. 2002).

The northern bottlenose whale, *Hyperoodon ampullatus* (Forster), represents the most studied member of this family (Whitehead et al. 1997, Hooker et al. 1999, Gowans et al. 2000, Hooker et al. 2002). They are a deep-diving species, thought to typically occupy deep waters over 700 m in depth, where their principle prey, squid of the genus *Gonatus* is abundant (Benjaminsen 1972, Clarke & Kristensen 1980, Reeves et al. 1993, COSEWIC 2002, Bjørke 2001, Santos et al. 2001). They appear to have a preference for cold waters, with Gray (1882) finding dense concentrations along the edge of pack ice in spring and summer. Norwegian whaling reports have suggested that northern bottlenose whales can even occur several nautical miles within the pack ice (Benjaminsen & Christensen 1979). Northern bottlenose whales have been observed in sea surface temperatures (SST) ranging from -2°C to 17°C (Reeves et al. 1993).

The best known population of northern bottlenose whales frequents the waters over and adjacent to a large submarine canyon on the Scotian Shelf known as the Gully (44°N, 59°W) (Whitehead et al. 1997, Wimmer & Whitehead in press). Here, a population of approximately 130 individuals is known to be resident year round (Gowans et al. 2000). This population has been listed as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) since November 2002 (COSEWIC 2002). Hooker et al. (2002) found a strong relationship between the

distribution of northern bottlenose whales in the Gully and the bathymetric features, depth and slope, with steep topography believed to be a major factor.

The status and specific habitat requirement of northern bottlenose whales in other locations is unknown. The Labrador Sea is known as a historic ‘hotspot’ of northern bottlenose whale abundance, with whales reported as far north as 70°N, down the west coast of Greenland, and along the continental shelf of Newfoundland and Labrador (Benjaminsen 1972, Benjaminsen & Christensen 1979). This area experienced significant whaling pressure following a shift in focus by Norwegian whalers from the eastern to the western North Atlantic between 1938 and 1971 (Benjaminsen 1972, Christensen 1975, Mitchell 1977, Mead 1989). From 1969 – 1971, a total of 818 northern bottlenose whales were taken off Labrador (Christensen 1975).

The Scotian Shelf and Labrador Sea populations are thought to be largely distinct, based on differences in mitochondrial (mt) DNA haplotype frequencies (Dalebout et al. 2001), and differences in the length of animals from the two populations, with individuals found on the Scotian Shelf being substantially shorter than those in the Labrador Sea (Whitehead et al. 1997). In the eastern North Atlantic, the northern bottlenose whale is believed to migrate northwards in the spring and southwards in the early summer (Benjaminsen 1972). It is not known whether similar movements occur between the Scotian Shelf and the Labrador Sea.

The approach used here is to highlight key areas of northern bottlenose whale habitat within the Northwest Atlantic Ocean through Ecological-Niche Factor Analysis (ENFA) (Hirzel et al. 2002a). ENFA is a multivariate, spatially-explicit method that can be employed to study the potential distribution of a given focal species (Hirzel et al. 2002a). It is a method that builds upon well established techniques using the power of Geographical Information Systems (GIS) to explore the relationship between species distributions and ecogeographical variables (EGVs) such as topographical features

(Gregn & Trites 2001, Hirzel et al. 2002a). The spatial distribution of marine species are determined largely by the distribution and availability of prey items, which are in turn influenced by topographical features and oceanographic variables such as SST, salinity, and chlorophyll concentration (Hui 1985, Brown & Winn 1989, Woodley & Gaskin 1996, Baumgartner 1997, Hooker et al. 1999).

Using GIS, it is possible to apply modelling techniques such as logistic regression in order to delineate the habitat requirements of a species, which can then be extrapolated to produce habitat suitability (HS) maps (Guisan & Zimmermann 2000, Hirzel et al. 2002a, Gibson et al. 2004). Such methods have been applied to range of species, including the northern right whale (*Eubalaena glacialis*) (Moses & Finn 1997), humpback whale (*Megaptera novaeangliae*), blue whale (*Balaenoptera musculus*), sperm whale (*Physeter macrocephalus*), fin whale (*Balaenoptera physalus*) (Gregn & Trites 2001) and the beaked whales (*Mesoplodon* spp. and *Ziphius cavirostris*) (Waring et al. 2001). Linking their distribution to a range of topographic and oceanographic variables, Waring et al. (2001) found that beaked whales were associated with deep, shelf-edge waters and significantly cooler SSTs than sperm whales, with the predicted habitat areas for these species showing small scale niche separation. Similar distribution patterns were found by Hooker et al. (2002) and Herfst (2004) for northern bottlenose whales in the Gully and Labrador Sea, respectively.

The main advantage of ENFA over the more established logistic regression techniques such as general linear models (GLMs) is that it requires only presence data, rather than presence/absence data (Hirzel et al. 2002a, Reutter et al. 2003). Absence data is difficult to obtain, especially for cetaceans, where there is a high chance that for a given location a species may erroneously be considered 'absent' simply due to not being detected when it is actually present (Hirzel et al. 2002a). It is for this reason that ENFA is recommended for rare or cryptic species (Reutter et al. 2003). As such, this

approach lends itself well to beaked whales such as the northern bottlenose whale, which like the other ziphiids is oceanic and spends a great deal of time beneath the surface (Hooker & Baird 1999).

Habitat suitability maps have broad applicability within conservation biology where detailed scientific information regarding species' distributions is often lacking, and difficult to obtain (Gibson et al. 2004). The production of such a map using even limited data can help focus future research and help decision makers to facilitate protection for the northern bottlenose whale. There is growing concern for this species over threats such as acoustic pollution, entanglement in marine debris (e.g., fishing gear), chemical pollution and collisions with ships (e.g., Whitehead et al. 1997, Hooker et al. 1999, COSEWIC 2002). Specifically, the aims of this study are: (1) to identify key areas of northern bottlenose whale habitat in the Northwest Atlantic, in relation to bathymetric features, and (2) to identify whether or not there is a viable habitat corridor that may allow interchange between the Scotian shelf and Labrador populations.

METHODS

Study area

The study area used extends from 40°N-75°N, and from 72°W-40°W, representing an area of 4,939,122.6 km² (Fig. 1). This area incorporates much of the territorial waters of eastern Canada, as well as southern and eastern Greenland. It is an area where oceanographic features such as the strong, cold Labrador Current create strong upwelling leading to high productivity on the wide continental shelf of eastern Canada (Drinkwater & Harding 2001, Fischer & Friedrich 2002). Such characteristics make the Northwest Atlantic Ocean an area of high biological diversity.

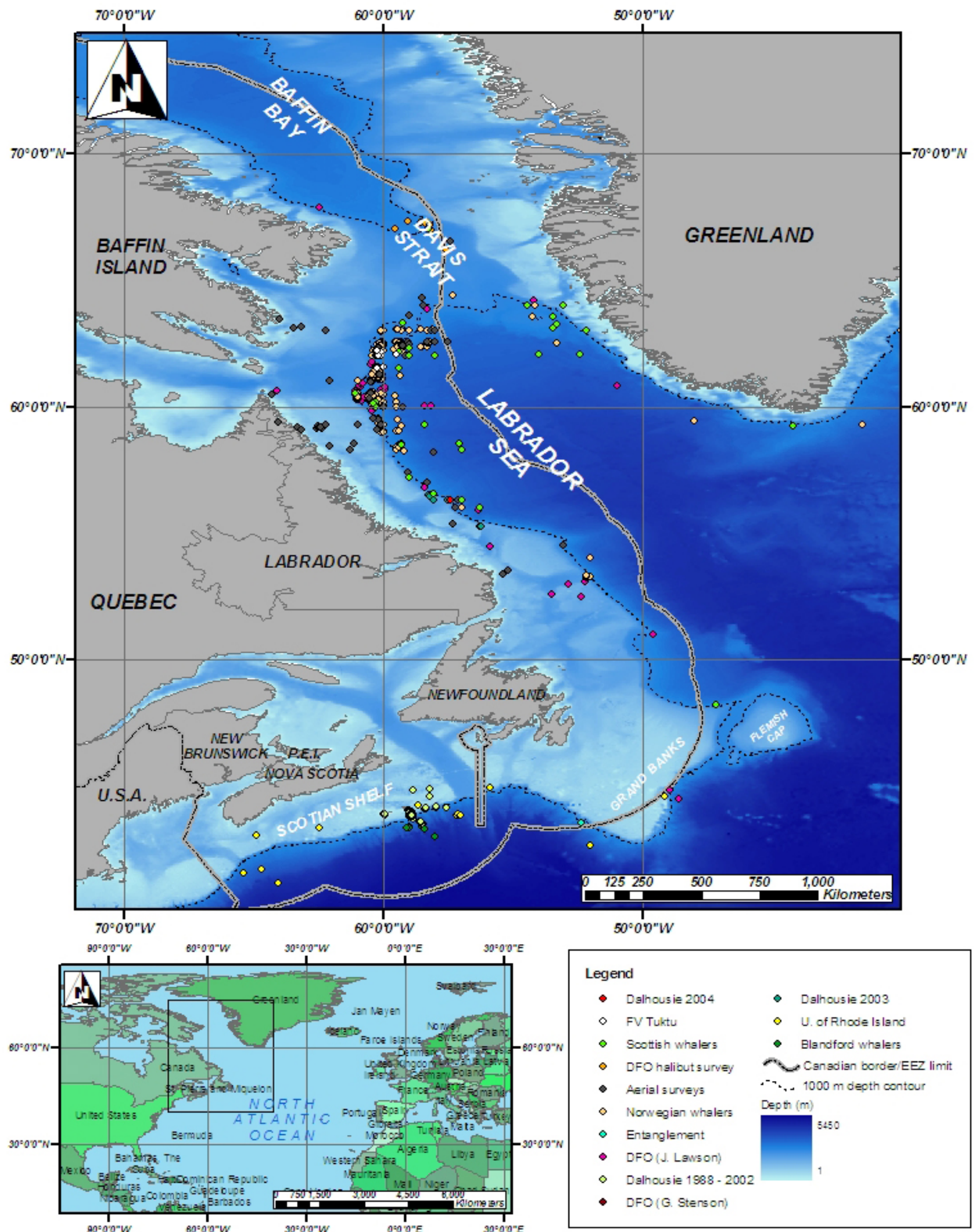


Fig. 1: map of the study area, with positions of all 2,103 records of northern bottlenose whales used within the ENFA

Cetacean sightings

Sightings and catch data was collated from published and unpublished sources, resulting in a database of 2,103 northern bottlenose whale records from the Northwest Atlantic Ocean (Table 2, Fig. 1). The bulk of this data comes from ‘reputable’ sources including Dalhousie cetacean surveys conducted between 1988 and 2004, Norwegian whaling catch reports provided by Nils Øien of the Institute of Marine Research, Norway, and Scottish and Canadian whaling catch reports (Blandford whaling station, NS) (Reeves et al. 1993).

Dalhousie surveys between 1988 and 2003 were conducted aboard a 12.5 m auxiliary sailing vessel. Surveys were conducted in the waters of and surrounding the Gully as well as the waters in close proximity to the 1000 m contour of the continental shelves of the Scotian Shelf (1988-2002) and Labrador (2003). Two observers searched for cetaceans with the naked eye during daylight hours and reasonable weather conditions (good visibility, Beaufort <5) (Whitehead et al. 1997, Wimmer & Whitehead in press). See appendix for details of survey protocol during a Dalhousie survey in the Labrador Sea, 2004.

Further data were obtained from Canadian Department of Fisheries and Oceans (DFO) fishery observer reports, a DFO halibut survey (upon which R. MacDonald, an undergraduate student was deployed specifically for cetacean research), a database held by the University of Rhode Island, a northern bottlenose whale entanglement reported by the DFO and a series of aerial surveys for marine mammals and seabirds (Reeves et al. 1993). Questions have been raised over the legitimacy of the data obtained from fishery observers due to the lack of experience with identifying marine mammals to species, and the aerial survey data (Reeves et al. 1993) which reported sightings in water <300 m deep. These data sources and their reliability is summarised in table 1.

Table 1; summary of sightings/catch data sources. Total $n = 2,103$. Source reliability is denoted as R (reputable) or Q (questionable).

Data source	Dates	n	Source reliability	Reference
DFO halibut survey	Oct. 2004	7	R	R. MacDonald, Dalhousie University pers comm
Dalhousie survey	Jul. – Aug. 2004	1	R	Dalebout et al. unpublished
Dalhousie survey	Jul. – Aug. 2003	15	R	Whitehead et al. unpublished
FV <i>Tuktu</i>	Apr. 2003	14	Q	S. Smith, DFO pers comm
Dalhousie survey	Jul. 1988 – Aug. 2002	1,056	R	Wimmer pers comm
DFO fishery obs.	Apr. 1980 – June 1999	41	Q	J. Lawson, DFO pers comm
Aerial surveys	Feb. 1977 – Aug. 1979	59	Q	Reeves et al. 1993, (Table 3)
Norwegian whaling reports	May 1969 – May 1971	808	R	N. Øien, Institute of Marine Research, Norway
Blandford whaling reports	June 1964 – June 1967	12	R	Reeves et al. 1993, (Table 1)
Scottish whaling reports	May 1885 – June 1913	30	R	Reeves et al. 1993, (Table 2)
Entanglement	Unknown	1	R	M. Schowell (Wimmer pers comm)
DFO fishery obs.	Unknown	41	Q	G. Stenson (Wimmer pers comm)
University of Rhode Island	Unknown	18	Q	R. Kenney (Wimmer pers comm)

EGVs

Four commonly used independent EGVs were used as predictors within the analysis: depth, slope, aspect and sea surface temperature (SST). Bathymetric data was obtained from the NOAA (National Oceanic and Atmospheric Administration) ETOPO2 database. From this database, a raster grid of 2-minute bathymetry was constructed within Idrisi 32 for Windows. Each 2-minute grid cell is 7.7 km^2 , or $\approx 2.75 \text{ km} \times 2.75 \text{ km}$. Slope and aspect for this study area were derived from the bathymetric base map using surface analysis tools within Idrisi, and were constructed as additional independent raster grids. SST data derived from the Pathfinder 4 Advanced Very High Resolution Radiometer (AVHRR) satellite was obtained from the NASA Physical Oceanography Distributed Active Archive Center (PO.DAAC) as 12 monthly composite images for 2003 (PO.DAAC 2004). These images were then combined and averaged to form a single yearly average raster layer. This data had a resolution of 9km, so was resampled within Idrisi in order to make the layer resolution match that of the bathymetric variables, such that the maps could be overlaid. The 2,103 sightings were first plotted as a vector map. Once converted to raster format at the same resolution as the bathymetric base maps, the resultant Boolean map contained 423 presence cells.

Analytical methods

ENFA and HS map computations were facilitated within the program *BioMapper 3* (Hirzel et al. 2004). *BioMapper* is a GIS and statistical tool-kit, developed for carrying out ENFA and producing HS maps from the comparison of a species distribution with a number of given EGVs (Hirzel et al. 2004). Once all EGVs are input into *BioMapper*, a box-cox transformation is performed to normalise the EGVs and

make them overlayable. After verification that there were no discrepancies between the maps, the ENFA was carried out. This process summarizes all predictors into a number of uncorrelated axes, similar to Principal Components Analysis (Reutter et al. 2003), except that the axes have ecological meaning.

The first axis represents marginality, which is the degree to which the mean of the species distribution differs from that of the available conditions of the study area. Marginality coefficients were calculated for each EGV, with positive values indicating that the focal species prefers EGV conditions that are higher than the average available, and vice versa for negative values (Hirzel et al. 2002a). An overall marginality (M) value was also calculated, for which values generally lie between 0 and 1, with larger values indicating that the focal species has habitat requirements that differ from the average conditions available.

Subsequent axes represent decreasing amounts of information about the specialisation of the focal species, which is based on how the variance of the species distribution differs from that of the available conditions. Specialisation coefficients for each EGV are calculated for each of the specialisation factors. For these values, signs are arbitrary, with only the absolute values of importance. The higher the value, the more restricted the range of the focal species with regard to a given EGV. Overall specialisation (S) and tolerance (T , inverse of specialisation) values were also calculated. A high specialisation value indicates that the focal species has a particular requirement for certain EGVs. A high tolerance value indicates that within a given study area, the species occupies a relatively wide niche (Hirzel et al. 2002a, Reutter et al. 2003, Engler et al. 2004).

Each EGV will vary in the amount of information it explains per factor, as shown by the marginality and specialisation coefficients. Each factor then explains a proportion of the specialisation of the focal species (Hirzel et al. 2002a). Once these

factors are computed, McArthur's broken stick model is used as a guide to select the number of factors that explain the greatest amount of information and should be included in the computation of the HS map. Each cell of the resultant map is given an HS value ranging from 0 – 100, with 100 being those cells that have the highest suitability.

The model can be validated by means of the jack-knife cross-validation procedure (Fielding & Bell 1997). This process partitions the species dataset into k equal size subsets. In this case, ten subsets were sampled, with nine used to calibrate the HS map, and the last 'validation' subset used to evaluate the result. From the ten subsets the number of cells which fall into a set number of HS value bin ranges was calculated. Each bin covers a portion of the maps area (A_i), and contains some proportion of the validation cells (N_i). The area-adjusted frequency of cells falling into each bin range can then be computed as $F_i = N_i/A_i$. A completely random map would result in $F_i \approx 1$ for each bin range. A good fit of the data to the model is indicated by a low F_i for low HS values and a high F_i for high HS values (Boyce et al. 2002). In this analysis, 3 bin ranges were used (HS values: 0 – 33, 34 – 66 and 67 – 100). These bin ranges were then used to reclassify the HS map into a simpler visualisation of *unsuitable*, *marginal* and *core* habitat types.

Data described as 'questionable' consisted of 173 records (120 presence cells) while data the 'reputable' data consisted of 1930 records (311 presence cells) (Table 1). To show the potential differences in accuracy between the two data sets, these data were partitioned, and overlaid onto the reclassified habitat map in order to calculate the proportion of presence cells falling within the unsuitable habitat class, in order. A separate ENFA was also conducted using each of these datasets in order to compare the M , S and T values between these two, and the overall dataset.

RESULTS

ENFA of the 2,103 bottlenose whale sighting/catch records and four EGVs resulted in an overall marginality value of $M = 0.487$, indicating that the required habitat of northern bottlenose whales differs from the average habitat available with the study area. The high, positive marginality coefficient for slope (0.95), shown in table 2, indicates that this species is linked primarily to slopes steeper than the average available. The remaining marginality coefficients show that northern bottlenose whales prefer lower aspects (-0.26) and temperatures (-0.18) than the average available. The low value for depth indicates little difference from the mean for this EGV.

Table 2; Variance explained by the ecological factors, with marginality and specialisation coefficient values. The amount of specialization accounted for by each factor is given between parentheses. Numbers in bold indicate the most important EGV for each factor

EGV	Marginality (24%)	Factor 2 (43%)	Factor 3 (17%)	Factor 4 (15%)
DEPTH	0.07	0.91	0.51	- 0.50
SLOPE	0.95	-0.06	0.05	0.28
ASPECT	- 0.26	- 0.23	0.66	0.42
SST	0.18	0.35	- 0.54	0.70

A specialisation value of $S = 1.577$ indicates that northern bottlenose whales are specialised in terms of the habitat they prefer, relative to the available habitats. The marginality factor alone accounted for 24% of the specialisation. Specialisation coefficients (Table 2) show that there is clear specialisation in terms of depth, with the remaining (though relatively little) specialisation explained by aspect and SST respectively. A relatively high tolerance value of $T = 0.634$ indicates that although northern bottlenose whales differ in their habitat requirements from the average available to them, and are also specialised with respect to certain topographical variables, there is a relatively large number of sightings over ‘unsuitable’ habitat.

Using the broken-stick model as a guide, an HS map was computed using the marginality factor and all three subsequent specialisation factors (Fig. 2), which together explained 100% of the marginality and 100% of the specialisation. The steep slope and adjacent deep waters of the continental shelf are the primary areas of predicted suitable habitat for northern bottlenose whales (Fig. 2) within the Northwest Atlantic, as predicted by the ENFA model.

Jack-knife cross-validation showed that predicted suitability exceeds 0.5 in 51% of the validation cells, which differs highly significantly from the value of 1% of cells expected if chosen at random ($P < 0.001$, bootstrap test). Area-adjusted frequencies showed that the majority of validation cells fall within the 'core' habitat category (Fig. 4), with $F_i < 1$ ($F_i = 0.375 \pm 0.0652$) for low habitat suitability values and $F_i > 1$ ($F_i = 11.95 \pm 1.884$) for high habitat suitability values, indicating that the model is a good fit to the data. The HS bin ranges shown in Fig. 3 were used to reclassify the HS map into *unsuitable* (HS 0 – 33), *marginal* (HS 34 – 66) and *core* (HS 67 – 100) habitat categories (Fig. 4).

This reclassification showed that marginal habitat extends all around the continental shelf-edge waters of the study area, though does not extend between the Labrador Sea and Baffin Bay. Core habitat areas are more restricted however, with the main core habitat areas being the northern and eastern edges of the Grand Banks including the area around the Flemish Cap, the Labrador shelf-edge and the area extending around the southern extent of the Davis Strait to western Greenland, and the area to the south and east of Greenland. This core habitat represents only 2.5% (Fig. 5) of the whole study area, which represents an area of $121,523 \text{ km}^2 \pm 19,452 \text{ km}^2$ (95% confidence limit) with over 80% of the study area classed as unsuitable.

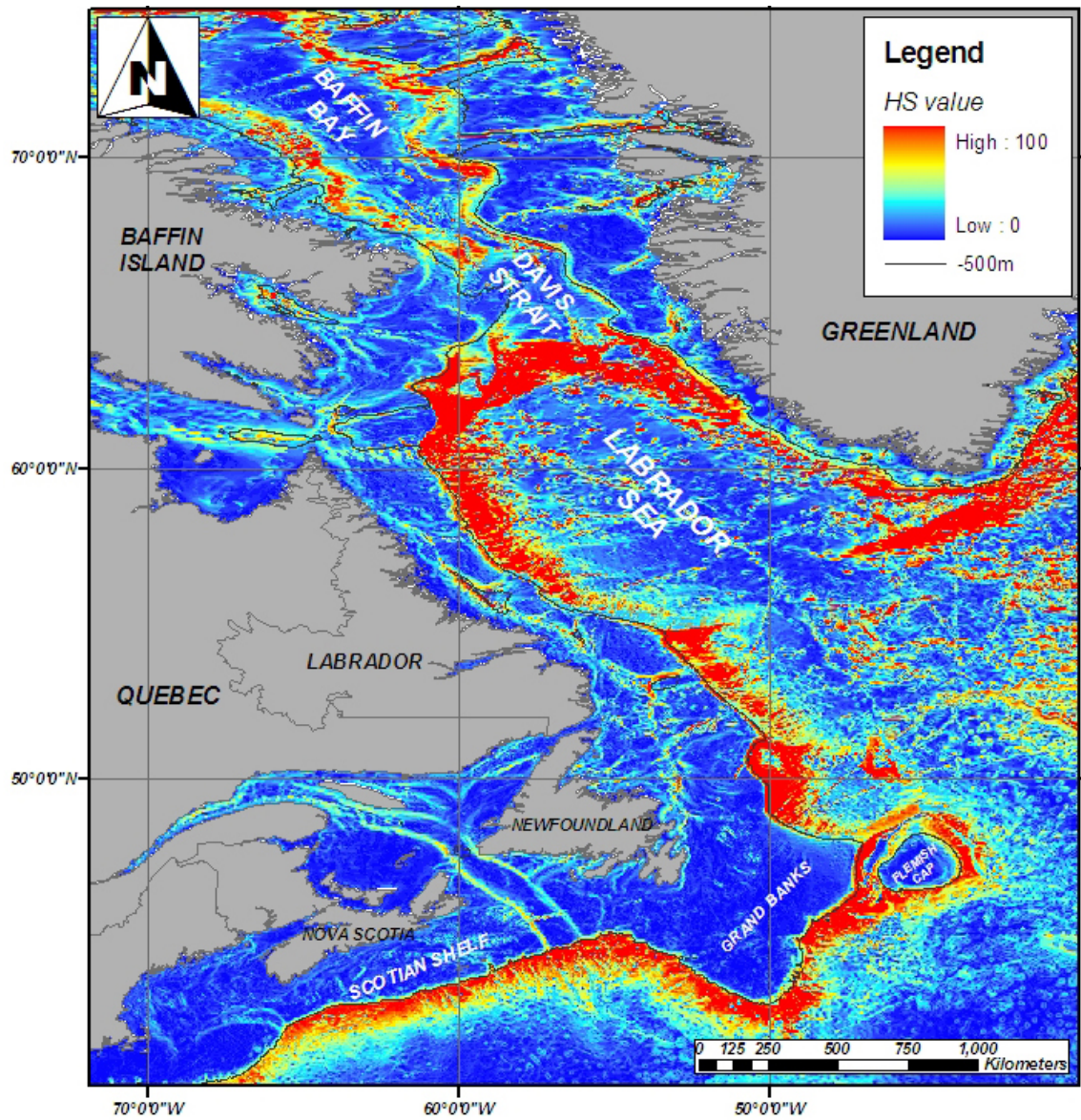


Fig. 2; HS map for northern bottlenose whales in the Northwest Atlantic Ocean. The 500 m contour is shown in order to illustrate proximity of high suitability areas to the continental shelf break

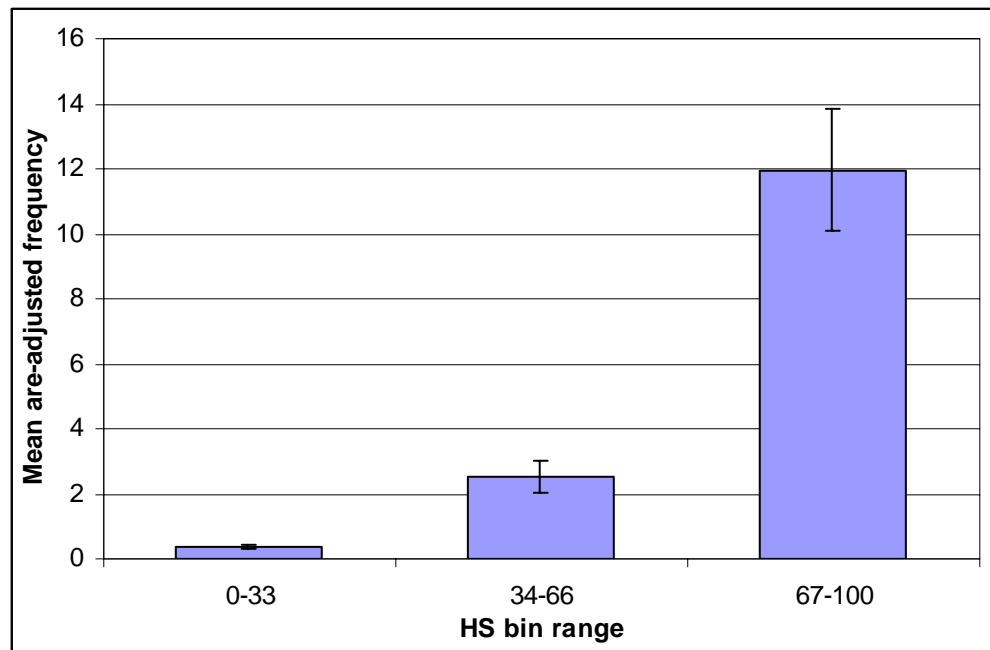


Fig. 3; mean area-adjusted frequency of validation cells within each HS bin range derived from jack-knife cross-validation (10 repeats). Error bars represent standard deviation from the mean

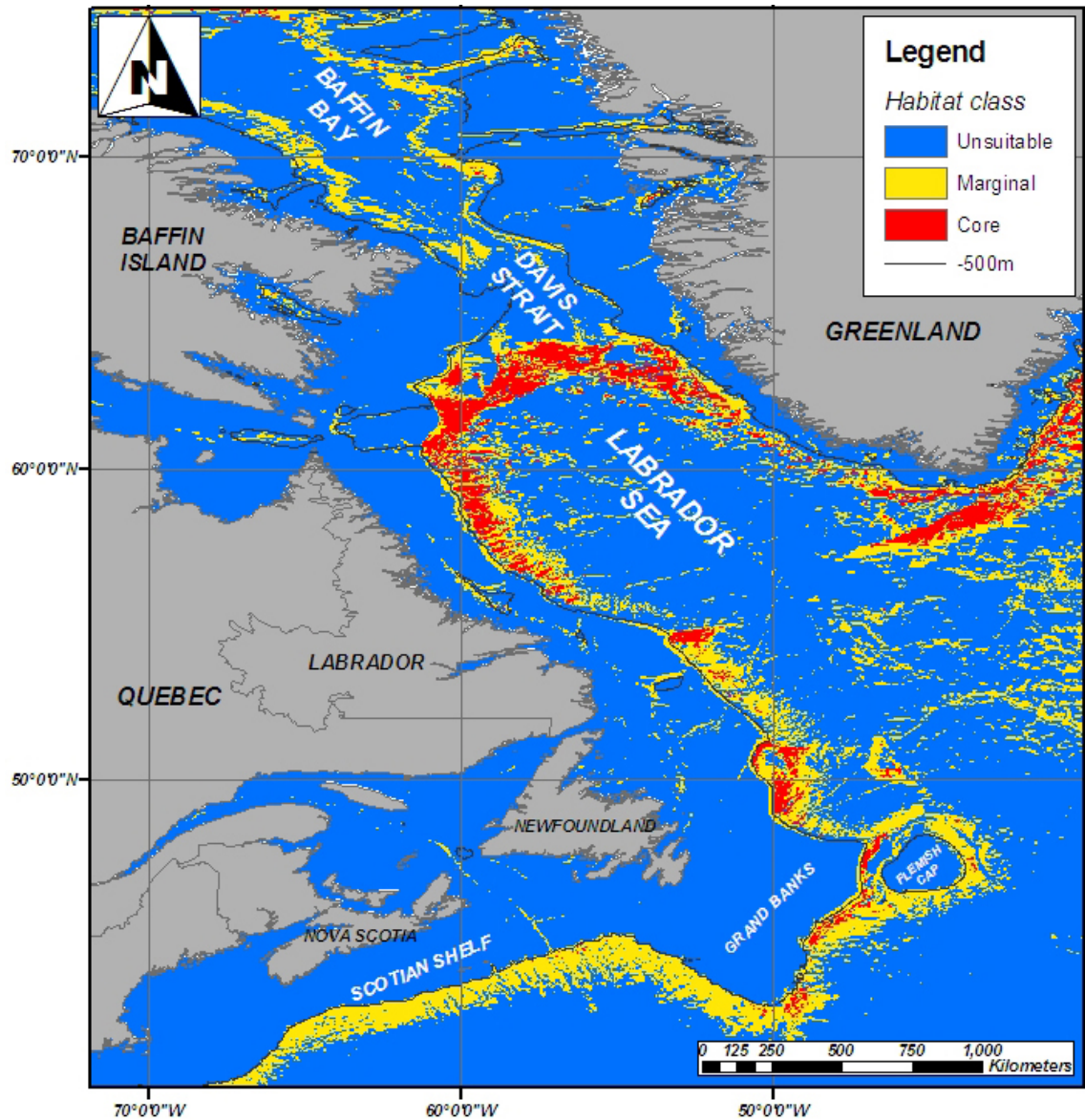


Fig. 4; reclassified HS map showing unsuitable (white), marginal (orange) and core (blue) habitats. The 500m contour is shown to illustrate the proximity of high suitability areas to the continental shelf break

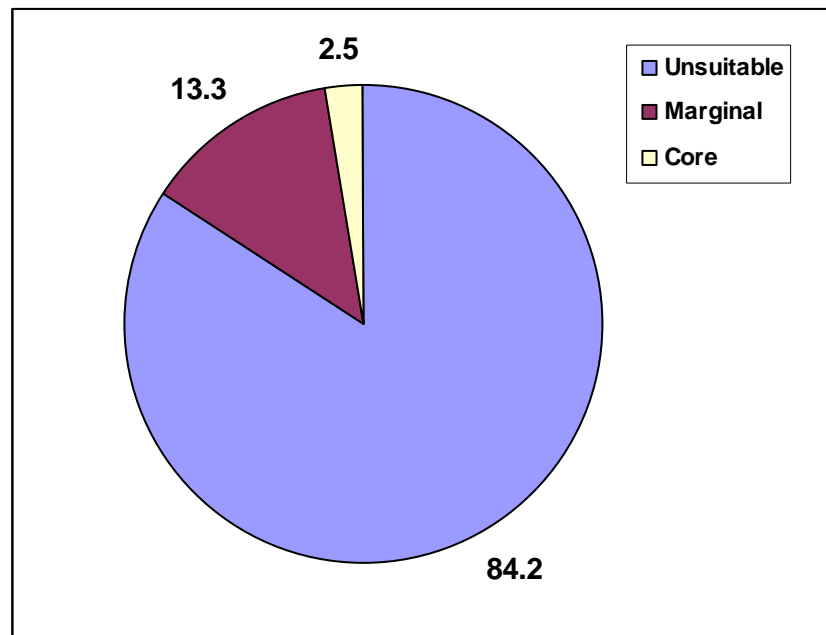


Fig. 5; percentage of study area represented by each HS category

The predicted core area for northern bottlenose whales differs greatly in terms of the environmental conditions within it relative to those available within the whole study area (Table 3), as previously indicated by the marginality and specialisation coefficients (Table 2). For each EGV, the core area covers a narrow range of values relative to the whole study area. For example, depth ranges from 508 – 3213m within the core area, whereas there is a range of over 5000m available within the study area as a whole. The core predicted area has an average depth of 1780m, a slope of 0.97, an aspect of 142° (south, south-east facing) and an average SST of 2.7°C. These values support the directionality of the northern bottlenose whale’s preference indicated by the marginality coefficients (Table 2).

Table 3; the range and average (in parentheses) for each EGV within the whole study area and the core predicted habitat area

EGV	Whole area	Core area
DEPTH (m)	0 – 5,450 (1,843)	508 – 3,213 (1,780)
SLOPE (°)	0 – 16.5 (0.56)	0.4 – 2.6 (0.97)
ASPECT (°)	- 1 – 360 (162)	22 – 265 (142)
SST (°C)	0.3 – 16 (4.2)	1 – 6.3 (2.7)

Comparison of the ‘questionable’ and ‘reputable’ data sets showed considerable difference between the two. Forty-three percent of presence cells from the questionable data set fell within the unsuitable habitat class, compared to only 29% of presence cells from the reputable data set. When analysed separately, the questionable dataset showed the northern bottlenose whale niche to be less marginal, less specialised and more tolerant (Table 4), than the results gained from the original analysis. Conversely, analysis of the reputable dataset described the niche as more marginal, more specialised and less tolerant, compared to the original niche description.

Table 4; overall marginality (*M*), specialisation (*S*) and tolerance (*T*) values for the three datasets

	All data	Reputable	Questionable
<i>M</i>	0.487	0.538	0.399
<i>S</i>	1.577	1.878	1.378
<i>T</i>	0.634	0.532	0.726

DISCUSSION

The four EGVs used within the model (depth, slope, aspect and SST) appear to be good predictors of northern bottlenose whale habitat, and results from the validation tests showed the model to be statistically robust. Bathymetric features such as shelf edges, submarine canyons and seamounts predicted by this model to be areas of potential habitat for this species are known to influence oceanographic processes. Upwelling leading to high biological productivity can occur in these areas, leading to the concentration of prey species (Hui 1985, Allen et al. 2001, Waring et al. 2001). Numerous studies have highlighted the relationship between a variety of oceanographic EGVs and cetacean distribution (Hui 1985, Brown & Winn 1989, Woodley & Gaskin 1996).

Northern bottlenose whales have been shown to exhibit high marginality in terms of slope, preferring the slopes of the continental shelf-edge. However, the steeper slopes within the study area, such as the Scotian Shelf and part of the shelf to the south west of Greenland and a part of the Labrador shelf in the region of 55°N, 55°W have been shown to be marginal or even unsuitable habitat. This may be due to steeper slopes providing a lack of structural diversity, resulting in lower biological diversity in these areas relative to less steep areas that may provide a variety of habitats and breeding grounds for different species (Sverdrup et al. 2003).

Northern bottlenose whales show greatest specialisation in terms of depth, with the predicted core habitat covering a depth range that closely matches that of the primary prey item, *Gonatus* spp (Dawe et al. 1998, Bjørke 2001, Santos et al. 2001). Little is known of the distribution and abundance of *Gonatus*, though this genus represents the most abundant squid genus within the Arctic and sub-Arctic waters of the North Atlantic, with a depth range of up to 2700 m (Dawe et al. 1998). *Gonatus* body size is known to increase with depth, and it is also known that northern bottlenose whales select for larger *Gonatus* spp. (Hooker et al. 2001, Santos et al. 2001). Santos et al. (2001) found that the majority of the *Gonatus* in the stomach contents of the whales studied were mature, ranging from 155 to 235 mm mantle length. This selective preference for larger prey is consistent with both the similarity highlighted in depth range, and the foraging ecology of northern bottlenose whales (Hooker & Baird 1999, Hooker et al. 2001).

The preferred average depth of northern bottlenose whales (1780 m) predicted by ENFA is close to the maximum depth of Greenland halibut, *Reinhardtius hippoglossoides* (2200 m; Dawe et al. 1998). Greenland halibut and several other deep sea fish species were shown to constitute a significant proportion of the stomach contents of northern bottlenose whales taken off Labrador in the late 1960's – early 1970's (Benjaminsen & Christensen 1979). Out of 108 animals from Labrador, 57 (53%) had a variety of squid, fish and other species present within their stomach contents. This is in contrast to northern bottlenose whales in most other areas which have been shown to feed primarily on squid (Lick & Piatkowski 1998, Bjørke 2001). For example, only 6 out of 46 (13%) individuals taken near Iceland had both fish and squid in their stomachs (Benjaminsen & Christensen 1979). This may indicate that northern bottlenose whales in the Northwest and Northeast Atlantic have different foraging habitats and therefore potentially have different habitat requirements.

However, analyses of stomach contents may potentially be biased due to the increased retention of relatively indigestible dietary items, such as squid beaks (Bigg & Fawcett 1985, Hooker et al. 2001). Stable isotope and fatty acid analysis can provide an alternative means to assess diet. Both are based on the idea that the pattern of fatty acids and composition of stable isotopes present within an animal's diet will be reflected in its tissues (Iverson 1993, Todd et al. 1997).

Fatty acid and stable isotope analysis carried out by Hooker et al. (2001) using biopsy samples from animals in the Gully indicated that *Gonatus* spp. were the most likely prey item of northern bottlenose whales in this area. *Gonatus* spp. are also a major prey item of Greenland halibut, representing 84% of the prey items in the stomachs of halibut caught on the northeast edge of the Newfoundland shelf ($\approx 50^{\circ}\text{N}$, 50°W) (Dawe et al. 1998). The fatty acid and stable isotope composition of Greenland halibut may therefore closely reflect that of *Gonatus* spp., which may in turn be passed on to northern bottlenose whales if these fish are also consumed. However, Hooker et al. (2001) did not include Greenland halibut data in their analyses for a comparison. The northeast edge of the Newfoundland shelf is one of the main areas identified by ENFA as core habitat for northern bottlenose whales. The potential importance of Greenland halibut in the diet of northern bottlenose whales in this and other areas should be further investigated.

There is also growing evidence for interactions between northern bottlenose whales and vessels fishing for Greenland halibut in the Northwest Atlantic. In summarising cetacean interactions with trawls, Fertl and Leatherwood (1997) reported 15 records of northern bottlenose whales following trawls during haul-back on the Scotian Shelf. Herfst (2004), found sightings of northern bottlenose whales in the Labrador Sea to be associated with the presence of large demersal trawlers targeting Greenland halibut. Northern bottlenose whales were reported as following trawls for a

number of hours during a recent survey of Greenland halibut in the Davis Strait by the DFO (R. MacDonald, pers comm).

Behaviour such as this has been reported for a range of cetaceans, such as sperm whales, killer whales (*Orcinus orca*) and bottlenose dolphins (*Tursiops* spp.) (Ashford 1996, Karpouzli & Leaper 2004). It is thought that such fishery interactions are due to the provision of wounded and easy to take fish that lead to benefits in terms of reducing foraging effort (Ashford 1996, Fertl & Leatherwood 1997). Stomach content analyses have shown that where such interactions occur, there can be overlap of prey species in the stomachs of cetaceans and the target species of the fishery, as well as overlap with the prey species of the target species of the fishery (Fertl & Leatherwood 1997).

The remaining specialisation predicted by the ENFA accounted for little of the overall information, but the effect of aspect and SST can be seen. The preferred aspect predicted was a south-southeast facing aspect, similar to the dominant aspect within the study area. SST was found to be the most important EGV for the last specialisation factor, which represented only 15% of the information. Despite this overall lack of importance, northern bottlenose whales were predicted to occur primarily in cool waters, with an average temperature of 2.7°C. This is consistent with the findings of Herfst (2004), and Bejaminsen and Christensen (1979) who state that northern bottlenose whales are found most frequently in water between 0°C and 2.5°C. This suggests an apparent preference for the boundary waters of cold polar and warmer Atlantic currents, indicating that northern bottlenose whales may select waters under the influence of the strong, cold Labrador Current. This is the dominant oceanographic feature within the Northwest Atlantic, with the influx of cold low salinity water from the Hudson Strait and Baffin Bay resulting in high levels of mixing leading to high productivity that increases southward to the Grand Banks (Drinkwater & Harding 2001, Fischer & Friedrich 2002).

Although direct comparisons cannot be made between the marginality and specialisation values here and those from other studies, the values lie within the range calculated for a variety of species. For example, the M of amphibian and reptile species ranged from 0.349 to 0.916, with S ranging from 1.066 to 2.722 (Williams 2003). M for three species of mice in Switzerland ranged from 0.8 to 1.04, with S ranging from 1.6 to 3.98 (Reutter et al. 2003). Both studies incorporated a greater number of predictor EGVs, and covered a much smaller area (Reutter et al. 2003, Williams 2003).

The relatively high tolerance value (0.634) may seem contradictory at first glance, given the specialisation of this species revealed by the rest of the analysis. However, this value suggests that despite having a preference for a narrow range of values on the given EGVs, northern bottlenose whales will tolerate unsuitable conditions in order to move from one suitable area to another. This hypothesis is supported by a number of the sightings occurring in areas that may seem too shallow for example. This is not unreasonable given that all cetaceans are mobile species.

Many of the shelf areas of the Northwest Atlantic have steep-sided channels running through them, sometimes linked to the open sea (e.g., Fig. 1). These represent small sections of marginal habitat, in otherwise unsuitable zones (Fig. 3). Although relatively shallow, these channels may provide corridors for the movement of this species across relatively unsuitable areas to more suitable habitat. Several of the marginal and core habitat areas identified are linked by these channels (Fig. 3). For example, the eastern side of the Davis Strait is deeper than the western side, with a steep slope and as such may provide the more favourable route for northern bottlenose whales to move from the Labrador Sea into the southern reaches of Baffin Bay. Several sightings have occurred above the channel that runs along the Labrador Shelf (Fig. 1).

However, the questionable legitimacy of some of these data led to the comparison of those data deemed to be 'questionable' and 'reputable'. This procedure

highlighted that uncertainties within the data can lead to potential inaccuracies in the analysis, with a greater proportion of presence cells from the questionable dataset falling within the unsuitable habitat category. The results of separate ENFA carried out on these two datasets described the niche to be wider and less specialised, and narrower and more specialised respectively for the questionable and reputable datasets. In terms of the core areas predicted from each of these datasets, an overestimate may result from the incorporation of data that may include false positives (the questionable dataset). An underestimate could also result from the distributional bias present within the reputable dataset. This bias is likely because both the whalers and Dalhousie University cetacean surveys focussed on known areas of northern bottlenose whale abundance, and are therefore likely to be correlated with environmental factors.

Although considered ‘reputable’, historic whaling data may also include some inaccuracies. The positional accuracy of older catch data is likely to be relatively low, especially for the Scottish whaling records from the late 19th century (Reeves et al. 1993). Combined with potential inaccuracies of the questionable dataset, this may have resulted in an overestimate of the size of the area represented by each habitat class, an underestimate of the marginality and specialisation, and an overestimate of the relative tolerance of this species as identified by the ENFA.

All data sources were nonetheless incorporated in the analysis, as the ‘questionable’ data is likely to have less bias with respect to environment. ENFA is designed specifically for use with datasets that are of potentially low or unknown quality and those lacking adequate absence data, such as opportunistic sightings data and even museum records (Hirzel et al. 2001, 2002a, Reutter et al. 2003). However it is clear that greater accuracy will result from data that are unbiased with regard to distribution across environmental variables (Hirzel et al. 2002a). Hirzel et al. (2002b) looked at what sampling strategy would be most suited to HS modelling and concluded

that it is advisable to cover a greater spatial extent by way of regular, or stratified random sampling methods. Clearly however, as data quality and quantity increase, the usefulness of ENFA in the face of potentially more accurate methods will decrease.

ENFA can over-predict the distribution of a given focal species relative to other models such as GLMs, due to the lack of discriminating absence data (Zaniewski et al. 2002, Brotons et al. 2004). However, ENFA has been demonstrated as being robust in terms of sample size and also with respect to data quality, which approaches such as GLMs are sensitive to (Hirzel et al. 2001).

Several small, relatively isolated areas of core habitat were identified within the study area. One example exists just to the south of Disko Island, western Greenland. This area is linked to Baffin Bay by a narrow channel of unsuitable/marginal habitat (Figs. 2, 4). Such a small core area may seem spurious and unrealistic, but subsequent to the analysis presented here, a sighting was reported from this area (68°00'70"N, 54°41'50"W) (Brian Petrie, pers comm). Other small isolated areas of potential habitat, such as within Cumberland Sound, Baffin Island, may therefore also represent real core areas utilised by this species.

Though northern bottlenose whales may be tolerant of unfavourable conditions in order to move from core area to core area, the maximum distance animals will travel through such unsuitable habitat in order to reach another core area is still unclear. The model identified a clear link between the Labrador Sea and Scotian Shelf, by way of the Grand Banks, though the Scotian Shelf and southern edge of the Grand Banks are of only marginal suitability. Northern bottlenose whales on the Scotian Shelf have been shown to concentrate largely within the Sable Gully (Whitehead et al. 1997, Gowans et al. 2000), though also utilise the adjacent Shortland and Haldimand canyons (Wimmer & Whitehead in press). This indicates that these canyons clearly provide conditions preferable to the Scotian Shelf itself, which may be due to the unique oceanographic

conditions that occur within these canyons, such as enhanced upwelling (Allen et al. 2001). Wimmer and Whitehead (in press) found that individuals appeared to have preferences for particular canyons, with limited movement between them such that the population was not fully mixed. Given this apparent reluctance to move even relatively short distances along the Scotian Shelf, it may be that the distance to the nearest area of core habitat on the shelf-edge of the Grand Banks is too far.

The current ENFA failed to recognise the canyons of the Scotian shelf as core habitat, despite their demonstrated importance for northern bottlenose whales (Whitehead et al. 1997, Gowans et al. 2000, Wimmer & Whitehead in press). This may be due to the limited range of EGVs within the analysis not representing the unique conditions occurring within the canyons. It may also be an artefact of the resolution used. The Sable Gully is approximately 50 km x 15 km at its shallowest depth. The approximate 7.7 km² grid cells of the EGVs used here may represent this area relatively poorly. However, relative whaling catches indicate that the Scotian Shelf population has always been smaller than that of the Labrador Sea (Reeves et al. 1993), so it may be that this difference in historic population size genuinely reflects that the Scotian Shelf is marginal habitat, relative to more northerly areas such as the Labrador Sea.

To increase the accuracy of future analyses, a greater variety of EGVs at a finer scale should be incorporated. This would reduce the generalisation caused by using few factors and relatively large spatial scales. Possible factors that may be incorporated include chlorophyll-*a* concentration as a measure of productivity and fish catch data as a proxy for the distribution of species such as Greenland halibut. Of greatest use would be good data concerning the actual distribution of the likely most important prey species, such as *Gonatus* spp. Consideration of specific areas on a smaller scale would facilitate increased understanding of a range of variables. Based on the same four basic EGVs, the current analysis could also be extrapolated to cover the whole of the current

known range of northern bottlenose whales. This may serve to identify further core habitat areas, and examine the potential for movement to some of the locations where extra-limital sightings of this species have occurred, such as the Azores, Novaya Zemlya (Bering Sea) and the Mediterranean Sea (Mead 1989).

The overall marginality, specialisation and tolerance values calculated by the ENFA are of limited use with regard to a single species. Expanding the current ENFA to other taxa would allow a comparison of species within the same ecological guild. This would be useful to identify those species that may potentially be most affected by changes in the composition and abundance of prey species and global environmental change. Williams (2003) used ENFA to compare the niche of a variety of amphibian and reptile species. Using analysis of variance to examine the differences in mean marginality and specialisation among taxa, turtle species were demonstrated to be more marginal than salamanders and lizards and snakes were shown to be more specialised than frog and toad species (Williams 2003). Reutter et al. (2003) did a similar comparison between three species of mice in Switzerland, showing one particular species (*Apodemus alpicola*) to be far more specialised and restricted in terms of suitable habitat, relative to two other species common within the Alps.

Such a comparative approach would build upon previous work identifying northern bottlenose whales as specialists in terms of diet, relative to other deep-diving marine mammals that feed primarily on cephalopods, such as Cuvier's beaked whale (*Ziphius cavirostris*), southern elephant seals (*Mirounga leonine*) and sperm whales (*Physeter macrocephalus*) (Whitehead et al. 2003). This approach may also help to identify multi-species core habitat 'hotspots', which may be of high conservation priority and which often occur in the region of prominent habitat features such as shelf-edges (Worm et al. 2003).

The analysis presented here has identified key areas of habitat for northern bottlenose whales in the Northwest Atlantic Ocean, the results were consistent with previous findings that this species is linked primarily to steep-sloped, deep shelf-edge waters and in primarily cold sea surface temperatures (Benjaminsen & Christensen 1979, Hooker et al. 2002, Herfst 2004). The model has identified that there is a continuous corridor of at least marginal habitat linking the Scotian Shelf and Labrador populations via the shelf-edge of the Grand Banks of Newfoundland. Despite potential inaccuracies identified within the data, ENFA has produced biologically-sensible results that could not have been obtained using more accurate modelling approaches. As such, it provides a useful picture of the distribution and habitat requirements of northern bottlenose whales in this region, and for the first time over a large scale.

Future research to assess the status of this species and its movements should focus on the areas identified here as core habitat. This is of particular importance given the potential for interaction between northern bottlenose whales and the large multinational Greenland halibut fishery in the Northwest Atlantic, which is concentrated in the same shelf edge waters identified as being the main habitat of this species. Given the limited range of this species identified here, it is recommended that a precautionary approach to the conservation of northern bottlenose whales be taken by granting this species as a whole, an appropriate listing under COSEWIC until further research confirms their status beyond the Scotian Shelf.

ACKNOWLEDGEMENTS

The author would like to thank supervisors H. Whitehead of Dalhousie University (DU) and L. Goodwin of the University of Plymouth (UOP). I would like to thank H. Whitehead and M. L. Dalebout particularly for giving me the opportunity to work with them and be a part of the 2004 field team in the Labrador Sea. Seeing northern Labrador is an experience I will never forget. Thanks to the other members of the 2004 field team S. Gero (DU) and M. De Boer (consultant to the Whale and Dolphin Conservation Society). Thanks to all those who provided me with additional data used within this study including; T. Wimmer (DU), N. Øien (Institute of Marine Research, Norway), J. Lawson, S. Smith (DFO) and R. MacDonald (DU). A big thank you to C. Walls, J. Boxall (DU) and A. Jones (UOP) for their GIS expertise. This study was supported by NERC grant NER/S/M/2003/11749.

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APPENDIX

Sailing from Cartwright, Labrador, a survey was conducted along continental shelf-edge waters of the Labrador Sea/Davis Strait aboard a 20 m chartered fishing vessel, '*What's Happening*' (registered St. John's, NFLD) between 28th July and 18th August 2004. The focus of the survey route was the 1000 m depth contour, as this has previously been noted as the focus of the bottlenose whales' distribution (Benjaminsen & Christensen 1979, Hooker et al. 2002). The vessel track-line during effort hours is shown on Fig. app. 1. A total of 1425.6 km were surveyed during this trip.

The field survey team consisted of a scientific crew of four persons, including myself, with three individuals on duty under normal survey effort. The mode of survey was divided into five types of effort (Table app. 1). During suitable conditions (visibility moderate or above, Beaufort ≤ 4), 'normal' survey effort was adopted, being either high basic, or high basic fast.

Under these effort modes, the field team rotated through the positions of port observer, wheelhouse data logger, starboard observer and break. Observers were in radio contact with the wheelhouse data logger at all times with use of hand-held frequency modulated radios. Data were logged onto an IBM laptop computer using the program Logger 2000 (developed by the International Fund for Animal Welfare, available at <http://www.ifaw.org/ifaw/general/default.aspx?oid=25653>), interfaced with a Garmin™ Map 76 GPS unit. Logger 2000 automatically logged the vessel's GPS position every minute.

Each observer was responsible for scanning a 90 degree sector from 0° (track-line) to 90° port or starboard, enabling full observer coverage of 180 degrees in front of the vessel. To aid sighting, each observer was equipped with a pair of 7x50 reticule binoculars. To aid the correct recording of animal bearing and heading, each observer

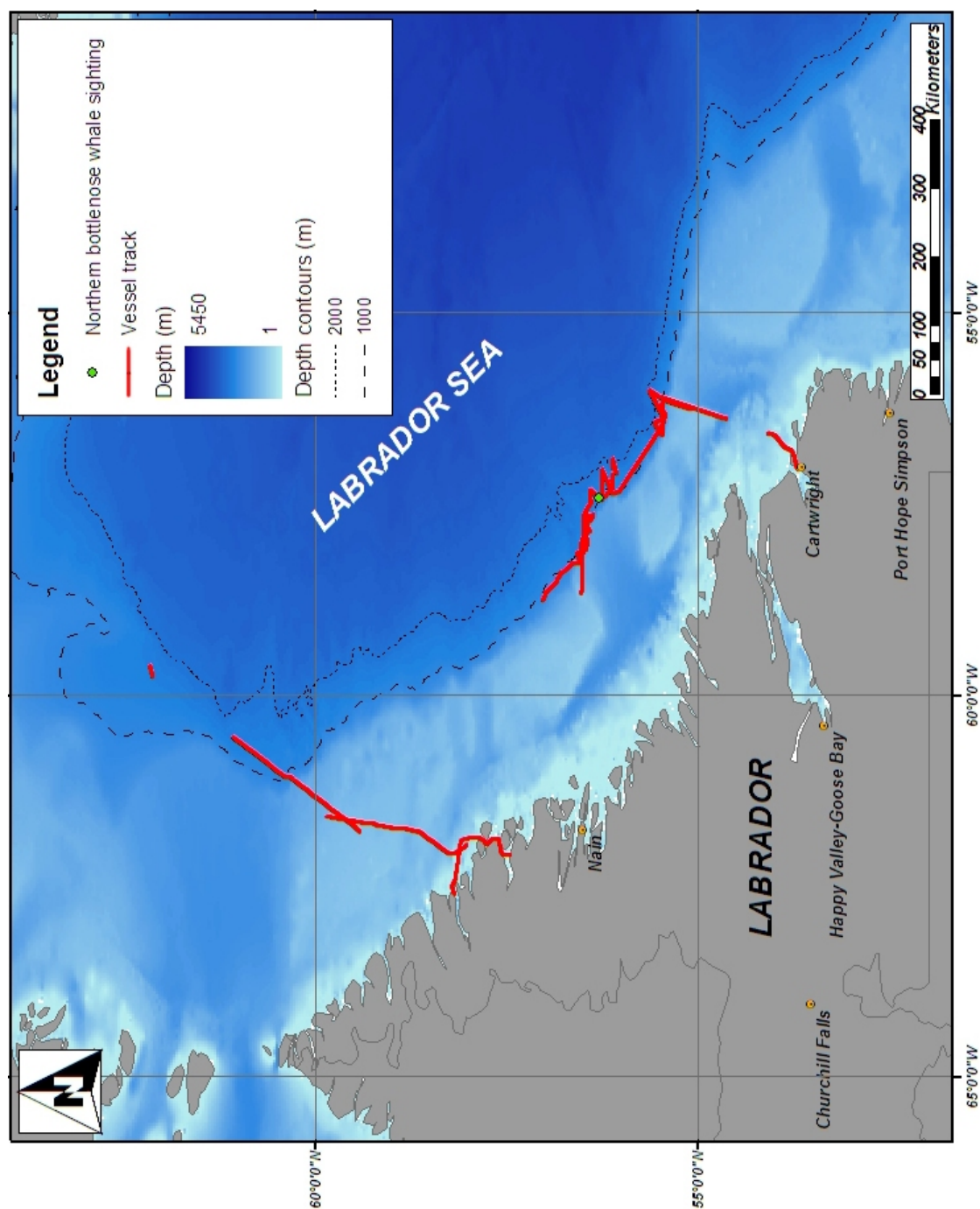


Fig. app. 1: map of survey area with survey track-line during effort hours and the single northern bottlenose whale sighting

utilised an ‘angle-board’, which was fixed to the vessel’s railing parallel to the bow. At the time of each sighting, the data logger updated the GPS position, and logged data reported from the observer with a visual cetacean sighting to include: animal bearing, animal heading, distance (in reticules), species identification (along with % certainty, including definite-100%, probable-75% and possible-50%), number of animals (minimum, maximum and best estimate), presence of juveniles, and sighting cue.

Table app. 1; the five modes of survey effort, adopted according to environmental conditions

Effort mode	Description
OFF	No dedicated observers on duty due to rest breaks or extremely poor weather (opportunistic observations made by vessel crew)
LOW	1 dedicated observer keeping watch from the vessel’s wheelhouse during unfavourable weather conditions (poor visibility/Beaufort >4)
HIGH BASIC	1 port and 1 starboard observer. 1 data logger in vessel wheelhouse. Vessel speed maintained at ≈ 6 knots. Adopted in conditions with moderate or better visibility and Beaufort ≤ 4
HIGH BASIC FAST	As above, but vessel speed variable between 7 – 8 knots. Adopted in place of high basic in order to cover more area due to time constraints caused by bad weather
ACTION MODE	Survey broken due to active data collection with cetaceans. All field crew on duty

The following environmental data were logged every 30 minutes, or as conditions changed: ship’s position, Beaufort sea state, swell height, wind speed and direction, visibility, type of precipitation, depth (from shipboard echo-sounder), cloud coverage (1-8) and amount of glare (in degrees). Only 2 northern bottlenose whales were encountered during a single sighting (Fig. app. 1) whilst surveying. This is principally due to very poor weather conditions, which made surveying difficult due to fog and rough seas, and combined with port calls for refuelling, forced a total of 8.5 days ashore.