Research papers

Distribution and relative abundance of humpback whales in relation to environmental variables in coastal British Columbia and adjacent waters

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ABSTRACT

Humpback whales are common in feeding areas off British Columbia (BC) from spring to fall, and are widely distributed along the coast. Climate change and the increase in population size of North Pacific humpback whales may lead to increased anthropogenic impact and require a better understanding of species–habitat relationships. We investigated the distribution and relative abundance of humpback whales in relation to environmental variables and processes in BC waters using GIS and generalized additive models (GAMs). Six non-systematic cetacean surveys were conducted between 2004 and 2006. Whale encounter rates and environmental variables (oceanographic and remote sensing data) were recorded along transects divided into 4 km segments. A combined 3-year model and individual year models (two surveys each) were fitted with the mgcv R package. Model selection was based primarily on GCV scores. The explained deviance of our models ranged from 39% for the 3-year model to 76% for the 2004 model. Humpback whales were strongly associated with latitude and bathymetric features, including depth, slope and distance to the 100-m isobath. Distance to sea-surface-temperature fronts and salinity (climatology) were also constantly selected by the models. The shapes of smooth functions estimated for variables based on chlorophyll concentration or net primary productivity with different temporal resolutions and time lags were not consistent, even though higher numbers of whales seemed to be associated with higher primary productivity for some models. These and other selected explanatory variables may reflect areas of higher biological productivity that favor top predators. Our study confirms the presence of at least three important regions for humpback whales along the BC coast: south Dixon Entrance, middle and southwestern Hecate Strait and the area between La Perouse Bank and the southern edge of Juan de Fuca Canyon.

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1. Introduction

Humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific feed from California to western Alaska (Perry et al., 1990). They are common off British Columbia (BC) from spring to fall and are widely distributed along the coast (Ford et al., 2010; Gregr et al., 2000; Williams and Thomas, 2007).

Until recently, most of what was known about humpback whales in coastal BC originated from whaling records. Humpback whales, as well as sperm (*Physeter macrocephalus*), fin (*Balaenoptera physalus*), sei (*Balaenoptera borealis*) and blue (*Balaenoptera musculus*) whales were intensively hunted during commercial whaling, between 1908 and 1967 (Gregr et al., 2000; Nichol and Heise, 1992). Additional information obtained mainly through

photo-identification studies have shown movements and migratory destinations and provided estimates of abundance (Calambokidis et al., 2008; Darling et al., 1996; Ford et al., 2009; Rambeau, 2008; Urbán-Ramirez et al., 2000). The Canadian Department of Fisheries and Oceans (DFO) maintains a catalog of humpback whales seen in BC waters containing over 2000 individuals photographed between 1989 and 2006. In recent years, systematic line transect surveys have also been conducted to estimate cetacean abundance, including humpback whales, in inshore BC waters (Williams and Thomas, 2007).

Concerns about the effect of climate change (IPCC, 2007) on the recovery of North Pacific humpback whales (Calambokidis and Barlow, 2004; Calambokidis et al., 2008) cannot be properly addressed without a better understanding of species–habitat relationships. Unfortunately, such studies on humpback whales and their habitat are still rare in most regions, including the feeding grounds of the eastern North Pacific. Humpback whales seem to be associated with bathymetry in the Bering Sea (Moore et al., 2002) and off northern Washington coast, where they also

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prefer relatively colder waters in comparison to other offshore species found in the area (Calambokidis et al., 2004). In the northern California Current System, sea surface temperature (SST), depth and distance to the alongshore upwelling front were the most important variables in a multiple logistic regression model for humpback whales during late spring 2000 and sea surface salinity, latitude and depth were the most important predictors during summer of the same year (Tynan et al., 2005). Depth and distance, SST and fluorescence in the top 50 m of the nearest Aleutian pass resulted in the most significant correlations with humpback whale occurrence along the Aleutian Islands in 2000 and 2001 (Sinclair et al., 2005). Nevertheless, additional habitat modeling studies involving multi-year surveys and a wide range of explanatory variables are necessary to identify what oceanographic processes influence the distribution of humpback whales.

Gregr and Trites (2001) produced predictive habitat models for five whale species, including humpback whales, in BC coastal waters, using whaling records for the period 1948–1967 and six predictor variables (month, depth, slope, depth class and climatologies of sea surface temperature and salinity). Their humpback whale models showed low correlation coefficients due to either small sample size or because of relatively weak association with the predictor variables. However, their annual model confirmed strong association of humpback whales with coastal waters (Gregr and Trites, 2001). Inferences of predictive habitat models are limited to the range of data (e.g. Hamazaki, 2002; Redfern et al., 2006), so habitat models based on contemporary data are necessary to make inferences about the present distribution and habitat use of humpback whales in BC waters. This is vital for providing scientific advice towards identifying critical habitat of humpback whales under DFO guidelines.

The currents and ocean structure along the BC coast, particularly in the semi-protected northern shelf region, are shaped by deep-sea processes, tides, winds and estuarine processes (Thomson, 1981). Therefore, waters with coastal, offshore or mixed properties may be found in the region, resulting in a dynamic oceanographic environment. In light of this, it is desirable to implement habitat models that include not only fixed physiographic variables, but also other potentially important predictors, such as primary productivity and proximity to eddies and fronts, at different spatial and temporal scales.

We sought to investigate the distribution and relative abundance of humpback whales in BC waters in relation to a range of environmental variables, including oceanographic and remote sensing data, using Geographic Information System (GIS) and generalized additive models (GAMs). We hypothesize that the higher densities of humpback whales will be positively correlated with areas of enhanced biological productivity through physical forcing.

2. Material and methods

2.1. Data collection

2.1.1. Surveys

Data on cetacean distribution were obtained during six ship surveys conducted between 2004 and 2006 off the coast of British Columbia, including the waters of Queen Charlotte Sound, Hecate Strait and Dixon Entrance, and the offshore waters on the west coast of the Queen Charlotte Islands, Vancouver Island and Washington State (Fig. 1). Five surveys were conducted during spring and fall months aboard vessels from the Department of Fisheries and Oceans (DFO), Canada (Ford et al., 2010). The first three of these surveys were part of the 'Structure of Populations,
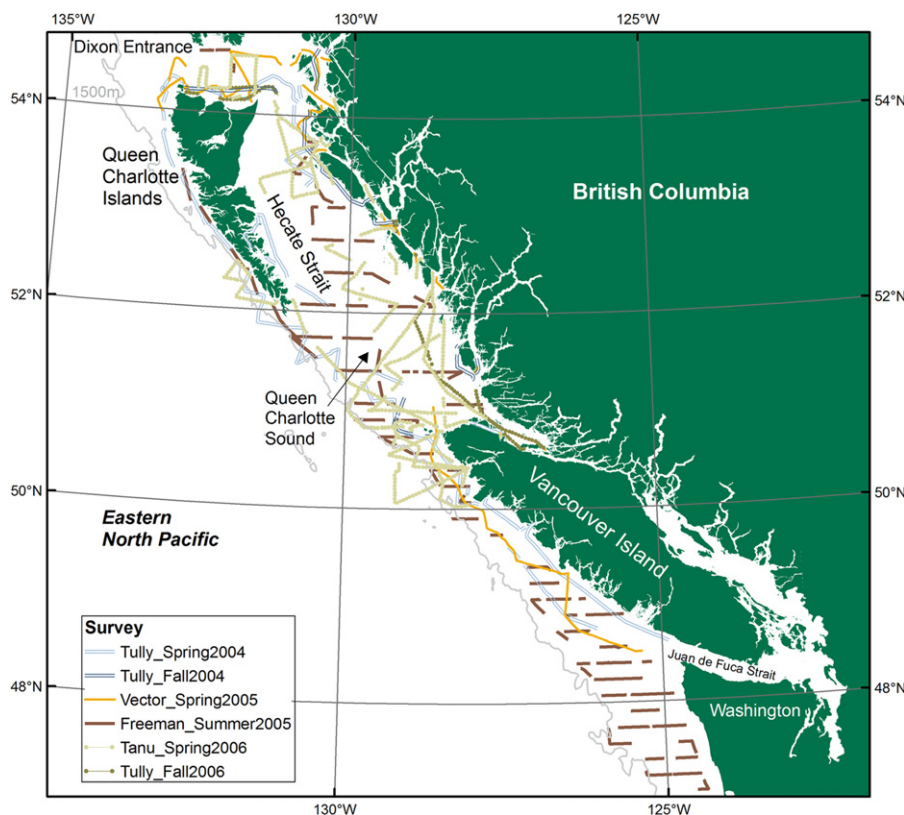

Fig. 1. Cetacean surveys conducted off the coast of British Columbia between 2004 and 2006. On effort transect lines are depicted for each survey, along with the 1500-m isobath in light gray.

Table 1
Survey periods and vessels used in the collection of cetacean sighting data.

Cruise	Year	Season	Period	Vessel
1	2004	Spring	10–23 May	CCGS *John P. Tully*
2	2004	Fall	14–21 October	CCGS *John P. Tully*
3	2005	Spring	10–21 May	CCGS *Vector*
4	2005	Summer	19 July–10 August	NOAA *Miller Freeman*
5	2006	Spring	29 April–20 May	CCGS *Tanu*
6	2006	Fall	21–29 October	CCGS *John P. Tully*

Levels of Abundance, and Status of Humpbacks' (SPLASH) project (Calambokidis et al., 2008), aimed primarily at photo-identification and genetic studies. The only summer survey, in July–August 2005, was part of a joint Canadian and U.S. Pacific hake survey aboard the NOAA ship *Miller Freeman* (MF), which was used as a platform of opportunity for cetacean observations. Survey periods and vessels are detailed in Table 1.

2.1.2. Effort and sighting data

Although surveys were non-systematic, searching effort followed strict protocols while vessels were in transit. Trained observers on port and starboard scanned with 7×50 Fujinon binoculars and naked eye from about $10°$ on the other side of the ship's bow to $90°$ on their side. Fujinon 25×150 binoculars ("big eyes") were occasionally used by the primary observers, and tended to be used by auxiliary observers to help with species identification or group size estimation. The observers rotated through port, starboard and data recorder positions every 30 or 40 min, depending on the cruise, with a minimum 2 h rest period which varied according to the number of extra observers on the cruise. For the MF cruise, the only two observers that were available at each leg worked together, with one observer reporting sightings to the other, who acted as data recorder. Port and starboard positions were switched every 30 min, and resting took place during fishing operations and CTD casts.

The ship's position, course and speed were continuously recorded on a laptop computer connected to the ship's GPS unit. Sightings and environmental conditions were recorded on datasheets on the first three cruises and in Logger 2000[1] on the remaining cruises. Sighting data included time, location, ship's true heading, number of reticles from the horizon to the sighting, bearing to the sighting, species identification, number of animals (best, minimum and maximum estimates), sighting cue and other comments. Weather and sea conditions (e.g. Beaufort sea state, swell height and visibility) were recorded on every observer rotation and when conditions changed. Searching effort was carried out only in good conditions, i.e., up to Beaufort 5 and with visibility of 3 nautical miles or higher. Observation platforms ranged in height from 8.2 m (*Vector*) to 15.5 m (*John P. Tully*).

Radial distance to each sighting was calculated from binocular reticle readings and platform height (Lerczak and Hobbs, 1998, erratum), and corrected based on distance to land when the coastline was at shorter distances than the horizon. The location of each whale group was then estimated from bearing and radial distance to the sighting and the ship's true heading at the moment of the sighting. On-effort sightings and tracklines were imported into geodatabases in ArcGIS 9.2 (ESRI, Redlands, CA). Tracklines were divided into 4 km segments. Segment length was chosen to closely match the resolution of the remote sensing data. If a segment at the endpoint of a trackline was shorter than 2 km, it was added to the previous segment; otherwise, it was left as a

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[1] Software developed by the International Fund for Animal Welfare (IFAW) to promote benign and non-invasive research.

separate segment. Each sighting was assigned to the closest segment. Segments were therefore the sampling unit, and the number of whales per segment represented encounter rates.

2.2. Environmental data

A series of GIS layers were produced or imported into ArcGIS containing physiographic, remote sensing and climatological datasets on a BC Albers equal area projection (Table 2).

Bathymetry data were obtained from a 75-m digital elevation model (DEM) produced by the Geological Survey of Canada (Pacific), Natural Resources Canada, Sidney, BC. A 250-m DEM of the Cascadia region (⟨http://geopubs.wr.usgs.gov/open-file/of99-369/⟩) was also used for the southern portion of the study area not covered by the first dataset. Bathymetric slope and 100-m and 200-m contour lines were originated from the DEMs using Spatial Analyst's slope and contour tools, respectively, in ArcGIS.

Chlorophyll *a* (chl-*a*) concentration (mg/m^3) was used as a proxy for primary productivity, and was obtained as seasonal, monthly and 8-day images from the Moderate Resolution Imaging Spectroradiometer (MODIS) onboard the Aqua satellite (available at ⟨http://oceancolor.gsfc.nasa.gov/⟩). These chl-*a* images consisted of the binned product, a 4.63 km resolution dataset stored in an equal area projection. Each image was re-projected, clipped and exported as point data to an ascii file using the SeaDAS 5.1 software, an image analysis package for ocean color data. Subsequently, each file was imported to a point geodatabase in ArcGIS and converted to raster. In addition, two mapped (equal-angle grid) chl-*a* image products were also downloaded: a MODIS rolling 32-day ~ 4 km composite and an 8-day MODIS-SeaWiFS (Sea-viewing Wide Field-of-view Sensor) ~ 9 km merged image. These were imported to ArcGIS using the Marine Geospatial Ecology Tools (MGET) (Roberts et al., 2010). The merged product has potentially increased image coverage, a desirable feature particularly with 8-day images which tend to be more affected by cloud coverage. Maximum chl-*a* concentration values in mapped images are scaled down to 64.56 mg/m^3, whereas the original maximum values were kept in the binned images.

Sea surface temperature (SST) was obtained as seasonal, monthly and 8-day MODIS 4.63 km binned data, and processed in the same way as the chl-*a* binned product. Fronts were identified in the SST raster images using MGET, which implements the Cayula and Cornillon (1992) single-image edge detection algorithm. Custom settings in the parameters of the algorithm which produced better results with the MODIS images included a histogram window size of 16×16 and a histogram window stride of 4 pixels. Weak fronts with mean temperature difference of less than $0.375 °C$ were not included. The fronts in the output rasters were converted to polylines to allow calculation of Euclidean distances between each effort segment and the closest front (Fig. 2).

The Oceanic Front Probability Index (NOAA CoastWatch Program) is an experimental dataset produced by applying an edge detection algorithm to daily SST images from the Geostationary-orbiting Operational Environmental Spacecraft (GOES) satellites (Breaker et al., 2005). The index is calculated as the number of times a pixel is classified as a front (gradient $> 0.375 °C$) divided by the number of cloud free days for the given time period. These data were acquired as monthly composites mapped to an equal angle grid (~ 5.5 km resolution) in Arcview gridded format. Each file was then imported to an ArcGIS raster and re-projected.

Monthly and 8-day net primary production (NPP) was obtained from the Ocean Productivity website (⟨http://www.science.oregonstate.edu/ocean.productivity/⟩). The selected product uses the Vertically Generalized Production Model (VGPM) (Behrenfeld and Falkowski, 1997) as the standard algorithm, where net primary production is a function of chl-*a*, available light and the photosynthetic efficiency which is temperature-dependent. The resulting

Table 2
Environmental variables sampled along survey segments and their corresponding names and transformation (if any) for the data analyses. Note that not all variables were considered in the modeling process (see methodology for more details).

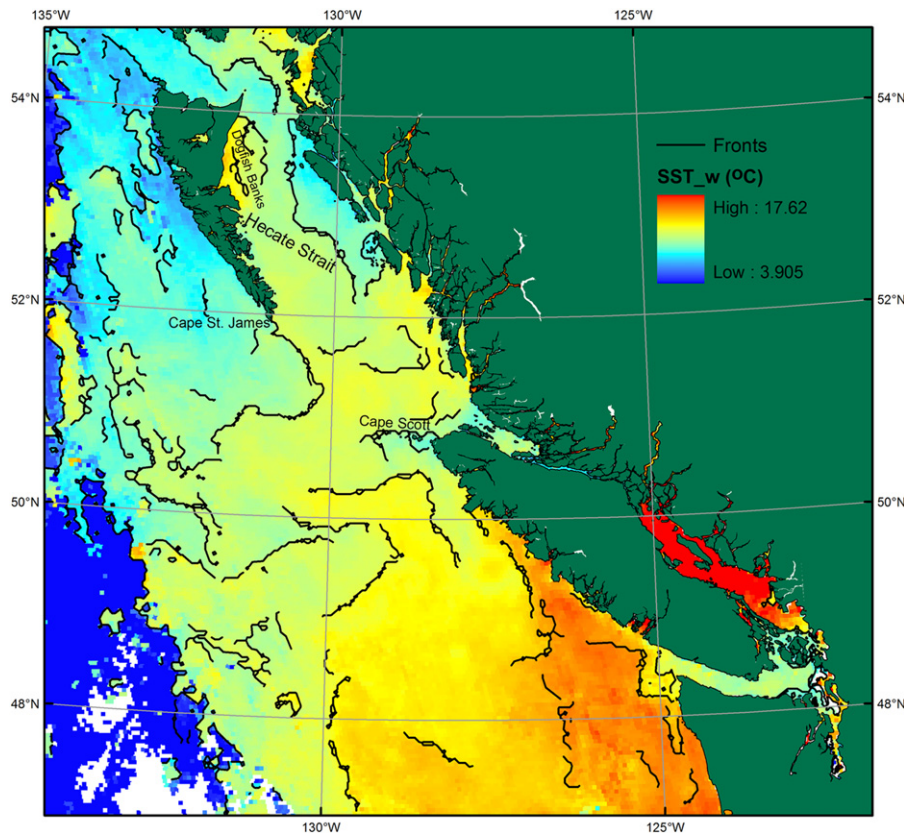| Environmental variable	Unit	Temporal resolution	Transformation	Reference name (s)
Latitude	m	–	none	Lat
Longitude	m	–	none	Lon
Depth	m	–	log	logDepth
Slope	deg.	–	log	logSlope
Distance to land	m	–	square root	sqrtdistland
Distance 100-m isobath	m	–	square root	sqrtcontour100 m
Distance 200-m isobath	m	–	square root	sqrtcontour200 m
Sea surface temperature	°C	Seasonal	none	SST_s
		Monthly	none	SST_m
		8-day	none	SST_w
Distance to SST fronts	m	8-day	square root	sqrtdistfront_w
Front probability index	prob.	Monthly		sqrtfrontspi_m
Chlorophyll a	mg/m^3	Monthly	log	logchla_m
				logchla_mlag
		8-day	log	logchla_w
				logchla_wlag
				logchla_wmerged
				logchla_wmerged_lag
Net primary production	mgC/m^2/d	Monthly	log	logNPP_m
				logNPP_mlag
		8-day	log	logNPP_w
				logNPP_wlag
Sea level anomaly	m	Monthly	none	SLA
Tidal speed	RMS	Climatology	log	logtidal_speed
Salinity (model)		Climatology	exponential	expsal_surf
			exponential	expsal_bottom
Temperature (model)	°C	Climatology	none	temp_surf
			none	temp_bottom

Fig. 2. Thermal fronts identified on an 8-day SST raster of 16–23 May 2004.

~9 km resolution NPP estimates were based on SeaWiFS chl-a values and on sea surface temperature from the Advanced Very High Resolution Radiometer (AVHRR).

Sea surface height deviation (SSHd) from the AVISO (Archiving, Validation and Interpretation of Satellite Oceanographic data) program was obtained as monthly averages at a 0.25° resolution. SSHd,

or sea level anomaly, is the difference between measured SSH and the expected mean SSH (see Ducet et al., 2000 for more details).

Five additional explanatory variables were extracted from datasets in a circulation model for the Northeastern Pacific Ocean maintained by M. Foreman (Institute of Ocean Sciences, Sidney, British Columbia). These include the root mean square of tidal speeds (RMS tidal speed) and four climatologies: bottom and surface summer temperature and bottom and surface summer salinity. These data were imported to point geodatabases in ArcGIS and interpolated to 500 m^2 resolution rasters using Spatial Analyst's inverse distance weighting (IDW).

2.3. Sampling environmental data

The GIS layers containing the environmental variables were sampled at each segment in two different ways: (1) all distances to features were measured as the shortest straight line distance from the midpoint of the segment to the feature; and (2) all rasters were sampled as the mean value of 5 points, i.e., the values extracted at the midpoint and at the vertices of a 2×2 km box placed over the midpoint following the segment's orientation angle. This latter approach aimed at providing a more balanced sampling for those segments falling near the margins of adjacent raster pixels with different values and whose searching effort certainly included at least part of them. The chl-*a* and NPP layers were sampled according to their corresponding time periods but also with time lags that included the previous month for the monthly data and a 2-week prior for the 8-day data.

Some environmental data to be used as explanatory variables in the models were not available for the inland waters of the Inside Passage and adjacent channels; therefore, segments and observations made in those areas were not included in the analyses.

2.4. Data analyses

2.4.1. Statistical modeling

Exploratory data analysis was conducted to identify outliers (e.g. boxplots) and other potential problems in the data that could affect model fitting (Zuur et al., 2007). Most explanatory variables were transformed to attain an even spread of values. Depth, slope, chl-*a* and NPP values were log-transformed and distances to features were square-root transformed (Table 2). Additionally, pairplots of all explanatory variables were produced to identify correlated variables. The variable with lower spatial/temporal resolution or coverage was dropped from further analyses when two variables were found to be highly correlated ($r > 0.75$). This approach avoided multicollinearity, which could have led to model performance issues (Zuur et al., 2007), and also identified and eliminated covariates that were not ecologically meaningful if put together in the same model, given their similar explanatory power (e.g. monthly and 8-day SST).

Humpback whale counts were modeled as a function of environmental variables using GAMs (Hastie and Tibshirani, 1990). GAMs are semiparametric models where the dependent variable is linked to an additive predictor through a nonlinear link function. The goal was, therefore, to investigate nonlinear relationships between humpback whale distribution and relative abundance and the environmental variables. A quasi-Poisson model with variance proportional to the mean was used to account for overdispersion. With a logarithmic link function, the general model structure was

$$\log(E[n_i]) = \sum_k s_k(z_{ik}) + \text{offset}(\log[\text{seg\_length}]_i)$$

where s_k are smooth functions of the explanatory covariates, and z_{ik} is the value of the kth explanatory covariate in the ith segment. The length of each segment was included as an offset, so that the encounter rates could be modeled as count data.

GAMs were fitted using the mgcv package v. 1.4-1 for the statistics program R (Wood, 2001). The degree of smoothness of model terms was estimated as part of fitting using penalized regression splines and parameters selected by generalized cross validation (GCV). Due to the tendency of GAMs to overfit, the argument gamma=1.4 was used (Kim and Gu, 2004), inflating the effective degrees of freedom by 1.4 in the GCV score (Wood, 2006). Also, the basis dimension parameter, k, was set to 8, thereby limiting the maximum allowable degrees of freedom of each term to 7 and further avoiding overfitting by restraining the wiggliness of the smoothing functions of the model terms, which leads to more ecologically defensible functions. An initial 3-year model combining all six surveys was fitted and, given the findings of this model, three individual year models, each containing two surveys, were also fitted to the data.

The mgcv package does not have a function to account for missing values of the covariates; therefore, segments containing missing values of one of the explanatory variables were automatically excluded from model fitting.

Model selection was based on GCV scores (Wood, 2001, 2006), percentage deviance explained and a visual examination of residual plots, and followed a backfitting procedure. First, model terms were dropped, one at a time, if the approximate 95% confidence interval of the smoothing function contained zero everywhere and, if by dropping the term, the GCV score also dropped. Next, each remaining term was also tested for lower GCV values and improvements in deviance explained and residual plots. Very small increases in GCV scores did prevent a variable from being dropped if it resulted in a simpler model with similar or improved explanatory power, as measured by the percentage deviance explained or if an improvement in residual plots was observed. Competing models were not compared with a formal statistical test either because the models started with different sets of variables (one of the explanatory variables was replaced by another variable which was highly correlated), or because the models were not nested.

Spatial autocorrelation in the residuals was investigated through a variogram analysis using the geoR package v. 1.6-22 for R (Ribeiro and Diggle, 2001). One of the model assumptions is that residuals are independently distributed. Violation of this assumption, which would suggest the need for a different type of model, was assessed by comparing the empirical variogram of deviance residuals with the Monte Carlo envelope of empirical variograms computed from 300 independent random permutations of the residuals, holding the corresponding locations fixed (Diggle and Ribeiro, 2007).

2.4.2. Predicting encounter rates of humpback whales

Maps of predicted encounter rates of humpback whales were produced to visually verify whether predicted areas of high whale densities matched with the observed distribution. A 4.63×4.63 km grid was generated for the study area and values for all explanatory variables selected in the 3-year model were extracted at the midpoint of each grid cell by overlaying the corresponding GIS layers on the grid. The resolution of the grid was chosen to be the same as the best resolution remote sensing data used. The outer boundary of the prediction grid was defined by fitting a line to locations in the 2500-m isobath (which is close to the largest depth values sampled) and the most offshore transect lines. Encounter rates were predicted for each grid cell by the 3-year model with the *predict.gam* function in mgcv and plotted for visualization. Three time periods corresponding to the larger surveys in each year were selected for prediction. Explanatory variables based on remote sensing data were obtained

from GIS layers that matched those time periods. Single survey or year models were not used for prediction because the limited range of some explanatory variables in the fitted models would result in extrapolation and unreliable predictions when applied to the whole study area.

3. Results

3.1. Surveys

Humpback whales were observed on all surveys throughout the study area (Fig. 3), and were the most commonly sighted large cetacean species in BC, followed by fin whales. The largest whale concentrations during individual surveys were observed east of Moresby Island (in the Queen Charlotte Islands=QCI), over the edge of the trough located in the middle of Hecate Strait and in the southern portion of Dixon Entrance (north of QCI).

A total of 541 humpback whale groups and 1041 individuals were recorded during 2167 segments of searching effort. However, due to missing values of some environmental variables, 2041 survey segments (8144 km) were used in the analyses (Table 3).

3.2. Generalized additive models (GAMs)

The combined 3-year GAM containing data from the six surveys resulted in 12 selected explanatory variables, an adjusted R-square of 0.27 and 39.2% of explained deviance (Table 4). All smooth functions for this model indicated nonlinear relationships (Fig. 4). The smooth function for latitude (which represents the variation of the fitted response surface holding all other predictors fixed)

showed a marked relationship with humpback whale encounter rates. A first peak occurred between 47°30′ and 48°30′N, off the Olympic Peninsula, followed by a drop that reached the lowest value around 50°N, just south of the Brooks Peninsula. Encounter rates then steadily increased northward, with latitude having a positive effect again around 52°20′N, the same latitude of Juan Perez Sound. The highest fitted values were obtained north of 54°N (Fig. 4), the area corresponding to Dixon Entrance.

Humpback whales appeared to be strongly associated with bathymetry. Encounter rates were higher between 50 and 200 m of depth (peak around 110 m) and, accordingly, were also higher around 2.5 km and dropped with increasing distance from the 100-m isobath. Slope was also significant, but the functional form was not so conspicuous. The steep curve increase from flat bottom was likely an artifact of the variable transformation, given that it represents a variation of only 0.3°, and has considerable uncertainty associated with it (see 95% confidence limits). After

Table 3
Total number of humpback whale groups and individuals sighted on each cruise along the survey segments used in the models. Note that segments with missing environmental variables are not accounted for here.

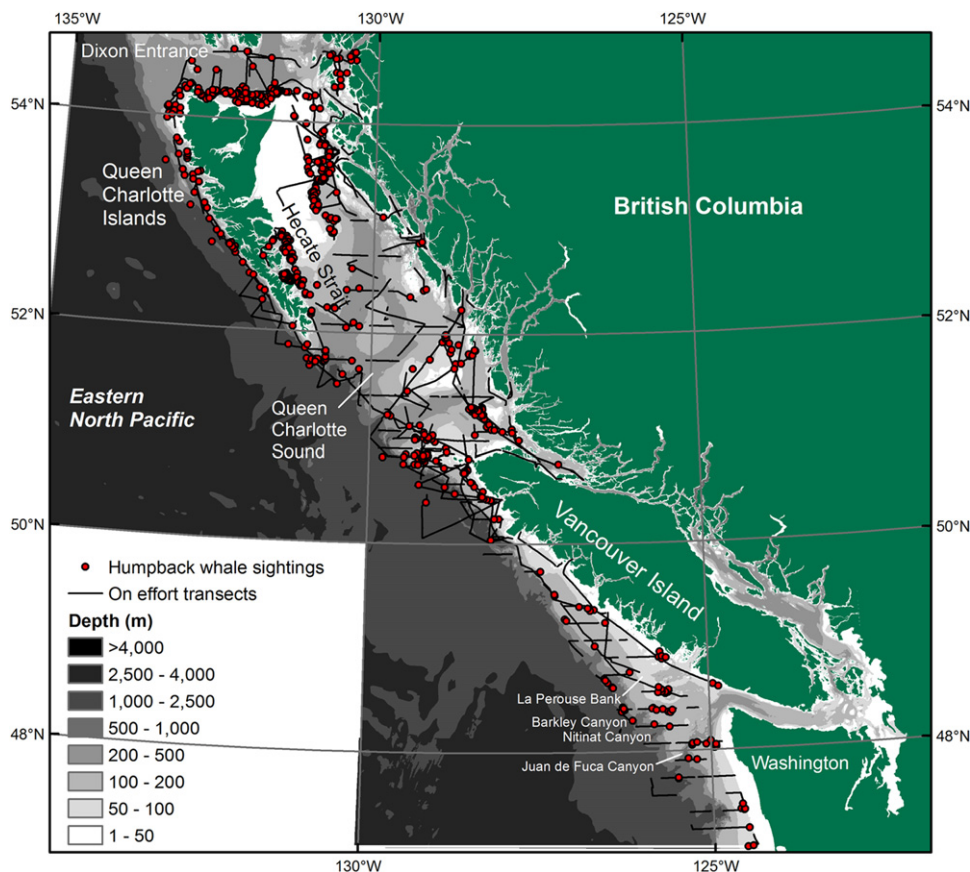| Cruise	Segments	HW groups	HW individuals
1	420	167	308
2	103	61	197
3	232	44	64
4	532	88	127
5	663	145	294
6	91	29	43
Total	2041	534	1033

Fig. 3. Locations of humpback whale groups (dots) sighted during six surveys conducted between 2004 and 2006. Survey tracklines and bathymetry are also shown.

Table 4

GAM results for the combined 3-year and the individual year models. The selected explanatory variables in each model are identified as factors (*F*) or smooth functions (*S*) along with their estimated degrees of freedom in parentheses and approximate *p*-value significance. Empty spaces correspond to non-selected variables and dashes represent variables that were not part of the initial model. Percent deviance explained and R^2 adjusted for all models are also presented.

Variable	3-year GAM	2004	2005	2006
Year	**F**	–	–	–
Month	**F**[*]		–	–
Lat	**S** (6.47)	**S** (6.38)	**S** (6.33)	**S** (6.55)
logDepth	**S** (4.73)	**S** (6.54)	**S** (4.39)	**S** (6.86)
logSlope	**S** (6.25)	**S** (6.95)	**S** (4.06)	**S** (6.76)
sqrtdistland				**S** (4.76)
sqrtdist100 m	**S** (4.26)	**S** (5.46)	**S** (1) [l]	**S** (4.92)
sqrtdist200 m		**S** (6.79)		**S** (6.4)
logchla_m	**S** (6.2)	–	–	**S** (7)
logchla_mlag		**S** (6.94)		**S** (4.66)*
logchla_wmerged			**S** (2.86)**	**S** (6.15)
logNPP_mlag	**S** (6.09)			**S** (5.63)
logNPP_wlag		**S** (6.11)	–	
SST_w	**S** (6.85)	–		**S** (5.93)
sqrtdistfront_w	**S** (5.8)	**S** (6.59)	**S** (5.53)	**S** (6.94)
sqrtfrontspi_m				
SLA		**S** (6.35)	**S** (6.83)	
logtidal_speed			**S** (6.46)	–
expsal_surf	**S** (5.92)	**S** (6.97)	**S** (6.85)	**S** (6.57)
temp_surf	**S** (4.77)		**S** (2.65)	**S** (6.30)
% Deviance explained	39.2	75.5	42	62.9
R^2 adjusted	0.27	0.76	0.31	0.65

All terms in bold = $p < 0.001$; l = linear term.

[*] $p < 0.05$.

[**] $p < 0.01$.

that point, the curve slowly decreased to around the 4.5° mark and started increasing again towards the steeper slopes (Fig. 4).

The smooth curve for monthly chl-*a* appeared to indicate a slight increase in encounter rates with increasing chl-*a* values, up to at least 20 mg/m^3, with the middle peak corresponding to about 2.7 mg/m^3. The relationship with lagged monthly NPP, on the other hand, indicated higher concentrations of whales in areas with relatively lower productivity in the previous month (peak around 990 mgC/m^2/day). The 8-day SST showed a negative effect at lower temperatures, with slightly higher encounter rates at around 8 and 11 °C, and the climatology of summer surface temperature presented a peak around 13 °C. The function for distance to weekly fronts suggested an initial drop in encounter rates from zero to 2.5 km, followed by an increase to around 15 km and a further increase with higher distances from the fronts (Fig. 4). This last increase was likely caused by the very high encounter rates observed close to shore, east of Moresby Island during the survey in May 2004, and the absence of fronts detected nearby. However, detecting fronts in nearshore areas with several fjords was problematic given the spatial and temporal resolution of the SST data used.

Higher humpback whale encounter rates were also associated with higher climatology values of summer surface salinity. The categorical variables year and month were both selected. The partial for year indicated a significant negative effect of 2005 relative to 2004 and 2006, whereas the partial for month resulted in significant effects of May and July. The suggested differences among years in the 3-year model motivated the fitting of the individual year models.

The 2004 GAM resulted in 10 explanatory variables, an adjusted *R*-square of 0.76 and 75.5% deviance explained (Table 4). The estimated smooth functions of latitude, slope and distance to the 100-m isobath were quite similar to those obtained in the 3-year model (Fig. 5). The function for depth, however, indicated higher

humpback whale encounter rates between 120 and 400 m. The lagged monthly chl-*a* curve showed two peaks, one at around 1.65 mg/m^3 and a higher one around 16 mg/m^3. The smooth term for the 8-day NPP with a two week lag was also similar in shape to the lagged monthly NPP from the 3-year model, including a peak around the same value, except for the clear drop at values larger than 3000 mgC/m^2/day. Encounter rates of whales increased with increasing distance to fronts and with higher values of summer surface salinity. There were also more whales either around 13 km or further than 40 km from the 200-m isobath. The smooth term for SSH deviation reached a peak just below zero and then increased again at positive values (Fig. 5).

The 2005 GAM resulted in 10 explanatory variables, an adjusted R-square of 0.31 and 42% deviance explained (Table 4). Latitude presented a similar functional form to the previous models (Fig. 6). Humpback encounter rates were higher at depths up to about 120 m and greater than about 600 m, and decreased linearly with distance from the 100-m isobath. The smooth curve of slope peaked around 1° and remained relatively constant. Higher encounter rates were also associated with higher values of chl-*a* (8-day merged), areas of higher summer surface temperatures and, apparently, faster tidal speeds. The curve for distance to fronts remained relatively constant at closer distances, with a slight peak around 15 km and a conspicuous drop afterwards. SSH deviation yielded a wiggly curve with three peaks and summer surface salinity had a negative effect at lower values and stabilized around 30.6 psu (Fig. 6).

The 2006 GAM resulted in 10 explanatory variables, an adjusted *R*-square of 0.65 and 62.9% deviance explained (Table 4). Humpback whale encounter rates in 2006 were lower on the segments south of 51°N and higher on the northernmost ones, as in the previous years (Fig. 7). The SST curve suggested lower encounter rates at temperatures below 8 °C, however with much uncertainty due to few samples in that range. Encounter rates were higher around 150 and 500 m of depth, and apparently decreased sharply over the steepest slopes. The smooth terms of lagged monthly and 8-day merged chl-*a* yielded similarly shaped curves suggesting higher encounter rates at both lower and upper ranges, with a peak in the middle for the latter. The curve of monthly chl-*a* also indicated there were more whales at the lower range of values, but with an apparent (given the wide confidence interval) decrease at the upper range. The lagged monthly NPP resulted in a bi-modal curve almost opposite in shape to the lagged monthly chl-*a*. The shape of the 'distance to 100-m' curve was similar to its equivalent term in the 3-year and 2004 models. The smooth term for distance to land and to the 200-m isobath showed peaks in encounter rates around 40 and 32 km, respectively. Higher humpback encounter rates were also associated with areas having an average summer surface temperature around 13 °C, similarly to the 3-year model, and an average summer surface salinity around 31.9 psu. The smooth curve of distance to fronts indicated that whales were more common close to fronts (under 2.5 km), and less common around 35 km and beyond 65 km (Fig. 7).

There was no evidence of significant spatial autocorrelation on the residuals of any of the models, as the semivariance was within the boundaries of the Monte Carlo envelopes on all variograms (Fig. 8A–D).

3.3. Predicted encounter rates

The predicted humpback whale encounter rates from the 3-year GAM compare favorably with the overall distribution patterns observed during the surveys (Fig. 9A–C). All areas where the highest concentrations were observed were consistently identified in the predictions. There seems to be some edge effect on the northernmost limit of the map, which could be fixed by
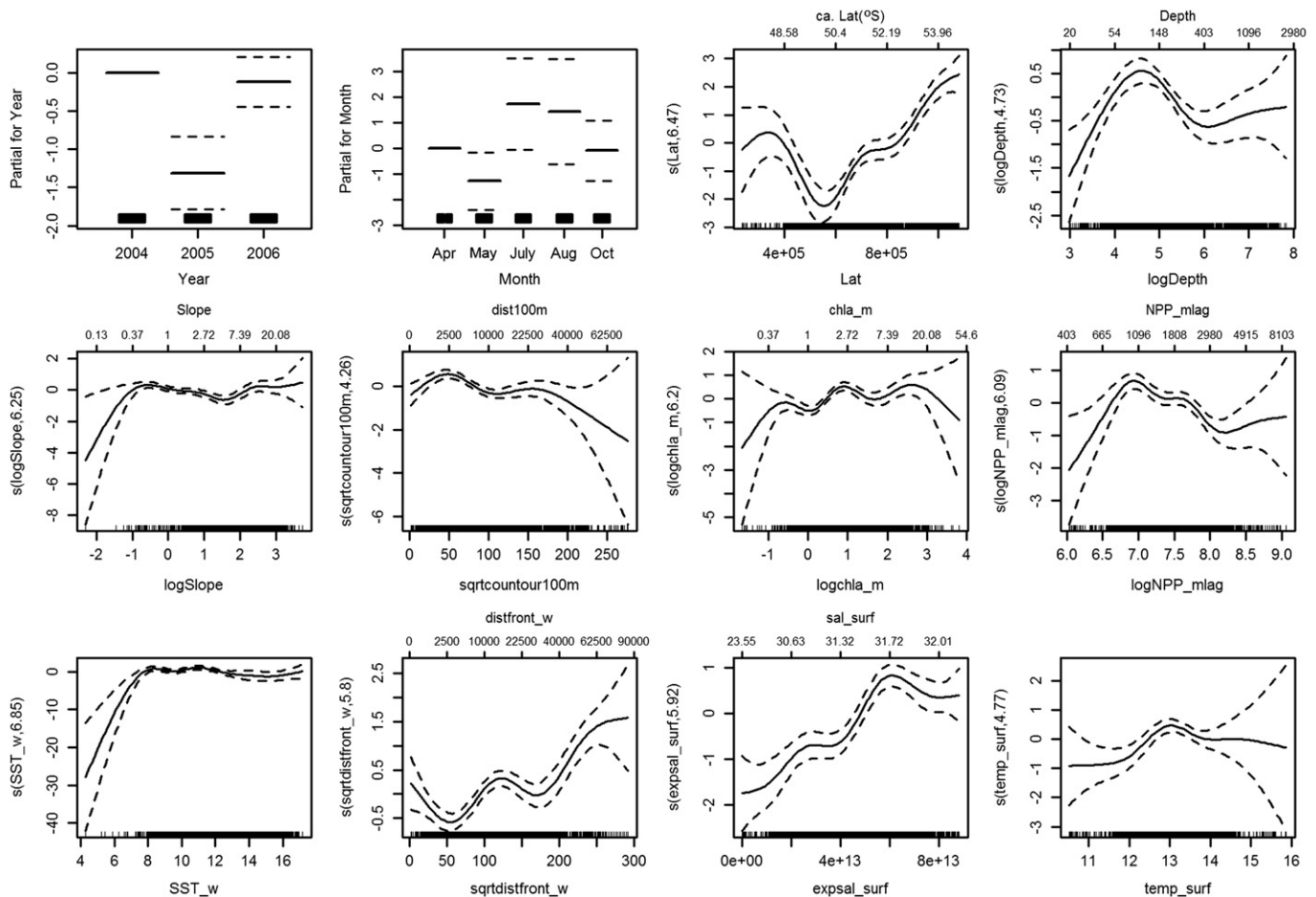
Fig. 4. Model terms for the 3-year generalized additive model (GAM) of humpback whale relative abundance. Estimated smooth functions (solid lines) with 95% confidence interval (dashed lines) are shown for each explanatory variable. y-axis=fitted function with estimated degrees of freedom in parenthesis; x-axis=variable range with rug plots indicating sampled values. Untransformed values are provided on the upper x-axis of transformed variables for easier interpretation. The partial effects of factor variables are also included.

adding longitude to the model. However, that would also increase the influence of spatial variables in the model, potentially affecting the effect of the explanatory variables more directly related to the physical and biological processes.

4. Discussion

4.1. Distribution patterns

The humpback whale was the most common large cetacean species in our surveys, as in other studies in British Columbia (Williams and Thomas, 2007) or elsewhere in shelf waters of the eastern North Pacific feeding grounds (e.g. Calambokidis and Barlow, 2004; Tynan et al., 2005; Zerbini et al., 2006). The exceptions are the Bering Sea, where fin whales are more abundant (Moore et al., 2002), or some localized areas such as the Channel Islands, where blue whales predominate (Fiedler et al., 1998).

Two of the largest concentrations of humpback whales were observed around the Queen Charlotte Islands (QCI), in areas where high densities of sightings have been previously reported: southwestern Hecate Strait, from photo-identification (Ford et al., 2009) and line transect (Williams and Thomas, 2007) surveys; and the southern Dixon Entrance, from opportunistic boat surveys (Nichol et al., 2010). Sightings made off the Olympic Peninsula during the 2005 summer survey were more numerous in the area

east of Barkley Canyon and between La Perouse Bank and Nitinat Canyon, and on the shelf edge near the southern portion of Juan de Fuca Canyon (see Fig. 3). These observations agree with the distribution patterns reported by Calambokidis et al. (2004) from line transect surveys conducted between 1997 and 2002.

As surveys were not systematic, we were unable to detect shifts in whale distribution among areas or changes in overall abundance, either within or between years. However, high variability in encounter rates was observed on the local scale, such as in the southern Dixon Entrance over the five surveys that crossed this area. We explored this variability in our habitat models by relating it to the dynamic variables from the weekly remote sensing images, and also by including month and year as factors on the 3-year GAM.

4.2. Environmental variables and oceanographic processes

Our models indicate that humpback whales were strongly associated with latitude and bathymetric features, including depth, slope and distance to isobaths. A number of studies have shown associations between latitude and cetacean distribution, either in terms of geographical ranges (e.g. Weir et al., 2001), latitudinal gradients (e.g. Forney and Wade, 2006) or as representing particular physiographic features (e.g. Tynan et al., 2005). Regardless of the type of association, latitude is always a proxy for some biological or physical property that ultimately affects distribution, such as prey availability or a physiologically limiting factor
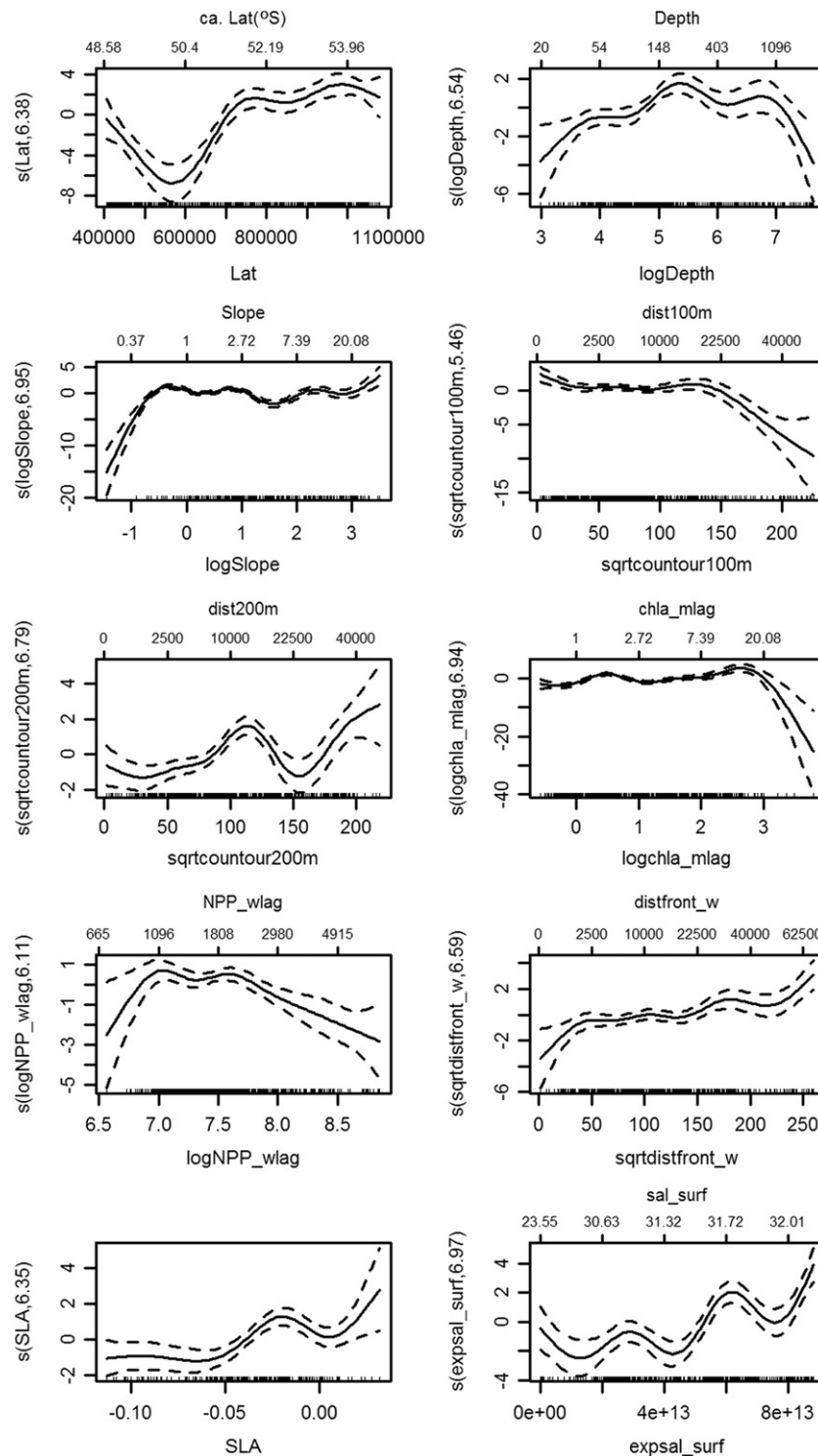
Fig. 5. Model terms for the 2004 generalized additive model (GAM) of humpback whale relative abundance. Estimated smooth functions (solid lines) with 95% confidence interval (dashed lines) are shown for each explanatory variable. y-axis=fitted function with estimated degrees of freedom in parenthesis; x-axis=variable range with rug plots indicating sampled values. Untransformed values are provided on the upper x-axis of transformed variables for easier interpretation.

(e.g. temperature). The seasonal increase in biological productivity towards high latitudes favors the use of mid and high latitude areas by migratory baleen whales during their feeding season (Gaskin, 1982). Therefore, on a large scale, the general pattern of increasing relative abundance with latitude observed in our models may partially reflect a latitudinal gradient of increased whale biomass towards the Arctic. Two subpopulations of humpback whales occupy our study area: the Eastern North Pacific subpopulation ranges from

California to Washington, and the Central North Pacific subpopulation inhabits British Columbia and Alaska (Calambokidis et al., 2001). Current abundance estimates are around 1400–1700 for the California–Oregon area, 200–400 for Washington–southern British Columbia and 3000–5000 for northern British Columbia and southeast Alaska (Calambokidis et al., 2008); see also Rambeau (2008).

From a regional perspective, however, the latitudinal differences may reflect the amount of suitable habitat available to the
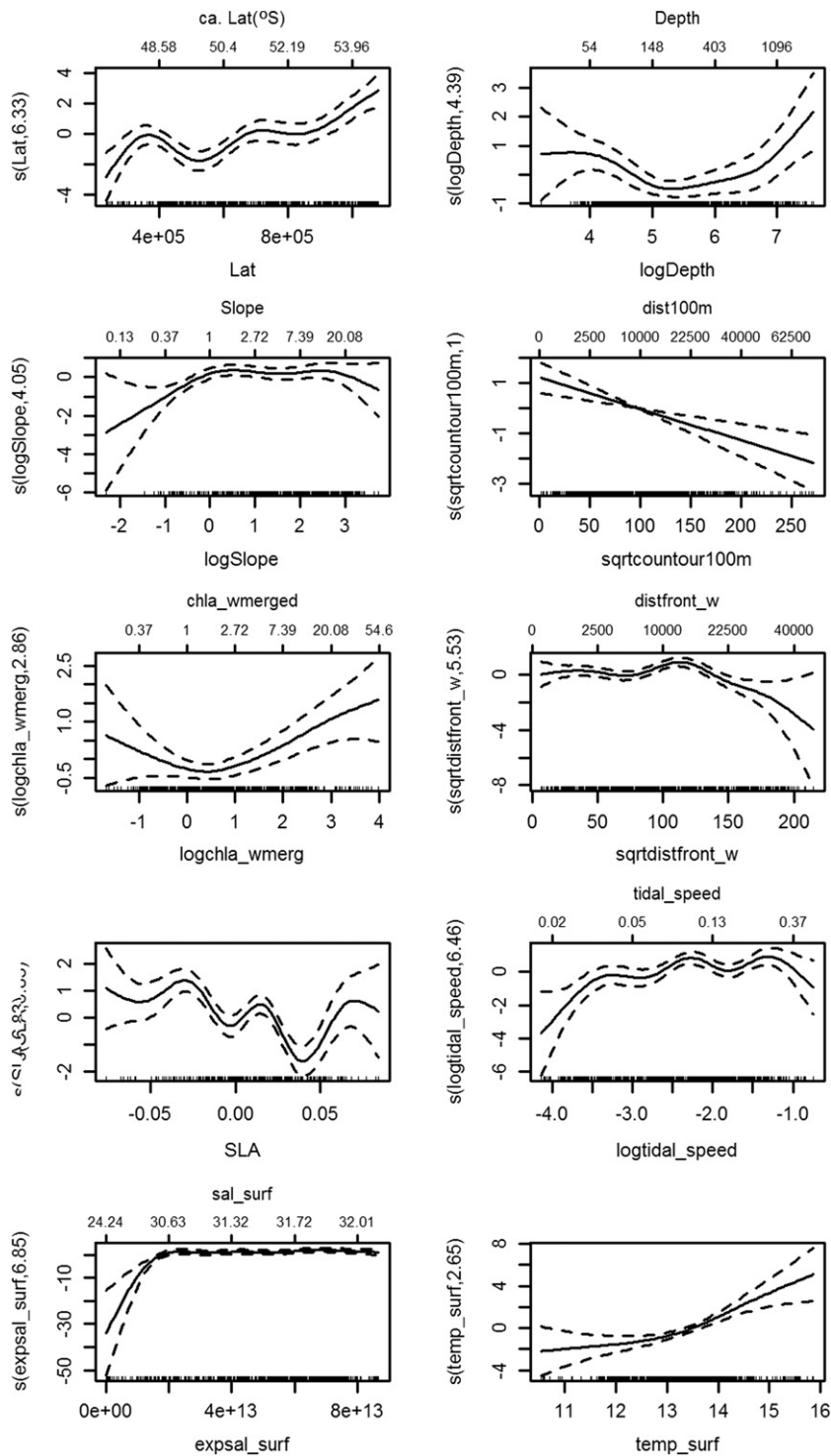
Fig. 6. Model terms for the 2005 generalized additive model (GAM) of humpback whale relative abundance. Estimated smooth functions (solid lines) with 95% confidence interval (dashed lines) are shown for each explanatory variable. *y*-axis=fitted function with estimated degrees of freedom in parenthesis; *x*-axis=variable range with rug plots indicating sampled values. Untransformed values are provided on the upper *x*-axis of transformed variables for easier interpretation.

humpback whales. That is, if humpbacks prefer mid-shelf waters, as we suggest below, then the latitudinal variation in the extent of shelf area along the BC coast seems to explain the observed pattern well. The lower encounter rates in our models occur off the northwestern side of Vancouver Island, where the shelf is relatively narrow. On a wider shelf, more of the primary production remains on shelf and becomes available to coastal food web (Ware and Thomson, 2005). And although mean annual chl-*a* and zooplankton concentrations and mean resident fish yields are

higher off Washington–southern BC than in northern BC (Ware and Thomson, 2005), the total area of ocean habitat with coastal influence is larger in the latter, which may provide more opportunities for humpbacks of finding predictable prey aggregations.

The relationships with bathymetry shown in our models suggest that humpback whales in BC waters prefer shelf waters between 50 and about 200 m of depth, especially near the 100-m contour. Where positive correlations with larger depths were observed, they appeared to be related to areas with a narrow shelf
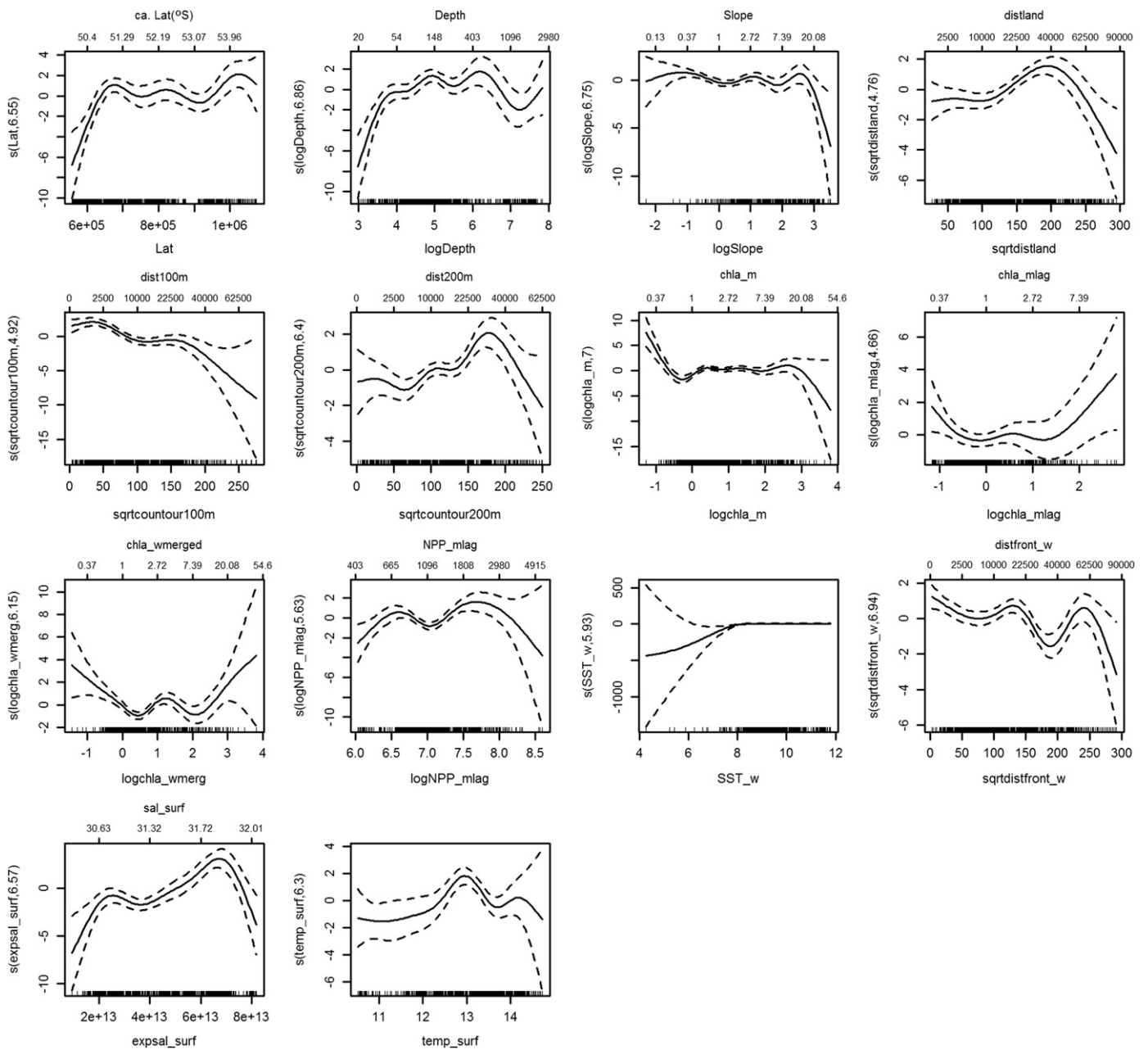
Fig. 7. Model terms for the 2006 generalized additive model (GAM) of humpback whale relative abundance. Estimated smooth functions (solid lines) with 95% confidence interval (dashed lines) are shown for each explanatory variable. y-axis=fitted function with estimated degrees of freedom in parenthesis; x-axis=variable range with rug plots indicating sampled values. Untransformed values are provided on the upper x-axis of transformed variables for easier interpretation.

(e.g. west coast of QCI) or deep channels (e.g. Juan Perez Channel, east Moresby Island) and cross-shelf canyons (e.g. off Juan de Fuca Strait). This idea is supported by the positive correlations within shorter distances to the 100-m isobath alone, or in combination with slope and distance to the shelf break. Calambokidis et al. (2004) reported a mean depth and distance to shelf break of 144 m and 8.4 km, respectively, for 153 humpback whale sightings made off the Olympic Peninsula. In the northern California Current System, humpback whales occurred over the slope in late spring, but were concentrated at water depths of 50–100 m over the Heceta Bank and off Cape Blanco in summer (Tynan et al., 2005). In the Bering Sea, humpbacks were primarily seen on the middle shelf (50–100 m depth), and also in deeper waters near the Unimak Pass (Moore et al., 2002), one of the Aleutian passes with the highest number of humpback whale sightings (Sinclair et al., 2005).

Bottom topography plays a determinant role on the oceanographic processes that lead to enhanced productivity in coastal regions. Through sometimes complex interactions with tidal flow, wind stress and ocean currents, bathymetry is the basis for such enrichment processes as tidal mixing and shelf-break upwelling, and also facilitates concentration and retention processes by simply acting as a physical barrier or by altering water flows (e.g. Taylor column over a submarine bank) and promoting frontal zones (Bakun, 1996). It is therefore not surprising that explanatory variables related to bottom topography were consistently selected in our models.

The preference of humpback whales in BC for shelf waters is presumably related to the horizontal distribution of prey, but may also be influenced by the energetic cost of diving and foraging efficiency. Dive depths of foraging humpback whales correlate significantly with dive and surface durations, as well as with
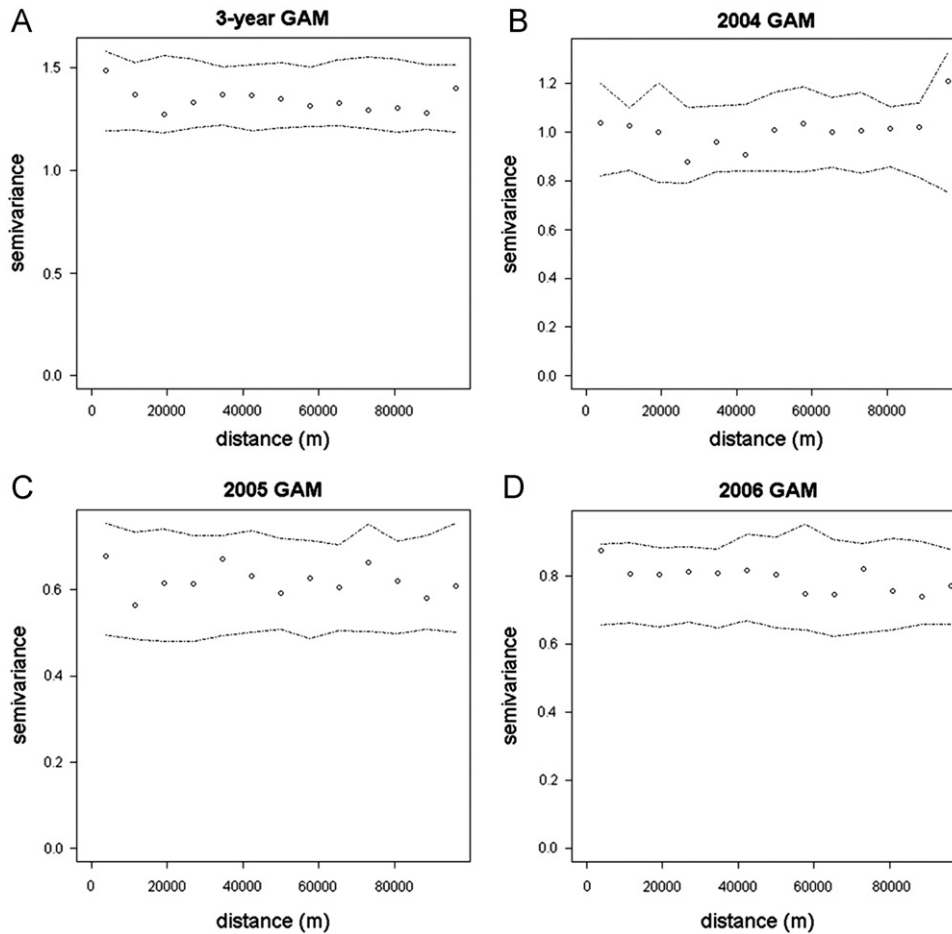
Fig. 8. A–D—Binned variograms with Monte Carlo envelopes of deviance residuals of the selected GAM models.

ventilation patterns (Dolphin, 1987b, 1987c), such that shallower dives should be more efficient than deeper dives when prey densities are comparable. In support of this, humpback whales tend to lunge feed on the upper boundary of dense aggregations of euphausiids (Goldbogen et al., 2008). In Frederick Sound, Alaska, humpback whales have been observed to dive as deep as 150 m in waters averaging over 300 m deep with dense euphausiid patches as deep as 200 m (Dolphin, 1987a, 1987c). Humpback whales should, therefore, benefit energetically by feeding in areas with shallower bottom depths where the vertical diel migration of euphausiids is depth limited and prey may be concentrated closer to the surface.

The concentrations of whale sightings off the Olympic Peninsula in summer 2005, mentioned above, are located on what appears to be the edge of the Juan de Fuca Eddy (Fig. 10). This seasonal and semi-permanent cyclonic feature is formed off the entrance of Juan de Fuca Strait in summer (Freeland and Denman, 1982), as a consequence of the geostrophic adjustment to doming isopycnals that arise from tidal or wind upwelling off Cape Flattery (Foreman et al., 2008). Its presence has been linked to enhanced phytoplankton biomass and primary productivity (Marchetti et al., 2004) and to increased biomass of euphausiids, pelagic fish and seabirds (Burger, 2003; McFarlane et al., 1997; Simard and Mackas, 1989). The whales observed could have been taking advantage of this feature given that edges of eddies may help concentrate euphausiids and pelagic fish such as herring (Johnston et al., 2005). During CTD/rosette and acoustic survey lines run across shelf at about the same area in 1991, Mackas et al. (1997) recorded the highest densities of euphausiids and Pacific hake between the 100- and

150-m isobaths, in a region of upward-domed isotherms and isohalines about 15 km from a strong surface front, and under a band of high chl-*a* concentration.

The shapes of the estimated smooth functions of chl-*a* and net primary productivity (NPP) were not consistent. The time lagged NPP variables showed positive effects in the relatively lower to mid-range of log values in two models (the 3-year and 2004 models), and in the upper range of values of the 2006 model. The different chl-*a* smoothed functions resulted in positive effects in the upper range of log values in all models and for most variables. The exception was the monthly chl-*a* for the 2006 GAM, although this model also included two other chl-*a* variables with positive effects in both upper and lower range of log values. Therefore, higher encounter rates of whales generally seemed to be associated with high primary production. Indeed, the areas with highest concentrations of humpback whales typically showed high chl-*a* concentrations in our satellite images.

There are at least four reasons why chl-*a* might not always be a good predictor of baleen whale distribution. First, grazing by herbivores can substantially reduce phytoplankton standing stocks (Strom et al., 2001). Second, phytoplankton can be advected away from the producing area by wind, currents and eddies (e.g. Hofmann and Murphy, 2004). Third, there may be higher phytoplankton concentrations at intermediate depths if vertical mixing is not strong enough (Denman et al., 1985; Prézelin et al., 2004), which are not detected by satellite sensors scanning surface waters and finally, the spatial and temporal scale of the study may not be the most appropriate (e.g. Jaquet, 1996). Spatial and temporal lags between peaks of phytoplankton and zooplankton biomass
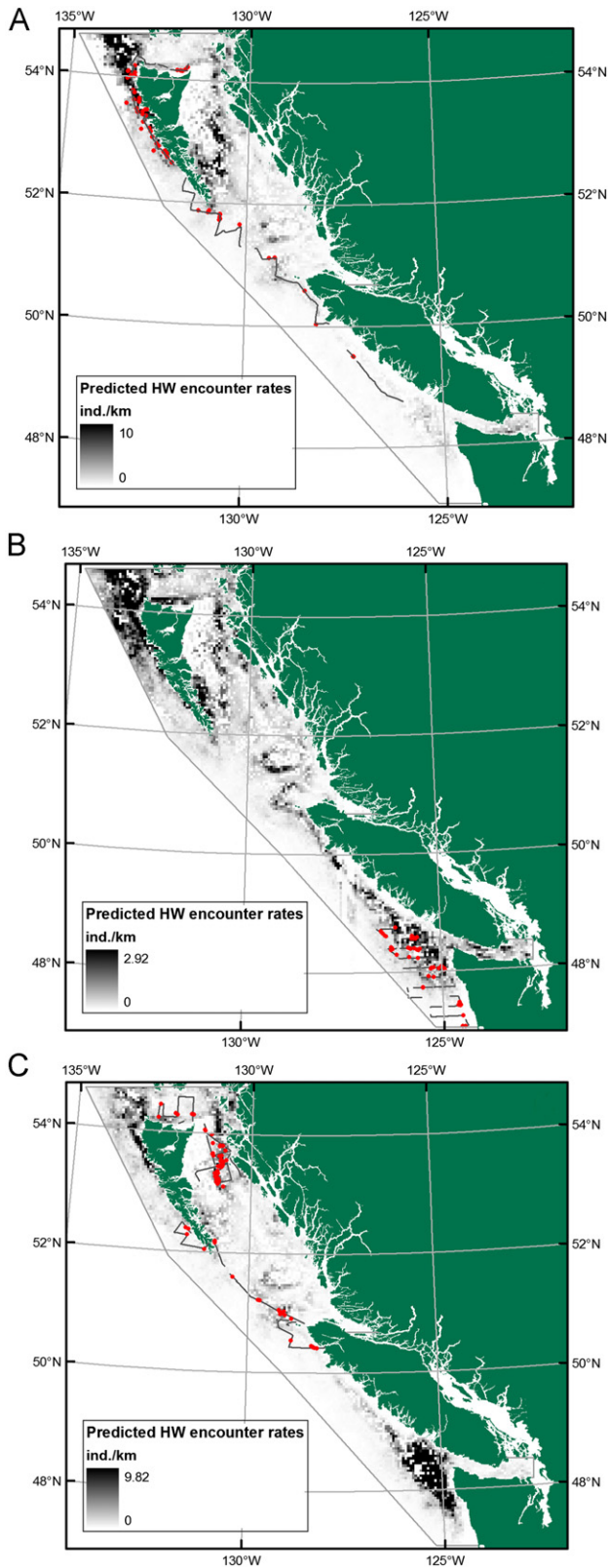
Fig. 9. Predicted humpback whale encounter rates for (A) 8–15 May 2004, (B) 20–27 July 2005 and (C) 9–16 May 2006 obtained from the 3-year GAM model. Actual sightings and effort during these periods are included for comparison. Note that the gray scale bars of the three images are not on the same scale.
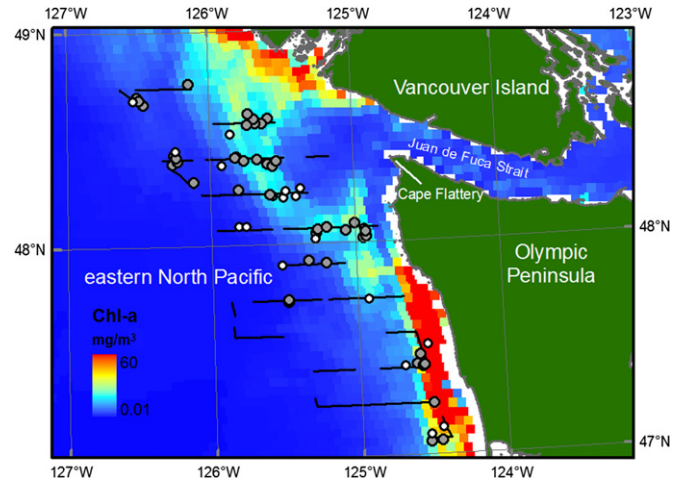

Fig. 10. Locations of humpback (gray dots) and unidentified (white dots) whales sighted off the Olympic Peninsula during 20–26 July 2005 on board the *Miller Freeman*, overlaid on a MODIS chlorophyll image for that week. Note that whale sightings concentrate around the edge of what appears to be the semi-permanent Juan de Fuca Eddy. On effort tracklines are also shown.

observed. Potential inaccuracies of satellite derived chl-*a* estimates and modeled NPP (Falkowski and Woodhead, 1992) combined with using variables with different spatio-temporal resolutions and time lags in our models could further explain some of the variability in our results.

As our surveys occurred at different times of year, seasonal events such as wind-driven upwelling could be another source of variability in our models, particularly for variables related to primary productivity. Coastal upwelling occurs along eastern boundary areas such as the west coast of Vancouver Island during northwesterly winds, typical of summertime conditions (Thomson, 1981). Even within a season, the onset and duration of coastal upwelling varies considerably. For instance, upwelling indices calculated by the Pacific Fisheries Environmental Laboratory (NOAA) for the area off Juan de Fuca Strait were positive for the period of our 2004 and 2006 spring surveys, but negative for the 2005 spring survey. The index also indicated that upwelling continued in this area in the fall of 2006, but apparently not in the fall of 2004. Additional surveys would be required to investigate the effects of the seasonality and within-season variation of upwelling events on humpback whale distribution in BC waters.

We had predicted that the concentration of chl-*a* would correlate better with humpbacks and their prey in areas where concentration and retention processes prevail. This appears to be the case in the southwestern Hecate Strait region, which typically has the highest estimated chl-*a* concentrations of the Gwaii Haanas National Marine Conservation Area (southern QCI). Phytoplankton blooms sometimes originate in this area (Robinson et al., 2004) of complex topography and coastline where three-dimensional simulation modeling indicates important particle retention at 30 and 100 m depths (Robinson et al., 2005). Comparisons of surface chl-*a* concentrations measured at Queen Charlotte Sound, Hecate Strait and Dixon Entrance suggested no significant differences between years or between sites, and showed a strong spring bloom and a weaker fall bloom (McQueen and Ware, 2006). Analyses of the IOS zooplankton database comparing euphausiid biomass among Queen Charlotte Sound (QCS), Hecate Strait (HS) and Dixon Entrance (DE) suggested no between-site differences using ANOVA, but sample variance was large, and a non-parametric test (Kruskall–Wallis) suggested significant differences: QCS > DE > HS (McQueen and Ware, 2006). Euphausiids peaked later in the summer and fall (McQueen and Ware, 2006).

ultimately affect large whale occurrence and distribution (e.g. Croll et al., 2005). Differences in oceanographic processes throughout the BC coastal areas might therefore have led to the variability

Sea surface temperature did not appear to have a strong influence on whale encounter rates, except for the negative effect in waters colder than 8 °C. The slightly bimodal SST smooth curve of the 3-year GAM apparently reflects the lower values encountered in Dixon Entrance and the higher values elsewhere.

Fronts are regions of enhanced horizontal gradients in temperature, salinity, density and other physical properties, often leading to enhanced phytoplankton, zooplankton and fish biomass (Mann and Lazier, 1996; Sharples and Simpson, 2001). Consequently, cetaceans may also be attracted to these frontal systems, either oceanic or shelf and slope fronts (e.g. Bluhm et al., 2007; Doniol-Valcroze et al., 2007; Gaskin, 1982). Humpback whales, for instance, appeared to be associated with the inside edge of the coastal upwelling front of the northern California Current System in June 2000 (Tynan et al., 2005). The distributions of blue, fin and humpback whales were also highly correlated with thermal fronts in the northern Gulf of St. Lawrence (Doniol-Valcroze et al., 2007). These authors observed, however, that most whales were not directly on top of the frontal areas. They hypothesized that this spatial lag could either occur because fronts are not necessarily straight lines under the surface, or because it takes time for passive prey to be aggregated by the fronts.

Except for the 2004 GAM, all of our models suggest that SST fronts had positive effects on whale distribution within distances of up to about 20 km. However, further increases in modeled whale numbers with longer distances were noted in both the 3-year and 2004 models, apparently as a consequence of problems with detecting frontal systems (and not necessarily a true absence of fronts). The temporal and spatial resolution of the SST images was too coarse to reliably detect alongshore fronts in areas with complex coastline, such as the east Moresby area. Similar issues with coastal front mapping were reported by Breaker et al. (2005). Ideally, daily 1 km resolution satellite images should be used to capture the fast dynamics and fine scale resolution of these areas very close to shore. Nevertheless, the edge detection algorithm we used frequently identified several of the recurring thermal features described for the region (see example in Fig. 2), such as the Dogfish Banks Front, the mainland coastal upwelling in the eastern Hecate Strait, the Cape Scott upwelling front, tidal jets at Cape St. James and the Haida Front (Belkin and Cornillon, 2003; Crawford et al., 1995; Jardine et al., 1993).

During our study, relatively high densities of humpback whales were observed over the edge of the trough in the middle of Hecate Strait. This area is bordered on the west by the Dogfish Banks Front, a tidal mixing and seasonally reversing front over shallow depths (Jardine et al., 1993) containing the highest near-surface concentrations of chl-a, nutrients, diatoms and copepods of the region (Perry et al., 1983). This front was also identified by Belkin and Cornillon (2003) as the northern part of a well-defined front, from July through March, between 52.5 and 54°N. Northwesterly winds lead to coastal upwelling along the eastern shores of Hecate Strait (Jardine et al., 1993), bordering therefore the east side of the trough.

Tidal streams and non-tidal currents at Dixon Entrance are generally characterized by the intrusion of cold high-salinity water on the southern portion and strong seaward flow of brackish water on the northern side, with a counterclockwise vortex in the middle of the channel (Thomson, 1981). We suspect that this circulation favors concentration and retention processes on the south side, and further investigation is warranted. An exploratory inspection of average humpback whale encounter rates against average values of remote sensing images for this area resulted in no apparent correlations, except for higher encounter rates with higher mean surface temperature (data not shown).

The values of the summer climatologies of sea surface temperature and salinity corresponding to positive effects in our models are spread throughout most of the shelf areas, except for Dixon Entrance and, in the case of salinity, for some areas near the mainland. Therefore, these values appear to simply reinforce the strong association of humpback whales with shelf waters. Sea surface height deviation, although selected in two models, did not appear to yield any interpretable results, with positive effects between −5 and 3 cm.

4.3. Modeling considerations

The explanatory power of the 3-year GAM was lower than that of the single year models. This was expected because the full dataset added additional variability to be explained. However, using the full dataset also provided more confidence in the results, as it reduced the chance of selecting spurious covariates. The year models were still a useful means to obtain a snapshot of potentially different conditions and correlations that could have disappeared in the 3-year model. In this context, we interpreted our results primarily in terms of what the models and groups of variables told us in aggregate. The selection of several explanatory variables in our models suggests the relationship between humpback whales and their environment is complex. Interactions between explanatory variables were not tested in our models due to the large number of covariates investigated. Although they can potentially improve model fit (Wood, 2006), they can also lead to complicated and uninterpretable functions, particularly if interactions are not expected a priori.

The partial effects of year and month in the 3-year GAM could potentially represent inter-annual and inter-seasonal differences in whale encounter rates. Nevertheless, we cannot rule out the possibility that these differences were caused by the non-systematic nature of the surveys. For instance, the fall surveys were limited in range, and there was only one summer survey.

4.4. Predicted encounter rates

The 3-year GAM appeared to perform well for the purpose of identifying the main areas of humpback whale concentration. It is unclear, however, if this model would be able to predict important shifts in whale distribution or perform well against new datasets. This logical next step was beyond the scope of our study. Williams and O'Hara (2010) predicted qualitatively similar high-density areas of humpback whales in the southwestern and middle Hecate Strait region in their analysis of ship strike risk.

4.5. Conclusions

We modeled humpback whale encounter rates in coastal British Columbia and adjacent waters with respect to oceanographic and remote sensing data using GAMs. Humpback whales were strongly associated with latitude and bathymetric features, indicating a preference for shelf waters. Distance to SST fronts and salinity (climatology) were also constantly selected as explanatory variables in the models. The shapes of smooth functions estimated for variables based on chl-a concentration or net primary productivity with different temporal resolutions and time lags were not consistent, even though higher numbers of whales seemed to be associated with higher primary productivity in all models and for most variables. These and other selected explanatory variables may reflect areas of enhanced biological productivity that favor top predators.

Areas where we observed high concentrations of humpback whales are generally associated with topographically induced oceanographic processes that are known to influence the patchy distribution of euphausiids, an important prey of humpback whales (e.g. Clapham et al., 1997). Off Vancouver Island, for example, euphausiids form dense aggregations over the steep

slopes of the shelf break and the edges of the midshelf banks. These areas are characterized by complex topography, domed isopycnals and slower cross-shelf flows (Mackas et al., 1997). The interaction between varying winds, tidal flows and the diverse topographic features on the BC coast likely create distinct conditions to concentrate prey. Thus whales may select habitat based on previous experience and foraging success (Weinrich, 1998), and may also use their knowledge of current tides and winds to choose predictable habitats that might be reached within hours.

Few studies have combined GIS with satellite images in cetacean habitat modeling, and fewer have included oceanographic processes such as sea surface fronts, and high resolution spatial and temporal data. We incorporated explanatory variables that have just recently been made available to researchers, and have shown the value of using remote sensed data when in situ oceanographic samples are unavailable. We cannot over stress the need to undertake finer scale studies to shed light on how humpback whales interact with prey fields and different oceanographic processes. The challenge is to integrate these fine scale studies into habitat models that take advantage of remote sensing data and provide knowledge on broader scale distribution patterns at the population level.

Our study indicates the presence of at least three important regions for humpback whales along the BC coast: (1) southern Dixon Entrance and northwestern Queen Charlotte Islands; (2) middle and southwestern Hecate Strait and (3) the area between La Perouse Bank and the southern edge of Juan de Fuca Canyon, off the entrance of Juan de Fuca Strait. Increased survey effort on the west coasts of the Queen Charlottes and Vancouver Island is needed to affirm the relative importance of these regions. Further humpback whale research in BC waters should also couple systematic surveys with oceanographic sampling in the inside mainland channels where remote sensing data are not appropriate. Studies are also needed on feeding habits to investigate preferences and interactions with prey.

Acknowledgments

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