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Small-scale spatial variability of sperm and sei whales in relation to oceanographic and topographic features along the Mid-Atlantic Ridge

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Abstract

The 2004 Mid-Atlantic Ridge (MAR)-ECO expedition on the R.V. *G.O. Sars* provided the first opportunity to correlate oceanic distributions of cetaceans with synoptic acoustic (ADCP to 700 m depth, multi-beam echosounders) measurements of high-resolution, three-dimensional (3D) potential habitat (spatial scale < 100 km). The identified habitat features were tested with independent observations from the Icelandic combined cetacean and redfish cruises in 2001 and 2003 using data from a 3D ocean general circulation model of the MAR region (Regional Oceans Modelling System (ROMS) model 5 km resolution). The spatial autocorrelation of sampled encounter rates of sperm *Physeter macrocephalus* and sei whales *Balaenoptera borealis* indicated scale-dependent variability in the distribution of both species. Despite the large area surveyed, the observations of both species exhibited a strong small-scale structure (range parameter 20–50 km), indicating affinities to cross-seamount or cross-frontal structures. Potential cross-seamount and cross-frontal habitat structures were derived from the acoustic transect data by analysing fine-scale gradients in the 3D flow patterns and bathymetry, including interactions between frontal and topographic parameters. PLS regression was used to determine the potential habitat drivers of sperm and sei whales, both during the *G.O. Sars* cruise and during the Icelandic cruises in 2001 and 2003. The selected parameters, which reflected flow gradients interacting with the steep topography, were finally applied for modelling the habitat suitability of both target species along the northern MAR using Ecological Niche Factor Analysis. The results suggest aggregations of sperm and sei whales along the MAR are primarily associated with fine-scale frontal processes interacting with the topography in the upper 100 m of the water column just north of the Sub-Polar Front (SPF) and the Charlie–Gibbs Fracture Zone (CGFZ). As moderate and high habitat suitabilities were estimated only for areas downstream from the SPF, the findings suggest that the animals capitalise on secondary production maintained by enhanced primary production associated with the frontal processes in the upper part of the water column in the CGFZ and at the Faraday Seamounts. Further studies are encouraged to evaluate the importance of the bio-physical coupling, and the significance of small-scale frontal processes in the surface and subsurface waters north of the SPF for the transfer of energy to higher trophic levels in the North Atlantic.

Keywords: Cetaceans; Oceanic fronts; Mid-Atlantic Ridge; Spatial structure; Bio-physical coupling; Habitat modelling

1. Introduction

Cetaceans inhabit the earth's most extensive habitat; open oceans outside continental shelf environments. Systematic surveys of cetaceans have occurred in many slope and deep oceanic regions, with the intent to derive abundance estimates for stock management. Limited ecological research has been carried out on cetaceans during assessment surveys or as dedicated projects to examine potential ocean habitats. Potential habitat studies have used topographic variables to correlate abundance of

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cetaceans with seabed structures at various scales (Baumgartner et al., 2001; Williams et al., 2006; Yen et al., 2004) or surface and three-dimensional hydrodynamic parameters averaged over survey periods (Burtenshaw et al., 2004; Panigada et al., 2006). Reduced effort has focused on the small-scale variability of cetaceans in relation to oceanographic variables in the open ocean. The *G.O. Sars* leg 1 cruise along the Mid-Atlantic Ridge (MAR) in June 2004 provided a unique opportunity to examine oceanic habitats of cetaceans using synoptic three-dimensional acoustic recordings of the fine-scale structure of the water column and the seabed.

The *G.O. Sars* cruise recorded aggregations of zooplankton and nekton in several parts of the MAR region, most notably at the Sub-Polar Front (SPF) and in the Charlie–Gibbs Fracture Zone (CGFZ) (Opdal et al., 2008; Gaard et al., 2008). Observations of cetaceans revealed concentrations of sperm *Physeter macrocephalus* and sei *Balaenoptera borealis* whales in the same areas. Detailed analyses of the association between observations of sei and sperm whales and the dynamic features of the water column and the seabed topography may assist in the determination of habitat features that are important to cetacean feeding. Aggregations of feeding cetaceans may be associated with the enhanced secondary production frequently reported at and downstream of seamounts (Dower and Brodeur, 2004; Genin, 2004). Sperm whales are essentially piscivorous but also feed on cephalopods, while sei whales are planktivorous (Roe, 1969; Martin and Clarke, 1986; Christensen et al., 1992; Santos et al., 1999). Identification of biological and physical factors associated with high density feeding aggregations of sperm and sei whales may help understand the role of biophysical interacting processes that transfer energy along different pathways to higher trophic levels in open ocean ecosystems such as the MAR. Specifically, knowledge of potential habitat drivers, i.e. type, scale and interaction of key factors, for whales along the MAR may assist in the assessment of the role of different processes (meso-scale processes of the SPF/smaller scale processes at seamounts downstream from the SPF) in the development of enhanced secondary production recorded in the MAR region.

2. Material and methods

2.1. Physical oceanography of the study area

The area covered in this analysis encompasses the northern MAR from 37° to 61° N and from 19° to 38°W (Fig. 1). The Icelandic cruises used to evaluate the identified factors that influence marine mammal habitat drivers and subsequent habitat predictions included the northern MAR and parts of the eastern Irminger Sea from 53° to 63° N and from 19° to 40°W. The topography of the area is dominated by the MAR, which is located centrally with depths varying between approximately 500 and 2000 m. Both within the MAR and on the slopes towards the Irminger and Iceland Basins steep gradients occur. The dominant feature of the MAR is a ridge structure with numerous hills, but only few of the hills classify as seamounts in the normal sense of the term. One cluster of seamounts is found at 48° N; Faraday Seamounts (Fig. 1). North of these seamounts a fracture zone opens the MAR and further north at 52° the CGFZ functions as the major pathway for exchange of water masses between the two basins (Bersch, 1995; Rossby, 1996; Bower et al., 2002).

The circulation along the northern MAR results from subpolar and subtropical gyres, feeding water masses and currents into the study area. Due to marked density differences between the water masses, most of the region has a complex vertical stratification pattern. Sperm and sei whales feed in different layers of the stratified water column. Sperm whales are deep divers while the planktivorous sei whales are shallow divers (Horwood, 1987; Gregr, 2003). Digital tags indicate an effective maximum diving depth of sperm whales during feeding to approximately 985 m (Watwood et al., 2006), while sei whales are believed to feed closer to the surface. Accordingly, acoustic current data from the upper 700 m from the *G.O. Sars* cruise have been included in the analysis of habitat drivers.

2.2. Acoustic measurements of currents and depth

Acoustic backscatter data were collected continuously along the MAR-ECO Leg 1 cruise track (Opdal et al., 2008). Current velocities in the upper 500–700 m of the water column were recorded by a 75 kHz RDI Ocean Surveyor ADCP (Søiland et al., 2008). The ADCP was run in the narrow band mode with 45 vertical bins each 20 m deep and recorded useable data to 500 m depth. Five frequency (18, 38, 70, 120, and 200 kHz) water-column data were collected by a Simrad EK-60 splitbeam echosounder. The RDI software WmDas was used for data acquisition and the CODAS system (http://currents.soest.hawaii.edu) was used for initial post-processing of the data in 300-s averages.

The bottom depth was continuously logged using a Simrad EK 60 split beam echosounder and by a Kongsberg EM300 multibeam sonar. Both systems were synchronised with the ADCP.

2.3. Hydrodynamic and flow modelling data

To describe the small-scale variability in oceanographic parameters throughout the northern MAR we used data from the Regional Oceans Modelling System (ROMS) set up for the MAR region. ROMS is a hydrostatic, 3D, primitive equation, free surface model using stretched, terrain-following coordinates in the vertical and orthogonal curvilinear coordinates in the horizontal (Lien et al., 2006; Shchepetkin and McWilliams, 2005). The North Atlantic ROMS model has a horizontal resolution of 5 km and a vertical resolution of typically 5–10 m in the upper 100 and 100–200 m resolution in the deeper parts of the water column. We imported mean U (eastern component)

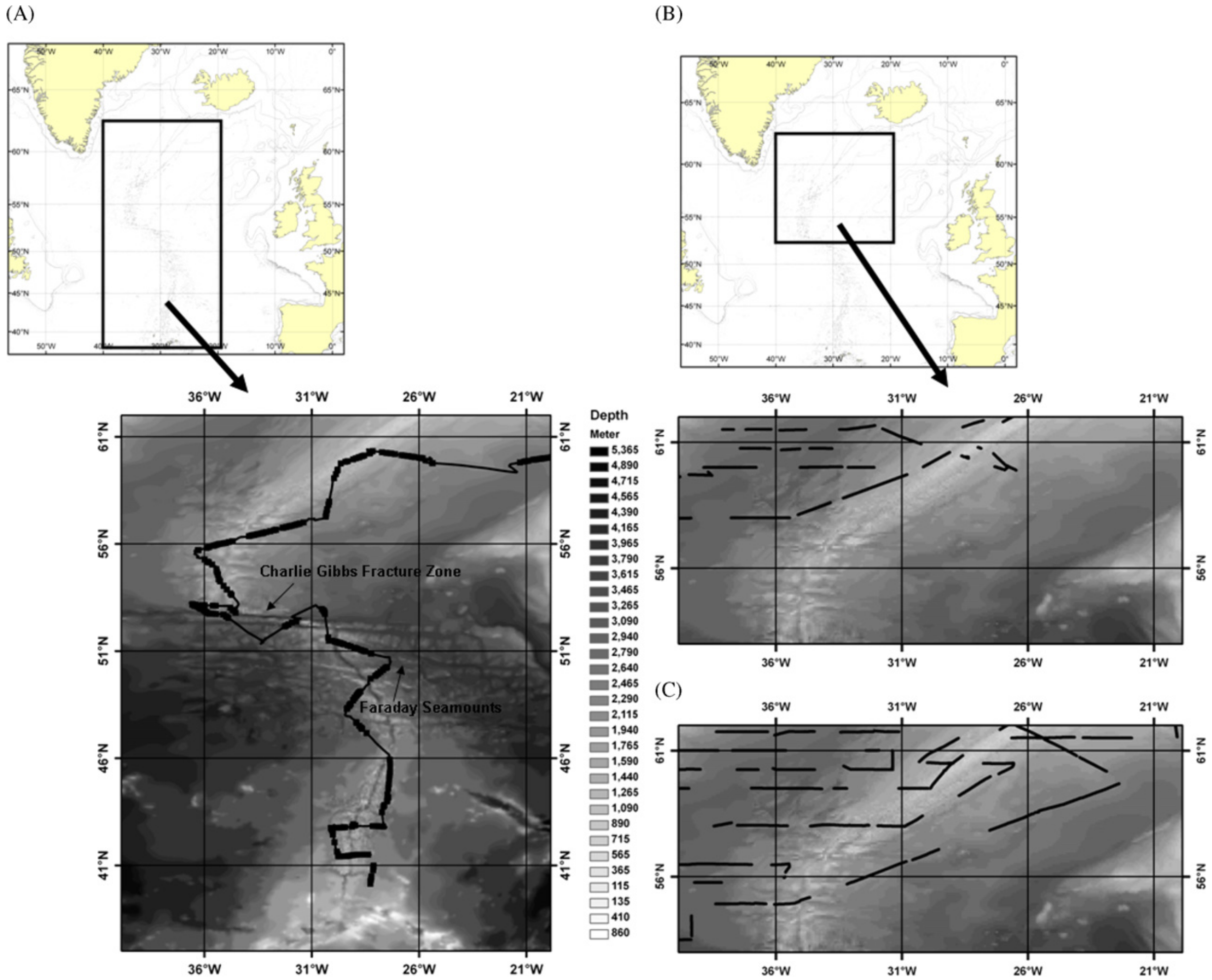

Fig. 1. Sampling area for the *G.O. Sars* 2004 (A) and the Icelandic combined cetacean and redfish surveys 2001 (B) and 2003 (C). For the survey in 2004 both cetacean density sampling effort and total cruise effort are indicated by bold and thin lines, respectively. For the Icelandic surveys only the cetacean recording effort is indicated.

and *V* (northern component) current velocities as well as salinity, temperature and water level (elevation in m from Earth geoid) for the periods covered by the three cruises.

2.4. Recordings of cetacean abundance

Recordings of cetacean abundance were collected during steaming between super stations by one to three observers located in an observer platform on the roof of the ship's wheelhouse at an eye height of 15.5 m above sea level. The ship's cruising speed during steaming was approximately 11 knots. Only very limited survey efforts were made as the vessel slowed down when approaching a sampling station and gradually increased speed when departing a station. Continuous observations were undertaken during daylight hours (04:00–23:00), except during adverse weather conditions (Beaufort sea state >6, rain and visibility <5 km). Generally two observers were present, but one extra observer assisted when passing areas with high densities of cetaceans. In areas of low densities or in association with meals one observer was working. The three observers were working overlapping shifts.

Each observer searched for cetaceans in a 140° arc centred along the track line. One observer searched using naked eye aided by 7×50 hand-held binoculars to identify possible sightings; the second observer searched using 7×50 hand-held binoculars. Observers recorded sightings and effort data onto data sheets, including data on time, species, group size, number of calves, radial distance, bearing, swim direction, behaviour, and association with seabirds. Due to the limited number of observers radial distances and bearings were only recorded at initial sightings as an absolute requirement, although frequently taken during re-sightings. Calibration of distance measurements was made by regularly using callipers with distance markings from 100 to 2000 m. Effort and environmental data included: transect number, date, time, course, speed, observer position, and environmental variables (e.g., weather, cloud cover, visibility, glare (severity and angle). Vessel sensor data (e.g., global positioning system (GPS), speed, wind direction and speed, etc.) were downloaded from the ship's computer system on a daily basis. Cetaceans were identified to the lowest taxonomic level possible based on key field characteristics, body size/shape and colour (Jefferson et al., 1993).

The Icelandic cruises were carried out in June–July 2001 and 2003 by the Marine Research Institute in Reykjavik combining cetacean and redfish surveys. The 2001 cruise was a part of the international North Atlantic Sightings Surveys (NASS-2001), conducted on two partially independent platforms (Víkingsson et al., in press), while the 2003 cruise had lower observer effort from one platform, the R.V. *Árni Friðriksson*. The general methods used for observation of cetaceans were comparable to those used during the *G.O. Sars* 2004 cruise. The transect design, however, allowed for a wider coverage of the cross-ridge area of the Reykjanes Ridge.

2.5. Post-processing and integration of oceanographic, model and cetacean data

Observations of cetaceans and seabirds were recorded to the nearest minute along the cruise track. These data formed a line transect database for sections of the track with observational effort for analyses of scale dependence and correlation with continuous acoustic data. The line transect database held details of densities (n/km^2) of each target species (group), position (dGPS), ship speed (m/s), surface area covered by marine mammal transect (km^2) and weather (Beaufort scale). Positions of all sightings were corrected to the position at the closest range to the transect instead of the position of the initial sighting, which for the larger whale species, could be several kilometres distant. The database of cetacean sightings was transferred to a digital database in Mercator projection (wgs 84 Datum) in ArcGIS Ver. 9.1 and Idrisi Ver. 8. for geo-statistical and spatial analysis. Encounter rates were calculated for each minute by dividing observed numbers by distance travelled along the transect.

Data from the acoustic 3D mapping of the seabed and currents were integrated with the mammal sightings by developing a $1 \times 1\,\text{km}^2$ transect raster matrix with 9 vertical bins (0, 50, 100, 200, 300, 400, 500, 600, and 700 m) following the ships path to be used as a basis for exploratory analysis of the *G.O. Sars* data. All cetacean sightings and acoustic transect data were re-sampled and merged into the 3D grid by allocating observations and recordings to one grid cell–vertical bin combination. ADCP data were filtered using a 7-point median filter in the horizontal on the 300-s averages, checked for outliers using the OLEX data and then added to the 1-km resolution matrix. For habitat modelling and exploratory analysis of the Icelandic cruise data cetacean observation, bathymetry and ROMS data were integrated into a $20 \times 20\,\text{km}^2$ digital transect with the same vertical bins as the 1-km transect matrix. The integrated physical–oceanographic variables used for exploratory analysis and habitat modelling are listed in Table 1.

2.6. Exploratory analysis: selection of potential drivers in habitat usage

To assist in the determination of the most relevant physical oceanographic features to select for the exploratory analysis of potential habitat drivers we examined the spatial auto-correlation of the sampled encounter rates of sperm and sei whales by geo-statistical analysis. The empirical variograms were used to evaluate the spatial scale of potential topographic and dynamic habitat features.

The 1- and 20-km 3D digital databases contained a large number of potential environmental habitat variables (including two-way interactions between topographic and hydrodynamic parameters approximately 100) that may influence the location of cetacean foraging. To develop habitat models and to determine primary influencing factors we used factorial models with PLS regression (Naes and Martens, 1985; Geladi and Kowalski, 1986) on the 1-km digital database for the *G.O. Sars* 2004 cruise and on the 20 km digital database for the Icelandic cruises. PLS regression is an extension of multiple linear regression and allows for the determination of complex responses in species data to colinear physical data. PLS regression in this study is especially useful as it enables the prediction of environmental factors underlying responses on the species from factors underlying the levels of the predictor variables extracted from cross-product matrices involving both the predictor and response variables. PLS regression has the advantage over linear regression in its ability to robustly handle non-orthogonal descriptors and has a lower risk of chance correlations (Cramer, 1993). Using the results of the PLS regression, a smaller number of parameters of combination of parameters were selected and used for habitat modelling.

2.7. Habitat modelling

We used Ecological Niche Factor Analysis (ENFA), a predictive presence-only model, to detect environmental gradients in the absence of standardised survey data. Cetacean observations on *G.O. Sars* were conducted using standard recording techniques, but we cannot rule out that uneven geographical coverage due to the zig-zag cruise track, incomplete observation effort, and variable observation conditions (i.e. waves, swell and rain) may have biased portions of the data. In such situations, presence only models like ENFA have proven efficient in determining gradients in species' habitat suitability (Guisan and Zimmermann, 2000; Manel et al., 1999).

We used ENFA to estimate habitat suitability of sperm and sei whales during the *G.O. Sars* and Icelandic cruises by calculating marginality and specialisation factors in the two species' oceanographic space as reflected by the linked physical oceanographic variables. Marginality was calculated as the absolute difference between the global mean of all oceanographic data in the matrix and the mean of the

Table 1
List of physical oceanographic variables used as input to exploratory analyses and habitat modelling for the *G.O. Sars* cruise and the Icelandic combined cetacean and redfish cruises

G.O. Sars cruise Variable	Value	Source
Exploratory analyses		
Bathymetry	Negative values/10	Simrad EK 60 + Kongsberg EM300 echosounders
Slope of seafloor	Tangent angle with max. downhill slope/1000	Bathymetry
Northern aspect of sea floor	Sine of the direction of max slope	Slope
Eastern aspect of sea floor	Cosine of the direction of max slope	Slope
Bottom complexity	*n* Classes-1/*n* cells-1	Bathymetry
Flow (m/s) gradient N component (*V*)	*n*/1000 at 10–50–100–300–500–700 m	OS ADCP
Flow (m/s) gradient E component (*U*)	*n*/1000 at 10–50–100–300–500–700 m	OS ADCP
Habitat modelling		
Bathymetry	Negative values/10	GOS 2004 + available depth data for North Atlantic
Slope of seafloor	Tangent angle with max. downhill slope/1000	Bathymetry
Northern aspect of sea floor	Sine of the direction of max slope	Slope
Eastern aspect of sea floor	Cosine of the direction of max slope	Slope
Bottom complexity	*n* Classes-1/*n* cells-1	Bathymetry
Water level (m) gradient	*n*	ROMS Model
Flow (m/s) gradient N component (*V*)	*n*/1000 at 10 m-50 m-100 m	ROMS Model
Flow (m/s) gradient E component (*U*)	*n*/1000 at 10–50–100 m	ROMS Model
Temperature gradient	*n* At 10–50–100 m	ROMS Model
Salinity gradient	*n* At 10–50–100 m	ROMS Model
Icelandic cruises		
Exploratory analyses		
Bathymetry	Negative values/10	GOS 2004 + available depth data for North Atlantic
Slope of seafloor	Tangent angle with max. Downhill slope/1000	Bathymetry
Northern aspect of sea floor	Sine of the direction of max slope	Slope
Eastern aspect of sea floor	Cosine of the direction of max slope	Slope
Bottom complexity	*n* Classes-1/*n* cells-1	Bathymetry
Water level (m) gradient	*n* At 10–50–100–300–500 m	ROMS Model
Flow (m/s) gradient N component (V)	*n*/1000 at 10–50–100–300–500 m	ROMS Model
Flow (m/s) gradient E component (U)	*n*/1000 at 10–50–100–300–500 m	ROMS Model
Temperature gradient	*n* At 10–50–100–300–500 m	ROMS Model
Salinity gradient	*n* At 10–50–100–300–500 m	ROMS Model
Habitat modelling		
Bathymetry	Negative values/10	GOS 2004 + available depth data for North Atlantic
Slope of seafloor	Tangent angle with max. downhill slope/1000	Bathymetry
Northern aspect of sea floor	Sine of the direction of max slope	Slope
Eastern aspect of sea floor	Cosine of the direction of max slope	Slope
Bottom complexity	*n* Classes-1/*n* cells-1	Bathymetry
Water level (m) gradient	*n* At 10–50–100 m	ROMS Model
Flow (m/s) gradient N component (*V*)	*n*/1000 at 10–50–100 m	ROMS Model
Flow (m/s) gradient E component (*U*)	*n*/1000 at 10–50–100 m	ROMS Model
Temperature gradient	*n* At 10–50–100 m	ROMS Model
Salinity gradient	*n* At 10–50–100 m	ROMS Model

part of the oceanographic matrix overlapping sperm and sei whale sightings divided by 1.96 standard deviations of the global distribution. Specialisation was defined as the ratio of the standard deviation of the global distribution of oceanographic variables to that of the species' distribution. On the basis of differences in the cetacean and global 'space' with respect to their mean and variances, marginality of cetacean sightings was identified by differences to the global mean and specialisation by a lower species variance than global variance. For large geographical areas, ENFA can be used to examine Hutchinson's concept of the realised ecological niche, defined as a hyper-volume in the multi-dimensional space of ecological variables within which a species can maintain a viable population (Hutchinson, 1957).

To incorporate multi-colinearity and interactions among oceanographic parameters, indices of marginality and specialisation were estimated by factor analysis. The first component is interpreted as the marginality factor passing through the centroid of all positive observations and the centroid of all background cells of the digital transects. The index of marginality measures the orthogonal distance between the two centroids. Several specialisation factors or components were successively extracted from the n-1 residual dimensions, ensuring their orthogonality to the marginality factor while at the same time, maximising the ratio between the residual variance of the background data and variances of the cetacean occurrences. A habitat suitability index ranging from 0 to 100 was computed using the marginality factors and the first three specialisation factors, as a high proportion (>70%) of the total variance was explained by the first few factors. We used the medians algorithm in BioMapper Version 3 (University of Lausanne, 2005) for habitat suitability computation. The central 33% of the suitability index (values from 34 to 66) were used as an indication of medium or moderate suitability and the upper 33% (values from 67 to 100) were used as an indication of high suitability.

3. Results

3.1. Distribution of sei and sperm whales

Effort was distributed along the entire length (3016 km) of the cruise track from the Reykjanes Ridge to north of the Azores (Fig. 1). The total line transect effort was 2321 km (1274 km N and 1047 km S of CGFZ). We recorded 13 cetacean species (Fig. 2), which were seen along the entire range of the MAR from Reykjanes Ridge south of Iceland to the Azores with notable areas of concentration in the CGFZ, as well as in association with seamounts and rises. A total of 199 sightings were made, of which 50 and 54 were of sperm and sei whale, respectively (Fig. 2, Table 2). The longitudinal distribution of both species showed a clear increasing trend towards the CGFZ, with both species being most concentrated at the distance of 50–100 km from the CGFZ (Fig. 3). Sperm whales, however, displayed a second aggregation extending over a wide area on the Reykjanes Ridge (3–500 km north of CGFZ).

During the Icelandic cruise in 2001, a total of 10 sperm and 412 sei whales were observed, while during 2003 a total of 5 sperm and 158 sei whales were observed (Table 2). Accordingly, only sei whale data were retained for statistical analyses. The total number of sightings of sei whale (schools) during the two cruises was 288 in 2001 and 98 in 2003.

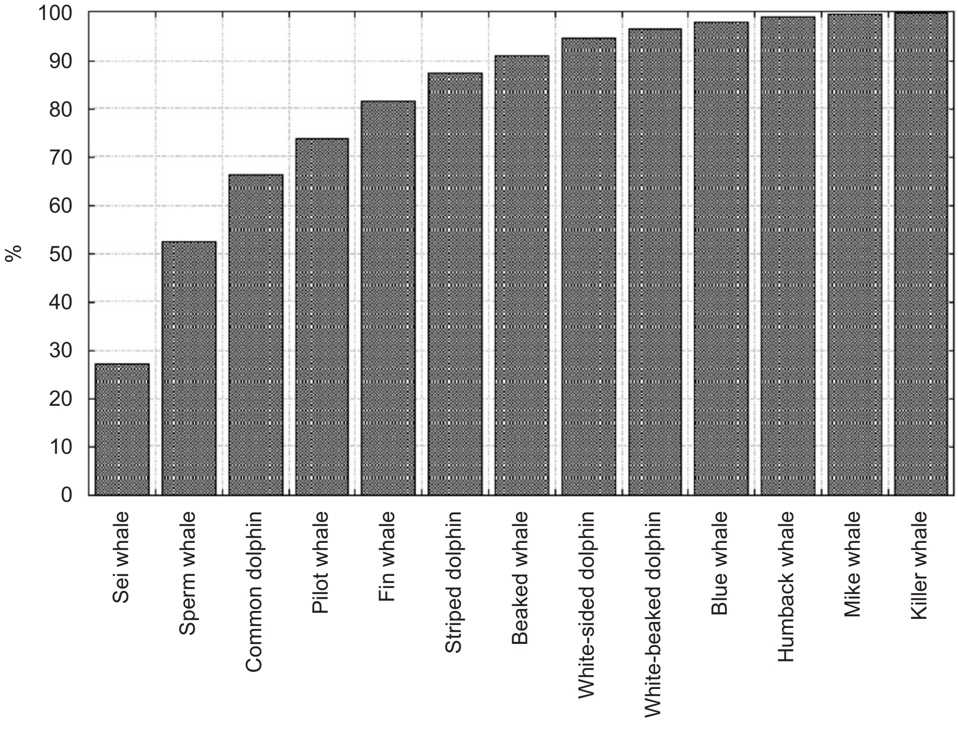

Fig. 2. Cumulative proportional abundance (numbers observed) of cetaceans observed along the *G.O. Sars* transect.

Table 2
Cruise statistics for observations of sperm and sei whales, summarized for the *G.O. Sars* cruise in June 2004 and the Icelandic cruises in July 2001 and 2003

	No samples	Mean	No observed	Variance	Std. dev.	Skewness	Kurtosis
Sei whale 2004	33,609	0.002618	88	0.0073	0.085	64.3	6182.0
Sperm whale 2004	33,609	0.002648	89	0.0113	0.105	96.5	12847.2
Sei whale 2001	8650	0.04764	412	0.0847	0.291	8.224	93.613
Sei whale 2003	3379	0.0468	158	0.100	0.317	9.372	112.389

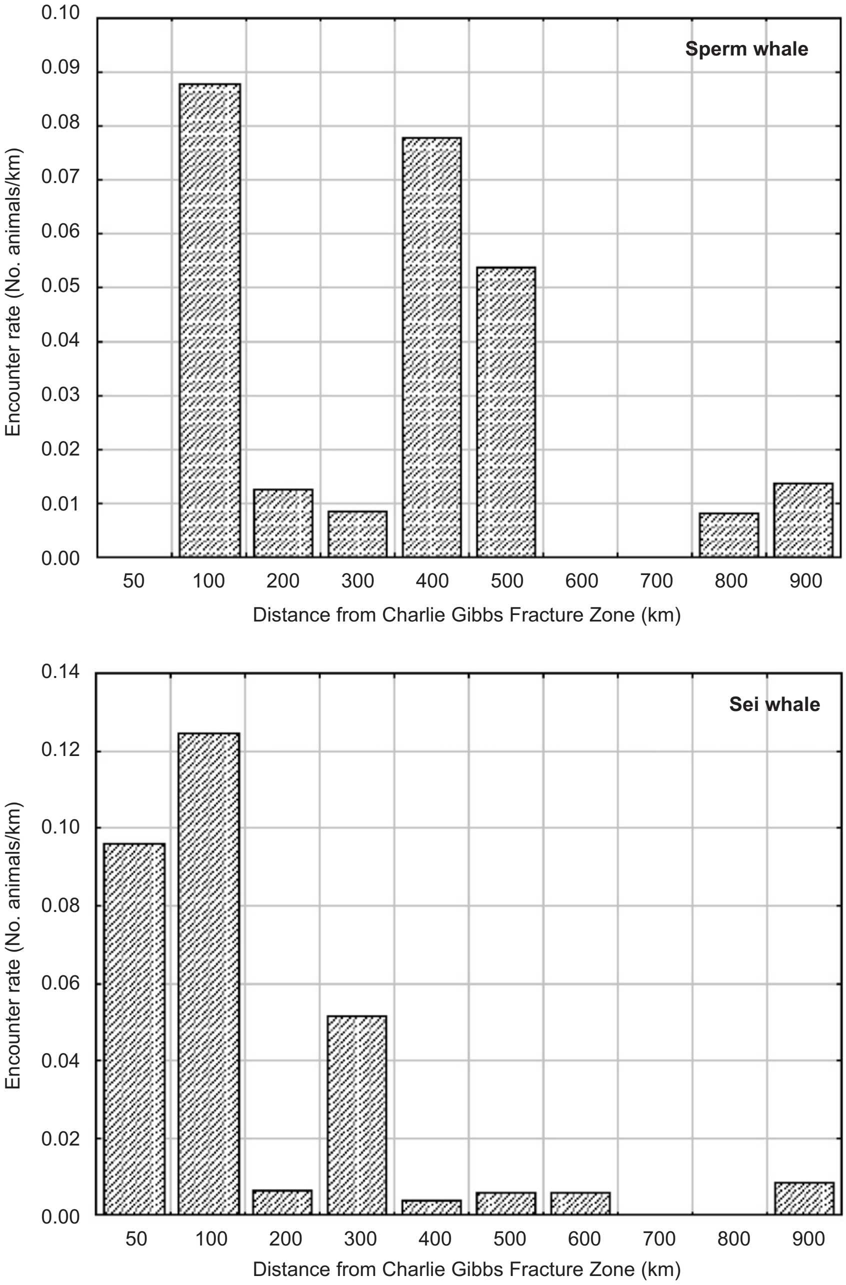

Fig. 3. Distribution of encounter rates (no. of animals/km) of sei and sperm whale during *G.O. Sars* cruise with distance from the Charlie–Gibbs Fracture Zone.

3.2. Oceanography

The transect covered relatively warm and relatively saline Modified North Atlantic Water (MNAW) on the Reykjanes Ridge in the northern part, colder less-saline Subarctic Intermediate Water (SAIW) further south to the CGFZ and warm high salinity North Atlantic Central Water (NACW) in the southern part. The region in and just south of the CGFZ was a frontal zone where both NACW and SAIW was observed in the upper 500 m of the ocean (Søiland et al., 2008). The depth of the base of the main thermocline was deeper than 1000 m just north of the Azores, and shoaled to less than 500 m south of the Frontal zone, and in the region dominated by SAIW no thermocline was observed. Farther north on the Reykjanes Ridge where MNAW was observed, the thermocline depth was about 500 m. The North Atlantic Current was observed to cross the ridge between 48° and 52°N (Søiland et al., 2008).

3.3. Potential habitat drivers

In Fig. 4 the empirical variograms of sperm and sei whales are shown for all cruises. Both the sperm whale during the *G.O. Sars* cruise and the sei whale data showed a clear small-scale spatial structure (range 30–50 km),

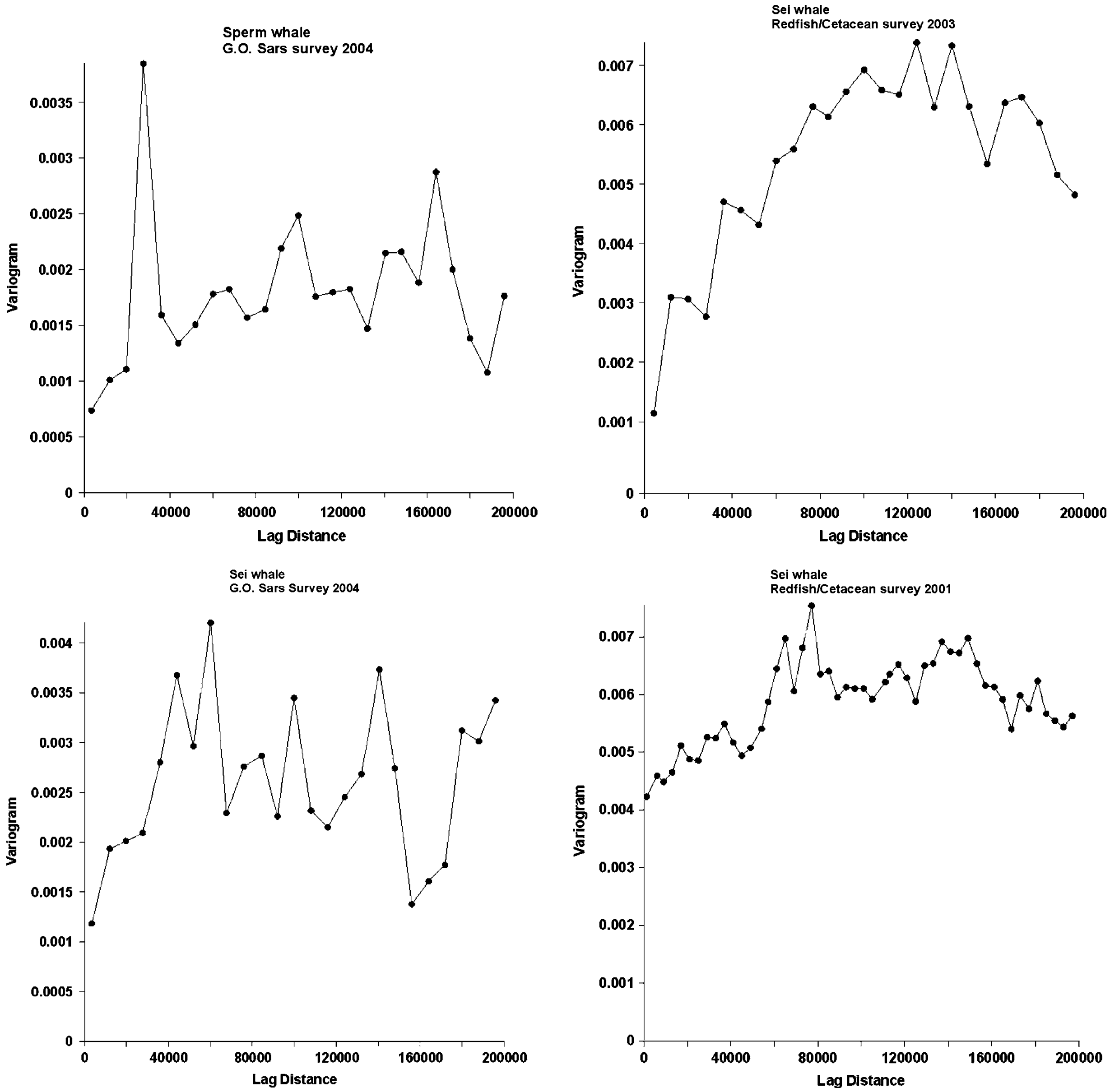

Fig. 4. Empirical variograms showing autocorrelations in sampled sei and sperm whale data for *G.O. Sars* 2004 as well as for Icelandic cruises (combined cetacean and redfish cruises in 2001 and 2003).

whereas the sei whale data from the two Icelandic cruises reflected both a small- and a medium-scale (80 km) structure. As a result, the *U* and *V* current velocities of both ADCP measurements and ROMS model data were transformed to velocity gradients in order to better account for small-scale structures associated with fronts and upwellings at seamounts and ridges. It should be noted that the gradient in the ADCP data is only used as a proxy for the real gradient in current velocities along the cruise track.

The results of the PLS regression for the synoptic 1-km transect data from the *G.O. Sars* cruise showed limited response of sperm and sei whale observations to most physical–oceanographic variables as main effects (Fig. 5). Sperm whales displayed a strong response to bottom complexity, while sei whales displayed a strong response to the northern aspect of the seafloor and to surface and subsurface fronts as determined by gradients in the east-component of the surface current and the north-component of the current measured at 700 m. Sperm whale displayed strong responses to the interactions between water depth (shallowness) and complexity and between flow gradient at the surface and at 100 m depth and topographic variables. Sei whales, on the other hand, displayed strong responses to the interactions between bottom topography and flow gradients at various depths, yet most notably at depths shallower than 100 m.

During the 2003 Icelandic cruise, sei whales showed strong responses to the northern aspect of the seafloor, and interactions between bottom topography and hydrodynamic and hydrographic gradients, especially flow

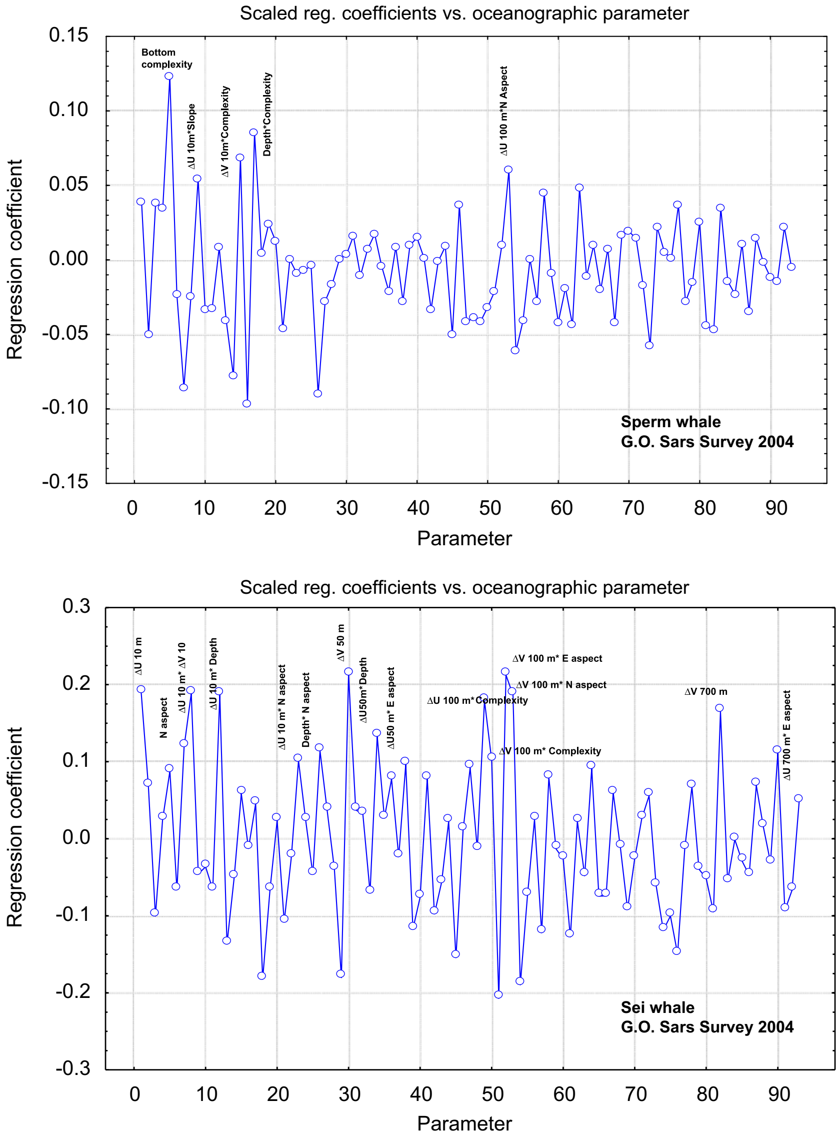

Fig. 5. Results of the PLS regression showing regression coefficients vs. oceanographic parameters for encounter rates of sperm and sei whales recorded during GOS 2004 survey. Parameters are marked for regression coefficients larger than 0.05 (sperm whale) and 0.1 (sei whale).

gradients in the surface layer. During the 2001 Icelandic cruise sei whale showed limited correlations with any of the physical parameters as main effects (Fig. 6). However, the animals showed strong responses to interactions between topographical variables and hydrographic and flow gradients in the upper (0–300 m) part of the water column.

3.4. Habitat modelling

As the results of the PLS regression showed only few instances of strong correlations with the dynamic parameters at depths deeper than 100 m all hydrographic and hydrodynamic variables in the upper (0–100 m) part of the water column were selected as potential habitat predictors together with the topographic variables. The three first components for the sperm whale data from 2004 summarised 79% of the habitat specialisation of the species, with the water depth (shallowness) and bottom complexity playing the major role in relation to the marginalisation, and the flow and water-level gradients in surface layers being more important in relation to the habitat specialisation (Table 3). For the sei whale, the two first factors accounted for 99% of the total specialisation, with the marginalisation, which accounted for 51% of the total specialisation, being determined mainly by the slope of the sea floor, and the specialisation mainly by the surface and subsurface flow and water-level gradients.

Overlays of observations of sperm and sei whales with the habitat suitability models produced by ENFA showed a reasonable degree of correspondence (Fig. 7). The prediction model for sperm whale in 2004 indicated a large area of medium suitability over the northern MAR and north of the Azores, and several higher suitability spots, including the area just north of the CGFZ and over the

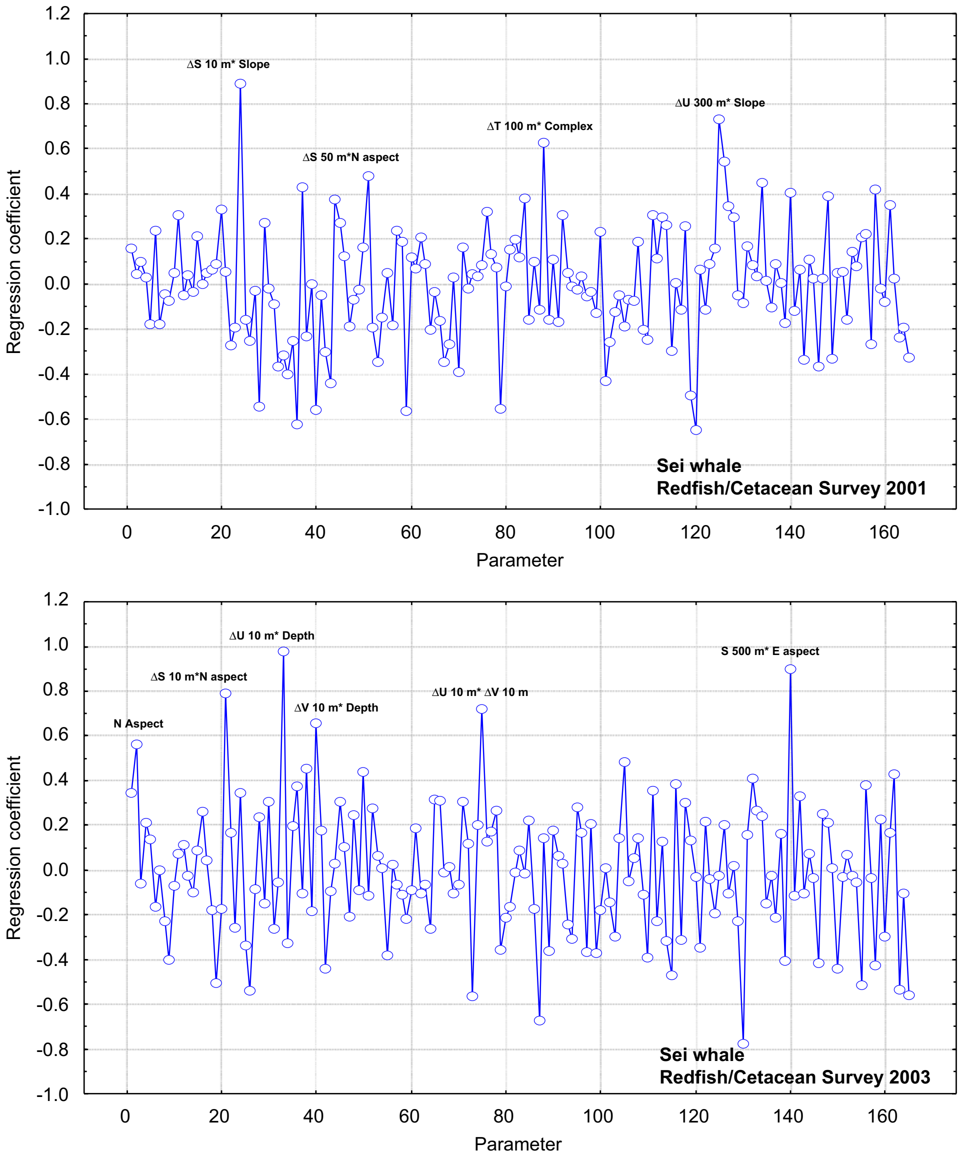

Fig. 6. Results of the PLS regression showing regression coefficients vs. oceanographic parameters for encounter rates of sei whales recorded during the Icelandic cruises in 2001 and 2003. Parameters are marked for regression coefficients larger than 0.5 (2001) and 0.6 (2003).

upper slopes of the Reykjanes Ridge, where most animals were seen. The area of suitable habitat to sei whales in 2004, as depicted by ENFA, was clearly smaller than for sperm whale. A small area of high suitability was estimated for the northern trench in the CGFZ and the associated area extending 100 km northwards from the trench, and medium suitability was estimated for the major part of the MAR area north of the CGFZ. Low suitability was estimated for almost the entire area south of the CGFZ, and for both species the deeper parts of the region received low suitability scores.

The zones of high habitat suitability to sei whales predicted during the Icelandic cruises in 2001 and 2003 covered larger zones of the central and western slopes of the Reykjanes Ridge than estimated for the *G.O. Sars* cruise (Fig. 8). In 2001, the marginality factor only accounted for 25% of the specialisation (Table 3).

4. Discussion

The spatial autocorrelation and the concurrent fine-scale transect of cetacean abundance, seabed characteristics and flow dynamics on the *G.O. Sars* cruise provided strong indications of the importance of fine-scale features in the shaping of the oceanic habitats of the two dominant species of large cetaceans in the MAR: sperm whale and sei whale. Correlations between cetacean distribution and oceanographic features and biological productivity have been widely reported, but have mainly focused on large- or meso-scale structures and processes (Ballance and Pitman,

Table 3
Amount of specialisation explained by the first four factors. Eco-geographical variables are sorted by decreasing absolute values of coefficients on the marginality factor. The amount of variation accounted for is given in parentheses

Eco-geographical variable	Marginality (59%)	Spec. 1 (27%)	Spec. 2 (6%)	Spec. 3 (3%)
Sperm whale G.O. Sars 2004				
E Aspect	−0.151	0.016	−0.010	0.013
N Aspect	−0.084	−0.021	0.006	0.030
Bathymetry	0.620	−0.060	0.041	−0.028
Bottom complexity	0.467	0.040	−0.011	−0.004
Easting	−0.241	0.028	0.012	−0.021
Northing	0.217	0.019	−0.025	−0.032
Bottom slope	0.168	0.005	0.007	0.038
Δ Water level 10 m	−0.075	0.497	−0.489	−0.521
Δ Water level 50 m	−0.075	−0.378	0.338	0.338
Δ Water level 100 m	−0.075	−0.224	−0.119	0.168
Δ Salinity 10 m	−0.132	−0.011	−0.029	−0.006
Δ Salinity 50 m	0.136	0.016	−0.04	0.011
Δ Salinity 100 m	−0.236	−0.087	−0.005	−0.131
Δ Temperature10 m	−0.146	−0.006	0.063	−0.078
Δ Temperature 50 m	−0.124	0.095	0.054	0.175
Δ Temperature 100 m	0.012	−0.019	0.028	−0.053
Δ E Flow 10 m	−0.041	0.056	0.031	−0.168
Δ E Flow 50 m	−0.042	0.346	−0.196	−0.349
Δ E Flow 100 m	−0.033	−0.380	0.153	0.573
Δ N Flow 10 m	−0.168	−0.007	0.401	0.034
Δ N Flow 50 m	−0.151	0.374	−0.476	−0.173
Δ N Flow 100 m	−0.185	−0.359	0.073	0.125

Eco-geographical variable	Marginality (51%)	Spec. 1 (48%)
Sei whale G.O. Sars 2004		
E Aspect	−0.181	0.005
N Aspect	0.064	0.015
Bathymetry	0.196	−0.017
Bottom complexity	0.55	−0.018
Easting	−0.33	−0.006
Northing	0.168	0.024
Bottom slope	0.437	−0.011
Δ Water level 10 m	−0.14	−0.343
Δ Water level 50 m	−0.14	−0.348
Δ Water level 100 m	−0.14	0.618
Δ Salinity 10 m	−0.168	−0.027
Δ Salinity 50 m	0.042	−0.097
Δ Salinity 100 m	−0.035	−0.073
Δ Temperature10 m	0.035	0.079
Δ Temperature 50 m	−0.116	0.017
Δ Temperature 100 m	0.088	0.069
Δ E Flow 10 m	−0.233	−0.052
Δ E Flow 50 m	−0.205	0.038
Δ E Flow 100 m	−0.192	0.017
Δ N Flow 10 m	−0.137	0.237
Δ N Flow 50 m	−0.120	−0.468
Δ N Flow 100 m	−0.125	0.267

Eco-geographical variable	Marginality (25%)	Spec. 1 (60%)	Spec. 2 (3%)	Spec. 3 (2%)
Sei whale Icelandic cruise 2001				
E Aspect	0.018	0	0.003	0.02
N Aspect	0.008	0	−0.001	0.007
Bathymetry	0.503	−0.001	0.002	−0.041
Bottom complexity	0.142	0.001	−0.002	0.03
Easting	−0.24	0.002	0.001	0.001
Northing	0.646	−0.001	−0.001	0.059
Bottom slope	0.112	−0.001	0.003	0.001
Δ Water level 10 m	0.011	−0.179	0.121	0.409
Δ Water level 50 m	0.02	0.778	−0.747	−0.458
Δ Water level 100 m	0.02	−0.602	0.635	−0.018

Table 3 (*continued*)

Δ Salinity 10 m	0.135	0.001	−0.002	−0.042
Δ Salinity 50 m	0.037	0	0.012	−0.203
Δ Salinity 100 m	−0.009	0.001	−0.006	0.201
Δ Temperature10 m	−0.04	−0.004	0.006	0.165
Δ Temperature 50 m	−0.067	−0.001	−0.004	0.024
Δ Temperature 100 m	−0.005	0.003	−0.015	0.035
Δ E Flow 10 m	0.176	0.005	−0.024	−0.257
Δ E Flow 50 m	0.267	−0.011	0.05	0.556
Δ E Flow 100 m	0.306	0.006	−0.031	−0.32
Δ N Flow 10 m	−0.084	0.001	−0.049	−0.122
Δ N Flow 50 m	−0.071	−0.008	0.111	0.101
Δ N Flow 100 m	−0.064	0.008	−0.061	0.033
Eco-geographical variable	Marginality (59%)	Spec. 1 (27%)	Spec. 2 (6%)	Spec. 3 (3%)
Sei whale Icelandic cruise 2003				
E Aspect	0.167	0.015	0.001	−0.013
N Aspect	−0.093	−0.012	0.011	0.005
Bathymetry	−0.17	0.096	0.128	−0.013
Bottom complexity	−0.151	0.01	−0.017	−0.029
Easting	−0.411	−0.011	0.027	−0.09
Northing	0.595	0.105	−0.02	0.033
Bottom slope	−0.072	0.046	0.004	0.038
Δ Water level 10 m	−0.084	−0.117	0.232	−0.001
Δ Water level 50 m	−0.084	0.386	−0.426	−0.108
Δ Water level 100 m	−0.084	−0.471	0.195	0.282
Δ Salinity 10 m	−0.057	−0.172	−0.082	−0.103
Δ Salinity 50 m	−0.342	0.151	−0.301	0.133
Δ Salinity 100 m	−0.344	0.004	0.175	−0.074
Δ Temperature10 m	−0.075	0.048	−0.067	0.093
Δ Temperature 50 m	−0.222	0.012	0.469	0.535
Δ Temperature 100 m	−0.161	0.159	−0.463	−0.671
Δ E Flow 10 m	−0.095	0.009	−0.009	0.083
Δ E Flow 50 m	−0.046	−0.174	0.118	0.128
Δ E Flow 100 m	−0.036	0.164	−0.066	−0.224
Δ N Flow 10 m	0.072	0.273	−0.129	−0.04
Δ N Flow 50 m	0.099	−0.525	−0.077	0.148
Δ N Flow 100 m	0.124	0.323	0.32	−0.146

1998; Baumgartner et al., 2001; Hamazaki, 2002; Moore et al., 2002; Reilly and Fiedler, 1994; Tynan et al., 2005; Waring et al., 2001). Both the spatial auto-correlation structure of the sightings data at spatial scales of 30–80 km and the PLS regression results show that oceanic habitat used by cetaceans in regions with ridges and/or seamounts has to be studied at equally high resolution as in shelf and shelf-break environments.

The analysis of responses of sperm and sei whale to the high-resolution flow and topographic data of the *G.O. Sars* cruise underlines the need to study cetacean habitats using concurrent 3D oceanographic transect data—dynamic variables which can allow for the identification of fine-scale habitat associations. The results point to the significance of interactions between seabed topography and surface and subsurface flow gradients as key habitat drivers to cetaceans along the MAR. Thus, resolving the three-dimensional habitat of cetaceans in oceanic ridge environments may require the use of complex statistical models that make it possible to identify discrete linkages between animals and physical variables. The results of the PLS regression and the ENFA are in line with the observations made during the *G.O. Sars* cruise that the recorded sperm and sei whale sightings were segregated with sperm whales being found mainly over the top of the ridge and sei whales mainly over the slopes. The results of the ENFA further showed that it is likely that the use of shallow and slope areas of the ridge may determine the marginality of both species as compared to the MAR at large, whereas the flow gradients may determine how specialised their habitat is.

The major aggregations of the two dominant large species of cetaceans at the MAR were generally found just north of the SPF in the area where SAIW was the dominant water mass in the upper ocean. Thus, the persistence of these aggregations will depend on the stability of the location of the SPF. The aggregation of sei whales at and just north of the CGFZ in 2004 overlaps spatially with the observations of the North Atlantic Sightings Survey (NASS-89) in July–August 1989, when large numbers of sei whales were recorded in the region (Sigurjónsson et al., 1991). It is still unclear whether

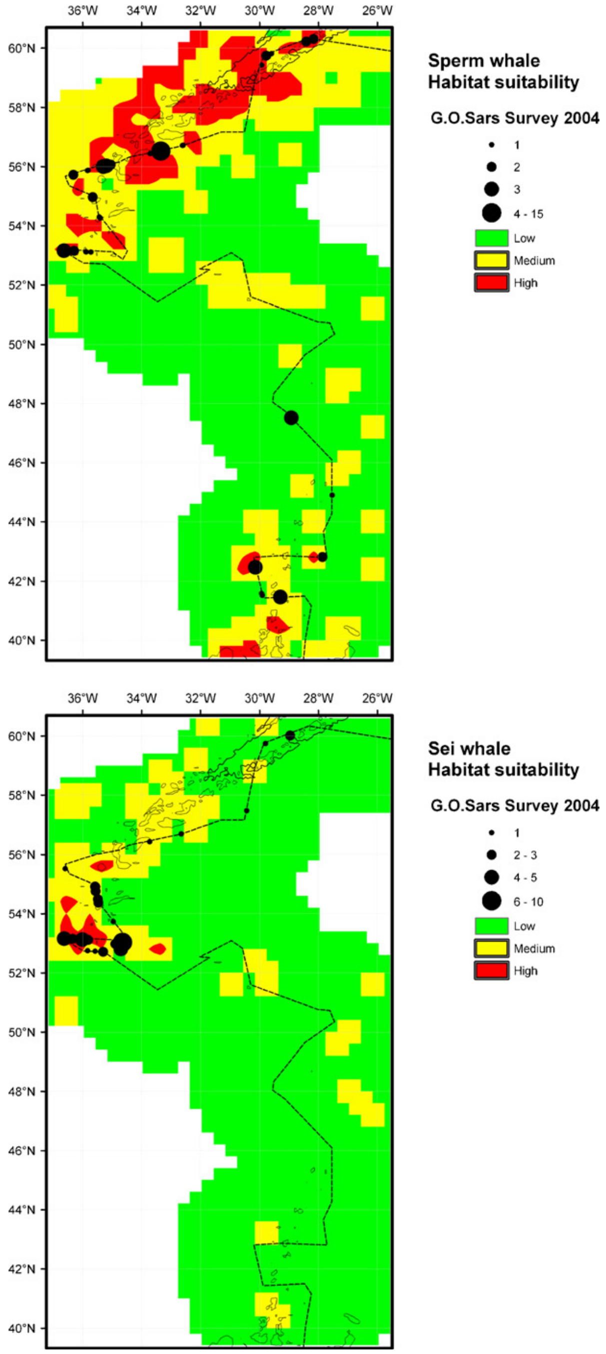

Fig. 7. The modelled habitat suitability of sperm and sei whales recorded during the *G.O. Sars* cruise. Habitat suitability values are split into moderate (50–66) and high (67–100) index scores. Sightings are indicated by black dots. Effort and 1500 m depth contour are indicated.

the differences between these two large-scale cruises and the two Icelandic cruises across the central part of the Reykjanes Ridge in June–July are due to changes in the overall distribution, and whether these changes are related to variations in the position of the SAIW–NAW front east of the Reykjanes Ridge. The low proportion of variance in the specialisation accounted for by the marginality factor for sei whales in 2001 may be explained by the limited coverage of the range of physical–oceanographic variables on the ridge during this cruise. The results of the PLS regression and the ENFA for the cruise in 2003, which covered a much larger sector of the MAR, gave similar results to the *G.O. Sars* cruise with respect to key habitat drivers. As for the cruise in 2003, habitat marginality of sei whales during this cruise was mainly determined by topographical variables, while habitat specialisation was mainly determined by surface fronts.

Sei whales are expected to feed in the upper 100 m of the water column; the linkage between feeding sei whales and flow gradients in the upper part of the water column may reflect a feeding association with concentrations of larger zooplankton, related to retention/advection processes north of the SPF Retention and advection may act to concentrate large zooplankton species over steep topography (Genin et al., 1994). During the *G.O. Sars* cruise concentrations of *Calanus finmarchicus* in the upper 100 m of the water column were limited to the area north of the CGFZ; thus overlapping with the concentration of sei whales (Gaard et al., 2008). Although maximum diving depths of sperm whales indicate deep diving and foraging at considerable depths, they do appear to be generalist feeders capable of utilising a wider range of prey items and depth strata than other deep diving ocean predators (Whitehead et al., 2003). Thus, the enhanced aggregation of prey in the upper water column north of the CGFZ may be effectively harvested by the sperm whales. Unfortunately, no detailed knowledge of the main prey to sperm whales is available for the MAR, but studies in the 1970s indicated a relatively higher proportion of fish to cephalopods off Iceland (Roe, 1969; Martin and Clarke, 1986).

Our analyses of fine-scale habitat features of the MAR have generated new knowledge of the significance of such features to cetaceans, knowledge that may help to manage fisheries and other human activities in the region. More importantly, the findings that steep topography and strong flow gradients in surface and subsurface layers may play an important role in meso-scale fluxes and in the transfer of energy to higher trophic levels along the MAR are of importance for future studies on the mechanisms controlling the maintenance of the unusually high secondary production, which the cetaceans capitalise on. Key questions to be addressed are whether the dense aggregations of zooplankton and fish/cephalopod prey in the northern part of the SPF are supported by presumed local production associated with the shallow thermocline over the whole SPF (Gaard et al., 2008), and whether such local production persists over sufficiently long periods to enhance secondary production in the same way as subsurface phytoplankton concentrations found over steep topography on the shelf (Richardson et al., 1998). Alternatively, as suggested by our results, the development of enhanced secondary production in the area may primarily be a function of advection and small-scale processes at seamounts downstream from the SPF.

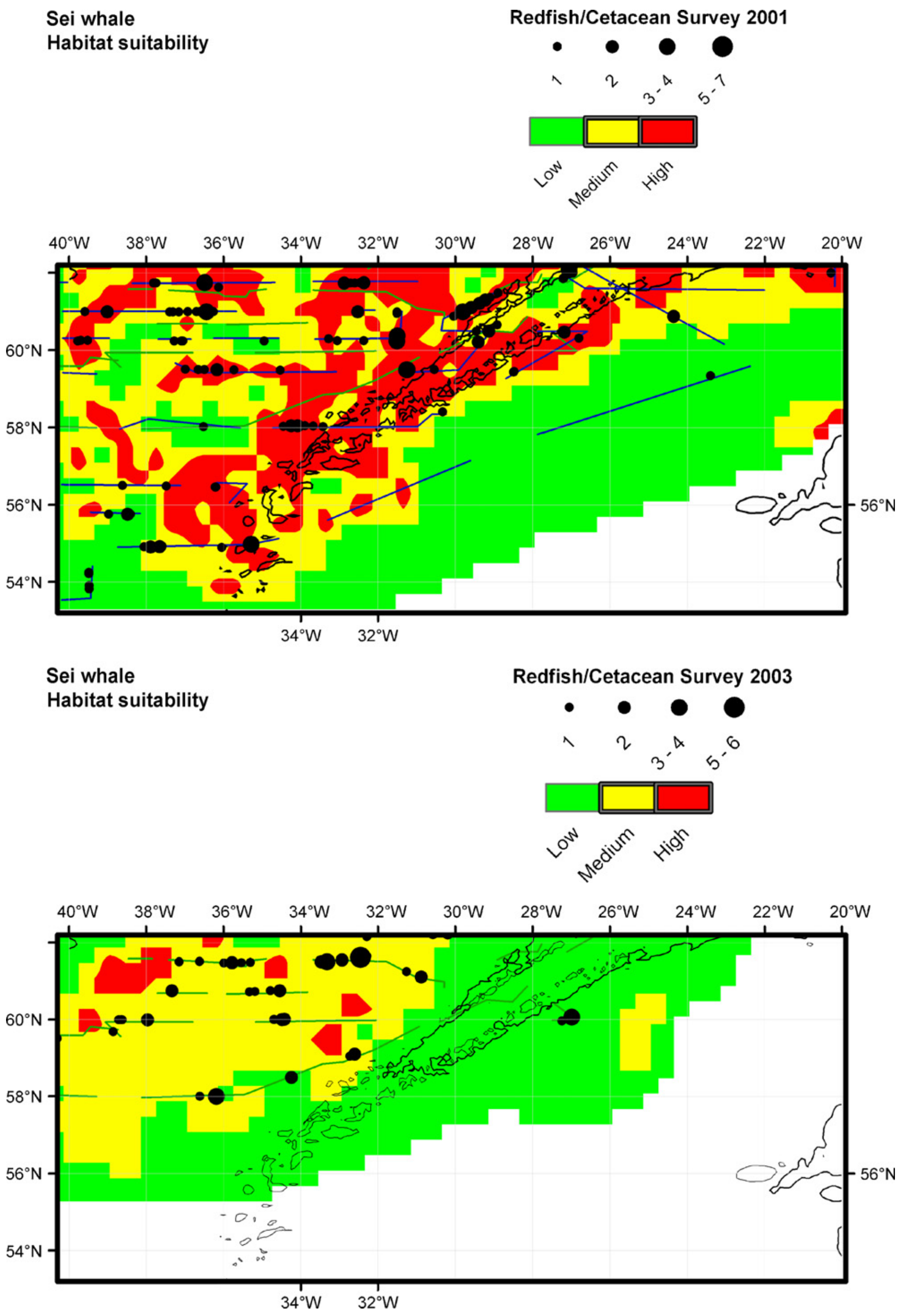

Fig. 8. The modelled habitat suitability of sei whales recorded during the Icelandic cruises in 2001 and 2003. Habitat suitability values are split into moderate (50–66) and high (67–100) index scores. Sightings are indicated by black dots. Effort and 1500 m depth contour are indicated.

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