Predictions of critical habitat for five whale species in the waters of coastal British Columbia

Edward J. Gregr and Andrew W. Trites

Abstract: Whaling records from British Columbia coastal whaling stations reliably report the positions of 9592 whales killed between 1948 and 1967. We used this positional information and oceanographic data (bathymetry, temperature, and salinity) to predict critical habitat off the coast of British Columbia for sperm (*Physeter macrocephalus*), sei (*Balaenoptera borealis*), fin (*Balaenoptera physalus*), humpback (*Megaptera novaeangliae*), and blue (*Balaenoptera musculus*) whales. We used generalized linear models at annual and monthly time scales to relate whale occurrence to six predictor variables (month, depth, slope, depth class, and sea surface temperature and salinity). The models showed critical habitat for sei, fin, and male sperm whales along the continental slope and over a large area off the northwest coast of Vancouver Island. Habitat models for blue, humpback, and female sperm whales were relatively insensitive to the predictor variables, owing partially to the smaller sample sizes for these groups. The habitat predictions lend support to recent hypotheses about sperm whale breeding off British Columbia and identify humpback whale habitat in sheltered bays and straits throughout the coast. The habitat models also provide insights about the nature of the linkages between the environment and the distribution of whales in the North Pacific Ocean.

Résumé : Les statistiques de chasse à la baleine accumulées par les stations baleinières de la côte de la Colombie-Britannique entre 1948 et 1967 indiquent de façon fiable les coordonnées géographiques des points de capture de 9 592 baleines. Ces données géographiques combinées à des informations océanographiques (bathymétrie, température et salinité) ont servi à prédire l'habitat critique des Cachalots macrocéphales (*Physeter macrocephalus*), des Rorquals boréaux (*Balaenoptera borealis*), des Rorquals communs (*Balaenoptera physalus*), des Rorquals à bosse (*Megaptera novaeangliae*) et des Rorquals bleus (*Balaenoptera musculus*) au large des côtes de la Colombie-Britannique. Des modèles linéaires généralisés à échelles annuelles et mensuelles ont permis de mettre en correspondance la présence des baleines et six variables prédictives (mois, profondeur, pente, classe de profondeur et température et salinité de surface de la mer). Les modèles ont révélé l'existence d'habitats critiques pour les Cachalots macrocéphales mâles, les Rorquals boréaux et les Rorquals communs le long du talus continental et sur une grande surface au large de la côte nord-ouest de l'île de Vancouver. En partie à cause d'un échantillonnage plus faible, les modèles d'habitat des Cachalots macrocéphales femelles, des Rorquals bleus et des Rorquals à bosse restent relativement insensibles aux variables prédictives. Ces prédictions sur les habitats viennent appuyer des hypothèses récentes qui veulent que les Cachalots macrocéphales se reproduisent au large de la côte de la Colombie-Britannique et qui indiquent que l'habitat des Rorquals à bosse se situe dans les baies et les détroits protégés tout le long de la côte. Ces modèles d'habitat laissent aussi entrevoir la nature des liens qui existent entre les conditions de l'environnement et la répartition géographique des baleines dans le Pacifique nord.

[Traduit par la Rédaction]

Introduction

Interest in the spatial distribution of whales in the world's oceans can be traced back to the Yankee sperm whaling industry and the charts of Townsend (1935) and Maury (1852). More recent efforts to relate whale distributions to oceanographic parameters can be traced to work by Uda (1954) who identified four types of oceanic fronts that were correlated with the presence of whales. This line of research culminated with Nasu (1966) who detailed the oceanographic conditions (mainly temperature and currents) that formed favourable whaling grounds in the North Pacific and described the seasonal effects of temperature and current on the distributions of blue (*Balaenoptera musculus*), fin (*Balaenoptera*

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E.J. Gregr[1] and A.W. Trites. Marine Mammal Research Unit, Fisheries Centre, Department of Zoology, University of British Columbia, Hut B3, Room 18, 6248 Biosciences Road, Vancouver, BC V6T 1Z4, Canada.

[1] Corresponding author (e-mail: ed_gregr@telus.net).

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physalus), humpback (*Megaptera novaeangliae*), and sei (*Balaenoptera borealis*) whales. The objective of these early studies was to improve the efficiency of the whaling fleets by reducing the amount of time spent searching for whales.

Recently, geographic information systems and remote sensing data have revived interest in the search for relationships between oceanographic conditions and marine mammal distributions. For example, relationships have been detected between marine mammal abundance and bathymetry (Hui 1985; Woodley and Gaskin 1996), sea surface chlorophyll concentrations (Smith et al. 1986), sea surface temperature (Woodley and Gaskin 1996), oceanographic circulations (Waring et al. 1993; Woodley and Gaskin 1996), and prey abundance (Woodley and Gaskin 1996; Fiedler et al. 1998). However, less work has been done to quantify habitat characteristics based on these relationships (e.g., Watts and Gaskin 1985; Moses and Finn 1997).

The objective of our study was to identify coastal regions that may be regarded as critical habitat for sperm (*Physeter macrocephalus*), fin, sei, blue, and humpback whales. We considered male and female sperm whales separately because of well-documented behavioural differences between the sexes (e.g., Best 1979). We adopted Hall et al.'s (1997) definition of critical habitat as the measure of an area's ability to provide the resources necessary for the persistence of a population. Since the baleen whales are highly migratory species, critical habitat could be expected to include feeding areas as well as common migration routes.

Our approach was based on work by Jaquet et al. (1996) and Moses and Finn (1997). Jaquet et al. (1996) analysed the correlations between nineteenth century Yankee sperm whaling records and satellite observations in the tropical Pacific at spatial scales of 220–1780 km^2 and found that historic sperm whale distributions were correlated with contemporary measurements of chlorophyll concentrations and that the degree of correlation increased as the spatial scale was increased. Moses and Finn (1997) used a logistic regression model to examine the relationship between right whale distributions off the coast of Nova Scotia on a 64 km^2 grid, using concurrent measurements of oceanography (depth and surface temperature) and whale presence–absence.

We sought to define critical habitat for five species of whales along the coast of British Columbia in terms of the physical environment. We did so using general linear models to determine whether the positions of historic whale catches recorded in British Columbia from 1948 to 1967 (our dependent variable) were related to six predictor variables: depth, slope, depth class, temperature, salinity, and month. Slope and depth class were derived from bathymetry, slope was a measure of topography, and depth class divided the study area into shelf, slope, and off-shelf regions. The models predicted the probability of occurrence of each species of whales based on these variables. Model results, identifying critical habitat for large whale species in British Columbia, are discussed in terms of northeastern Pacific oceanography, whale biology, and whale behaviour.

Methods

We used the positional data recorded between 1948 and 1967 by British Columbia coastal whalers and a simple oceanographic model based on depth, temperature, and salinity to create geographic probability distributions for sei, fin, humpback, blue, and sperm whales. We divided the coastal region of British Columbia into grid cells and used Cause&Effect software (Facet Decision Systems, Inc. 1999*a*) to create a habitat model, which spatially associated the dependent and independent data for each grid cell. We then exported data sets from the habitat model for regression analysis in S-Plus (Mathsoft 1999). We incorporated the results of the regression back into the Cause&Effect habitat model for display. Positional data, recorded in latitude and longitude, were converted to a regular universal transverse mercator grid for analytical and display purposes. Universal transverse mercator grids, which are measured in metres, are the preferred representation for spatial analysis because latitude and longitude measures do not reflect consistent distance measures.

We began the analysis by exploring the relationships between the predictor variables and the probability of whale presence. We then postulated an a priori "biological" model using the exploratory results. This biological model identified the terms subsequently used in the stepwise regression to create the generalized linear models. A separate regression model was generated for each species, at annual and monthly time scales. Predictions (the probability of whales being present in any given cell) were plotted on a spatial grid for visual interpretation and tested using cross-validation techniques. We also tested the sensitivity of the predictions to the predictor variables by comparing predictions from cold years with those from warm years because the temperature and salinity predictors (1980–1998) were not concurrent with the biological data (1948–1967).

The dependent variables consisted of the position, species, and date of capture for whales killed between 1948 and 1967 as part of the British Columbia coastal whaling industry. Sex was included for sperm whales only. Coastal whaling during this period was conducted solely from Coal Harbour on the west coast of Vancouver Island (Fig. 1). The whaling data used in the regression analysis were restricted to an area within 150 nautical miles (nmi) (275 km) of the mouth of Quatsino Sound ($n = 8164$ whales). This is where whales were often left for pickup by shore vessels. Whales killed within the 150-nmi radius represented about 85% of the georeferenced whale kills. Choosing this restricted area increases the likelihood that the whalers searched with equal effort throughout the study area and is well within the range of the whaling vessels (approximately 200 nmi) (Pike and MacAskie 1969). Regions within the 150-nmi search area that had no recorded kills were assumed to be empty of whales. Thus, we assumed that the spatial patterns of whales killed within the study area were primarily a function of whale distributions and less a function of concentrated whaling effort. Shortcomings of this assumption and the consequences of nonrandom sampling are considered in the Discussion.

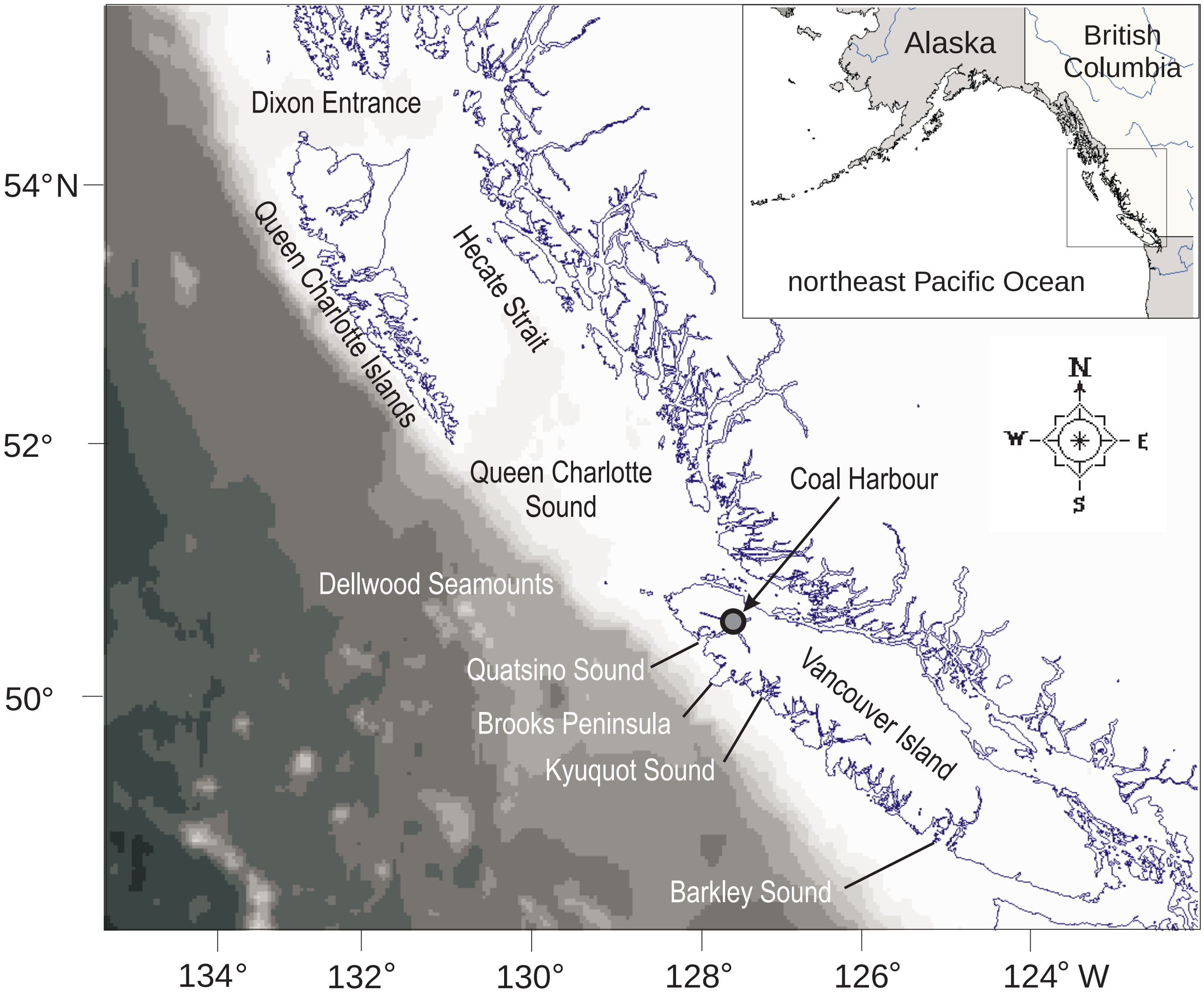
Independent variables

We used three continuous and three categorical predictor variables. The continuous variables included a 5-minute grid of bathymetry (PICES 1997) and long-term point data on surface temperature and salinity. The categorical variables consisted of month, slope, and depth class.

To maximize the spatial resolution and minimize interannual variability, the most recent 18 years (1980–1998) of conductivity (salinity), temperature, and depth point data were obtained from the Department of Fisheries and Oceans. We reduced this large, multidimensional data set (latitude, longitude, year, day, time, depth, temperature, and salinity) to mean monthly surface temperature and salinity values. For each depth profile, we used only the mean of the values in the top 1.5 m of the water column.

In addition to these three continuous predictors, we included the categorical variables month, slope, and depth class. We included

Fig. 1. British Columbia coastal waters showing the location of the Coal Harbour whaling station and other place-names mentioned in the text. Bathymetry is shaded from shallow to deep (light to dark) using 200-m bathymetric contours.



month to capture the significant species-specific monthly changes in the mean distance from shore (Gregr et al. 2000). This monthly effect (at least partially due to annual migration behaviour), combined with significant monthly changes in the temperature data (Fig. 2), shows the need to include month as a factor in the analysis. We only used the months April–September when the majority of whaling occurred (Gregr et al. 2000).

Slope was included to provide a measure of undersea topography, since topographic upwelling may play a role in biological productivity (Mann and Lazier 1996). This categorical predictor was defined to have slope classes from 0 (flat) to 6 (steepest). Although derived from the bathymetry, the slope at a particular location is independent of its depth. However, the two are strongly correlated in the area of the shelf break where there is a dramatic transition from on-shelf to deep waters.

We created the categorical predictor depth class to normalize the distribution of the depth variable, which was clearly bimodal (Fig. 3). While generalized linear models do not require the normally distributed independent variables, this does tend to yield a better fit (Tabachnik and Fidell 1996). We therefore divided the study area into three depth classes: shelf (≤200 m), slope (between 200 and 1800 m), and deep water (>1800 m). In addition to creating a more normal distribution of depths at each depth class (Fig. 3), this allowed us to capture the interaction between depth class and salinity (Fig. 2).

The study area was divided into grid cells, which thereby became the observational units in the study. We assigned annual and monthly temperature and salinity values independently to the grid cells by interpolation using triangular irregular networks (TINs) (Fig. 4). Interpolation was done equally in all directions. We did not correct for any potential spatial autocorrelation. For the annual and monthly models, we generated mean annual and monthly temperature and salinity TIN surfaces. All years were treated equally when generating the mean values, and no attempt was made to correct for the annual variance.

The bathymetric grid of point data was also mapped to the study grid using a TIN surface. The slope and depth class predictors were calculated for each grid cell after the depth was assigned. Depth class was simply a function of the depth at each cell, while slope was calculated for each cell based on the difference between the elevations of its neighbours (Facet Decision Systems, Inc. 1999*b*).

We examined the grid cells for colinearity between the assigned values using the tolerance statistic $1 - R_x^2$, where R_x^2 is the variance in each independent variable x explained by the other independent variables. A low tolerance is an indication of colinearity, with a tolerance below 0.20 considered cause for concern (Menard 1995).

Fig. 2. Mean effects of the categorical variables month, depth class, and slope on the distribution of the continuous predictor variables temperature and salinity for the grid cells within the 150-nmi search area (*n* = 9029).

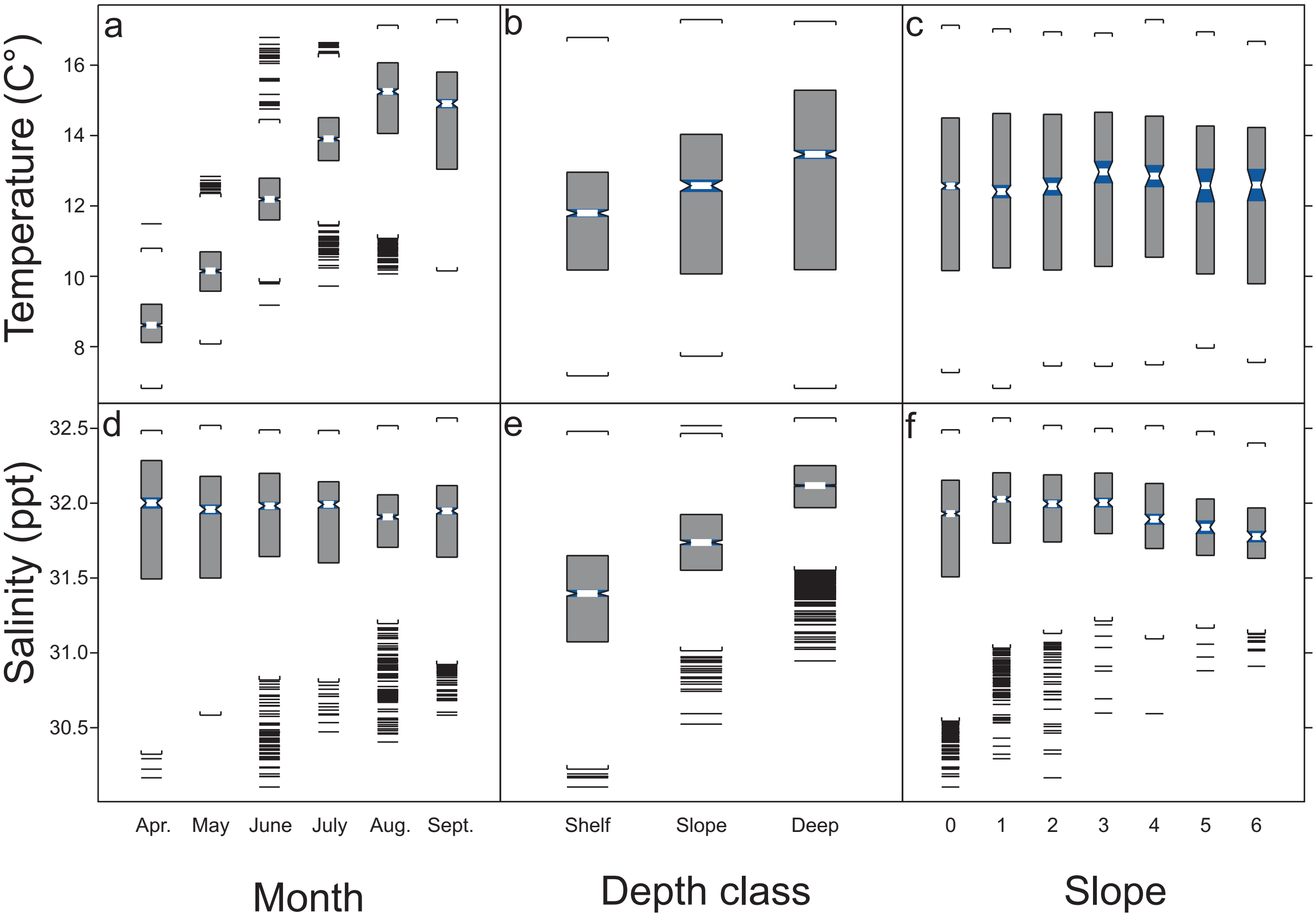
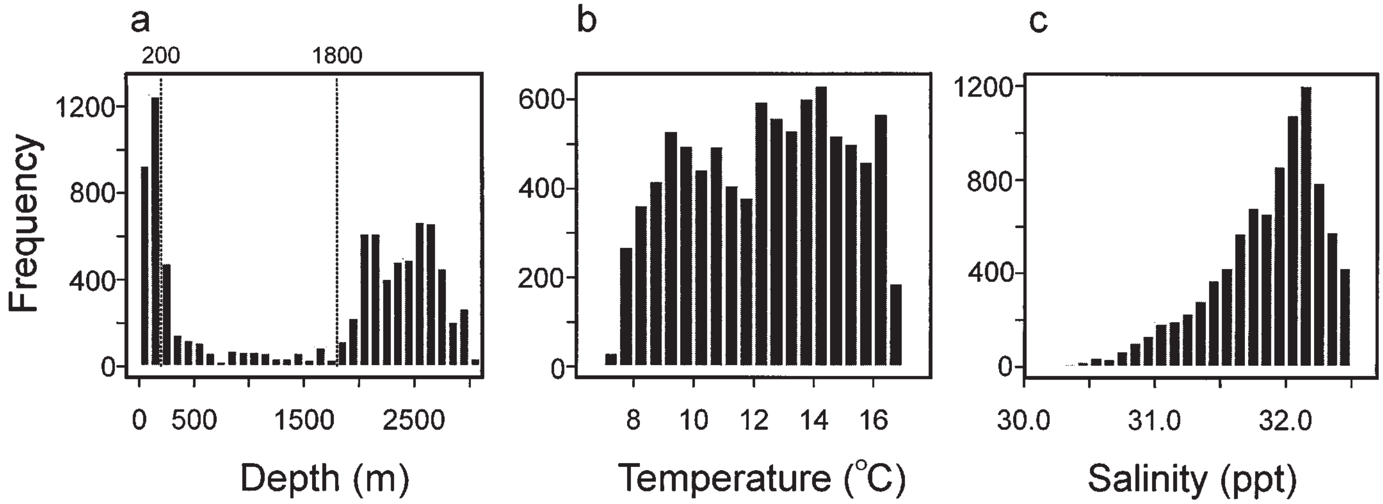


Fig. 3. Frequency distribution of the continuous predictor variables depth, temperature, and salinity for the grid cells within the 150-nmi search area (*n* = 9029). The vertical dashed lines on the depth–frequency plot show the three levels of the depth class categorical variable.



The tolerances for the independent variables in our study ranged from 0.47 to 0.97, indicating that the amount of colinearity was not significant at the spatial and temporal scales that we used. While some correlation between temperature and salinity might be expected, it may exist at a spatial scale (either finer or coarser) different from the one that we considered. Finally, to realistically bound the study area to reasonable oceanographic conditions, grid cells with depths of 10 m or less or with salinities less than 30 ppt were excluded.

Scale selection

Underlying all of the work on habitat characterization are two key assumptions. First, whales are generally found where their food is abundant, and second, these food sources are somehow related to oceanographic conditions. The relationship of common baleen whale prey species (zooplankton) to oceanographic conditions can take two forms: conditions can be ideal for primary production or oceanographic conditions can work to concentrate prey species in specific areas. In the first case, there is likely to be a temporal lag while the zooplankton blooms develop. For baleen whales feeding on zooplankton, which are trophically close to primary production (trophic levels 2.0–2.3 versus 1.0; Trites et al. 1999), this lag may be on the order of several weeks. However the lag may be considerably greater for sperm whales where the primary prey items (cephalopods, trophic level 3.7; Trites et al. 1999) are removed from primary production by approximately 4 months (Vinogradov 1981). These temporal lags typically result in corresponding spatial lags due to oceanic transport.

If the relationship between animal distributions and oceanographic predictors is more a function of prey concentration or aggregation caused by small-scale eddies or gyres, very little temporal and no spatial lag would be expected. Similarly, if certain bathymetric features (i.e., areas of high relief) caused prey species to aggregate, these lags would also be absent.

Thus, the time periods and spatial scales over which data are pooled may affect our ability to detect possible relationships between species abundance and any independent predictor variables, with different relationships or processes potentially being captured at different scales. The consequence of this fundamental scale problem was emphasized by Wiens (1989) who pointed out that just because we can provide clever explanations of the patterns that we observe, it does not necessarily follow that the patterns are anything more than artifacts of scale.

The effect of spatial scale was well treated by Jaquet et al. (1996) who demonstrated how multiscale analysis can help elucidate the effective scale of a relationship between a dependent variable and a single predictor. However, our objective was to evaluate the degree to which physical oceanography could be used to describe habitat for five different whale species. So rather than focus on a single predictor over multiple scales, we chose to examine the relationship between the catch distributions and a multivariate oceanographic model at two time scales. Using annual and monthly time scales allowed us to investigate the scale problem along an alternative axis (temporal versus spatial) and to assess the temporal variability in the habitat predictions. While multispatial scale analyses are the logical next step to explore the relationships proposed in our study, they are beyond the scope of this paper.

In selecting our spatial scale, we chose to use the finest possible resolution because fine-scale studies may be more informative than generalizations about the biological processes underlying the patterns (Wiens 1989). We selected a spatial resolution of 10 × 10 km based on an examination of the catch data, which showed that whalers tended to round their location to the nearest 5 minutes of both latitude and longitude (Gregr 2000). We therefore assumed this to be the precision of the positional data. Five minutes corresponds to approximately 10 km in these latitudes.

Regression modeling methods

Generalized linear models apply linear regression techniques to nonlinear data with heterogeneous variances (Chambers and Hastie 1993). Poisson and logistic regression are two types of generalized linear models that are used to model counts and binomial values (i.e., presence–absence), respectively. To capture the number of whales in the grid cells, we used Poisson rather than a logistic regression. Using a simple transform, we then converted the predicted number of whales (generated by the Poisson model) into probabilities. We mapped these probabilities onto the study area to generate the habitat predictions. An overview of these generalized linear modeling methods is contained in Gregr (2000). The transformation of counts into probabilities is described in the Appendix.

Model building

For each of the five species, we began with an exploratory analysis of how each of the continuous variables independently affected the presence of whales. We fit lowess (locally weighted scatterplot smoothing) curves to scatterplots showing the presence or absence of whales versus the independent variables. We examined the mean effects as well as the effects for each month and for each depth class. We used the results of this analysis to hypothesize a relationship between the presence–absence of whales and the independent variables based on biological significance. We used this a priori biological model to define the upper limit on the complexity of the regression models.

To generate the predictive models for each species, we used forward stepwise selection (Chambers and Hastie 1993). This technique repeatedly adds terms to the model from a pool of potential independent variables. The terms are added in order of the amount of variance that they explain. Thus, the most significant variables enter the model first. The pool of variables available for selection was defined by the biological model. We found that this approach consistently produced simpler models than stepwise backward elimination, which repeatedly removes terms from an overspecified model until the remaining terms are all statistically significant.

We applied forward stepwise selection to all the data within the 150-nmi search radius for each species to select the model terms. We determined the model coefficients using these same data. We then produced the habitat maps for the entire British Columbia coast from the annual and monthly probability predictions.

Model testing

We tested the predictive power of the models using cross-validation and classification tables. Cross-validation requires dividing the data into a fitting set and a testing set. The fitting set is used to fit the model (i.e., to generate equation coefficients). The fitted model is then tested against the testing data set. For each species, we used half of the grid cells within the 150-nmi search area for fitting and the other half for testing. Since the predictions generated by our models were probabilities, we used classification tables to evaluate the model fit.

Classification tables provide a measure of the efficiency of a predictive model. This predictive efficiency represents, in percent, how successfully a model predicts presence and absence. The tables compare the observed presence–absence in the testing data with predicted model values. In order to evaluate the predictive efficiency of our models, we needed to define a cutoff value that would convert probability into a presence–absence result. We set this cutoff value individually for each model such that the fitted model produced the same number of presence cells as found in the fitting data set.

To assess the effects of using mean surface temperature and salinity values from a 19-year period (1980–1998) that was not concurrent with the 20 years of whaling data (1948–1967), we conducted a simple analysis of the sensitivity of the predictions to the oceanographic model. We compared predictions obtained from warm years with predictions from the remaining years. Ware (1995) analysed the patterns in climate records from the northeast Pacific and related the warmest years in British Columbia (based on air temperature anomalies) to the El Niño – Southern Oscilla-

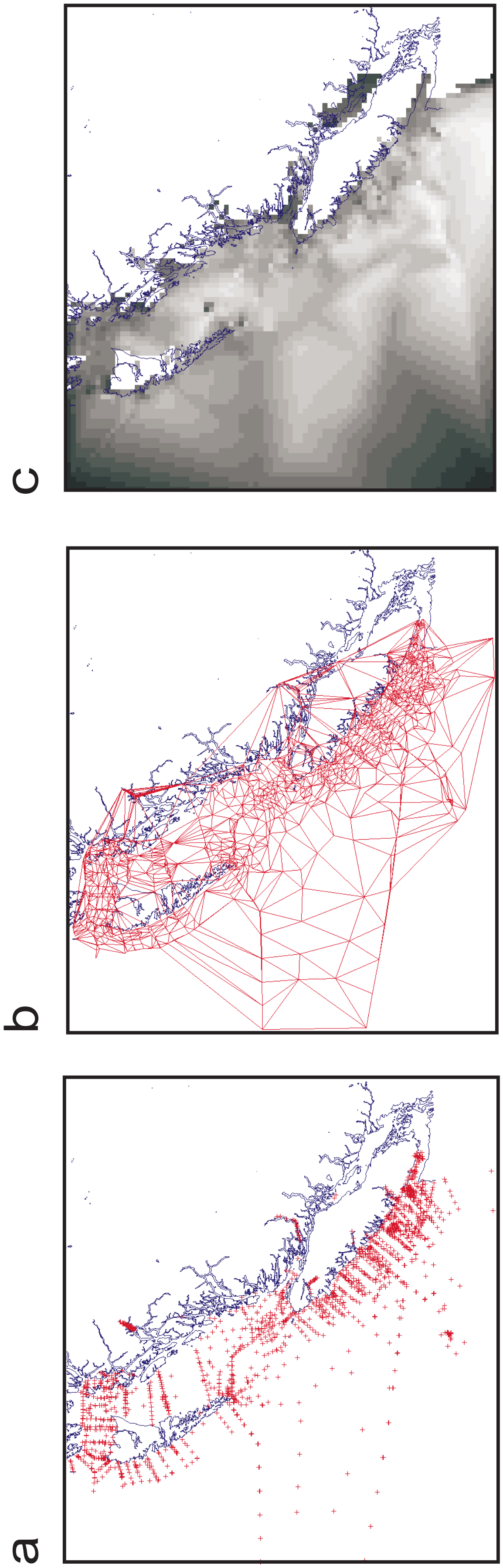


Fig. 4. Example of how point data were mapped onto the study grids using TINs. (*a*) Point temperature data for July; (*b*) TIN used to interpolate temperature to unsampled areas; (*c*) temperature grid resulting from the interpolation. This process was used to produce mean monthly and annual temperature and salinity grids.

tion (ENSO) events. Four of the warmest years since 1895 were associated with strong or moderate ENSO events (1983, 1987, 1992, and 1994) (Ware 1995). We chose these four years as representative of an extreme in temperature and used them to divide the temperature and salinity predictor data into "hot" and "other" years. We then generated two sets of model coefficients and compared the predictions quantitatively using a paired sample *t* test and qualitatively by comparing actual habitat predictions.

Results

The total number of each species killed, the number within the search area, the number of grid cells at the annual and monthly scales, and the mean probabilities of finding a whale (Pr(Wh)) in a grid cell are shown in Table 1. The effect of creating the observational units (grid cells) at annual and monthly time scales from whale locations can be seen by comparing the respective mean Pr(Wh) values.

Biological model

The preliminary analysis of whale presence–absence as a function of each of the independent variables showed two types of general trends: (*i*) linear trends that were either increasing or decreasing and (*ii*) trends that peaked at particular values (Gregr 2000). We examined the first-order (mean annual) effects of all six predictors on presence–absence as well as the interactions between each of the continuous variables for each level of month and depth class because of the apparent interactions between the continuous predictors and these two categorical variables (Fig. 2). This analysis confirmed the interactions between depth class and salinity and between temperature and month.

All species were most commonly found at particular depths and salinities. The response to temperature was linear for all species except humpback whales. Significant differences observed in the mean response of male and female sperm whales to temperature and salinity supported treating the sexes of this species independently.

Based on this exploratory analysis, we constructed a biological model that encompassed all of the observed effects. We defined the logit (linear component) of this a priori biological model as

$$(1) \qquad \mathrm{Pr(Wh)} \propto f[m + slope + zClass + z^2 + (S^2 \text{ in } zClass) + (T^2 \text{ in } m)]$$

where the probability of whale occurrence (Pr(Wh)) is only proportional to *f*[] because *f*[] is the logit, or linear component, of the generalized linear model, not the actual probability. Equation 1 contains all of the six predictor variables: the categorical variables month (m), *slope*, and depth class ($zClass$), the quadratic relationship in depth (z^2), and salinity (S^2) and temperature (T^2) nested in $zClass$ and m, respectively. The biological interpretation of this model is simply that whale presence is dependent in some way on the month, slope, and depth class and that there is an optimum salinity at each depth class and an optimum temperature in each month.

Model building

The regression terms, the amount of variance that each explained (R^2_{L}), and the degrees of freedom for the annual models are summarized in Table 2. In all cases, when quadratic terms entered the models, their respective linear components were included. The variable *slope* was significant for all species except blue whales. *zClass* was significant for all species except female sperm whales. Among the continuous variables, z^2 was significant for all species, S^2 was significant for fin, blue, and male sperm whales only, and T^2 was significant only for sei and male sperm whales. The total amount of variance explained (R_{L}^2) by the annual models ranged from a low of 0.23 (humpback whales) to a high of 0.49 (fin whales). Generally, R_{L}^2 values were higher for the groups (sei, fin, and male sperm whales) with higher sample sizes (i.e., number of whales killed).

The monthly models (Table 3) showed a higher diversity of model terms but provided marginally lower R_{L}^2 values than their annual counterparts. All three categorical variables were significant for all species with the exception of *zClass* for female sperm whales. For the continuous variables, z^2 was significant for all species, as was S^2, which was nested in *zClass* for both humpback and male sperm whales. *T* was omitted only from the female sperm whale model and was nested in *m* for sei and male sperm whales. The R_{L}^2 values ranged from 0.24 (humpback whales and male sperm whales) to 0.39 (sei whales).

Model predictions

The left-hand panels of the annual predictions (Figs. 5–7) show the prediction grids, while the right-hand panels show the locations of all the catches where position was recorded. Both panels show the 150-nmi search radius, which encompasses the data used in building and fitting the models. The positions shown in the right-hand panels include the small number of records from the Kyuquot Harbour, Naden Harbour, and Rose Harbour stations, which operated prior to 1948 and where positions of kills were recorded periodically.

Annual predictions for the baleen whales (Figs. 5 and 6) show sei, fin, blue, and humpback whales occupying habitats that are increasingly on-shelf, with sei whales in the areas furthest offshore. Predictions for humpback whales are almost exclusively on the shelf, while the habitat predicted for fin whales is in between that of the sei and humpback whales. Both the sei and fin whale predictions encompass a large area that includes the shelf break and an offshore area extending from the south end of the Queen Charlotte Islands southeastward, approximately one third of the way down Vancouver Island and reaching almost 100 nmi (185 km) offshore. This “habitat patch” is also apparent in the annual blue whale prediction. The annual humpback whale prediction includes large areas of the on-shelf region from the outer coast of both Vancouver Island and the Queen Charlotte Islands to the protected waters on the inside of these islands.

The annual sperm whale predictions (Fig. 7) highlight the difference between the sexes, with the males showing a much tighter distribution along the shelf and in the same habitat patch as identified for the baleen species. The prediction for female sperm whales is much more diffuse, although a stronger signal is evident in the habitat patch described above.

The seasonal predictions (Figs. 8–12) show monthly probability plots overlaid with the monthly positional data for the species. These predictions not only contain an expected monthly effect but also generally appear to refine the annual predictions, showing that the predicted probabilities shift as a function of month. This is most apparent with fin and humpback whales (Figs. 9 and 10), which have the highest probability of being on-shelf and in sheltered waters in the middle months (June–August for humpback whales and July and August for fin whales). Both sei (Fig. 8) and fin whales show an increasing probability of occurrence in the habitat patch off Vancouver Island.

Visual inspection of the correlations between the predictions and the data for sei whales shows good correlation until August, when the model fails to capture an apparent offshore movement of sei whales. The fin whale model agrees well with kills recorded in Dixon Entrance (north of the Queen Charlotte Islands) but only predicts whales in Hecate Strait in August. The seasonal humpback whale model performs well in July and August, but the month of May is poorly represented.

Seasonal predictions show a dramatic difference between male and female sperm whales (Figs. 11 and 12). Male sperm whale distributions appear to be similar to those of the baleen species, while female probabilities are distributed much more diffusely. The seasonal model for male sperm whales captures the majority of the data points in all months. The model predicts that female sperm whales should be virtually absent after May, which does not reflect the small numbers that were killed through September.

Model testing

The predictive efficiencies of the species models were defined using classification tables. The cutoff values selected consistently generated classification tables where the number of presence cells was predicted with much less efficiency than the absences. Overall monthly predictive efficiencies ranged from 0.60 (humpback whales) to 0.82 (male sperm whales), while the overall annual efficiencies ranged from 0.58 (blue whales) to 0.79 (fin whales).

For each group, we also compared the annual probability distributions generated by the “hot” (1983, 1987, 1992, 1994) and “other” predictor sets using a paired two-sample *t* test (Zar 1996). The resulting predictions were significantly different ($p < 0.0001$) in all cases. However, a qualitative comparison of the probability plots generated by annual models based on the “hot” and “other” data sets showed little apparent difference (Gregr 2000).

Discussion

The annual models predicted that fin, sei, and male sperm whales occurred, with near certainty, sometime over the course of the summer along the entire shelf break and in a large area extending 75–100 km beyond the shelf at the north end of Vancouver Island. This offshore region stretches from the continental shelf to approximately 100 nmi offshore and ranges from Kyuquot Sound, just south of Brooks Peninsula, to the northwest as far as the Dellwood Seamounts. Both the annual and the monthly models predicted a high probability of sei, fin, blue, and male sperm whales in this habitat patch, with lower predicted use in this area by humpback and female sperm whales. The monthly models served to capture some of

Table 1. Comparison of sample sizes and probability of whale occurrence (Pr(Wh)) for each species at annual and monthly time scales.

	Number of whales		Annual (total grid cells = 1507)		Monthly (total grid cells = 9029)	
Species	Total	Within 150 nmi	Presence cells	Mean Pr(Wh)	Presence cells	Mean Pr(Wh)
Sei	2716	2560	574	0.38	1004	0.11
Fin	3233	2613	680	0.45	1409	0.16
Humpback	598	433	212	0.14	288	0.03
Blue	249	146	118	0.08	138	0.02
Male sperm		1800	522	0.35	909	0.10
Female sperm		612	234	0.16	263	0.03

Note: Pr(Wh) is the mean probability of finding a whale in a grid cell. Pr(Wh) reflects the proportion of grid cells that contained whale kills. Monthly grid cells were created by extending the study grid across six months (May–October). Cells where depth was >10 m and salinity <30.0 ppt were removed. Whales were distributed by month and location of capture. The coefficients for the regression equations are shown in the Appendix.

Table 2. Annual regression models showing model terms (selected using stepwise forward regression), total variance explained (R^2_{L}), and degrees of freedom.

Species	Model					R^2_{L}	df
Sei	*slope*	+ *zClass*	$+ z + z^2$	$+ T + T^2$		0.48	1495
	0.021	0.275	0.182	0.005			
Fin	*slope*	+ *zClass*	$+ z + z^2$		$+ S + S^2$	0.49	1495
	0.027	0.147	0.284		0.029		
Humpback	*slope*	+ *zClass*	$+ z + z^2$			0.23	1497
	0.104	0.040	0.081				
Blue		+ *zClass*	$+ z + z^2$		$+ S + S^2$	0.25	1501
		0.098	0.128		0.026		
Male sperm	*slope*	+ *zClass*	$+ z + z^2$	$+ T + T^2$	$+ S + S^2$	0.38	1493
	0.172	0.084	0.097	0.008	0.020		
Female sperm	*slope*		$+ z + z^2$			0.25	1499
	0.010		0.235				

Note: The contribution of the terms to the R^2_{L} is shown below each term. Degrees of freedom are based on the number of grid cells in the analysis (n = 1507) and are uncorrected for spatial autocorrelation. The coefficients for the regression equations are shown in the Appendix.

Table 3. Monthly regression models showing model terms (selected using stepwise forward regression), total variance explained (R^2_{L}), and degrees of freedom.

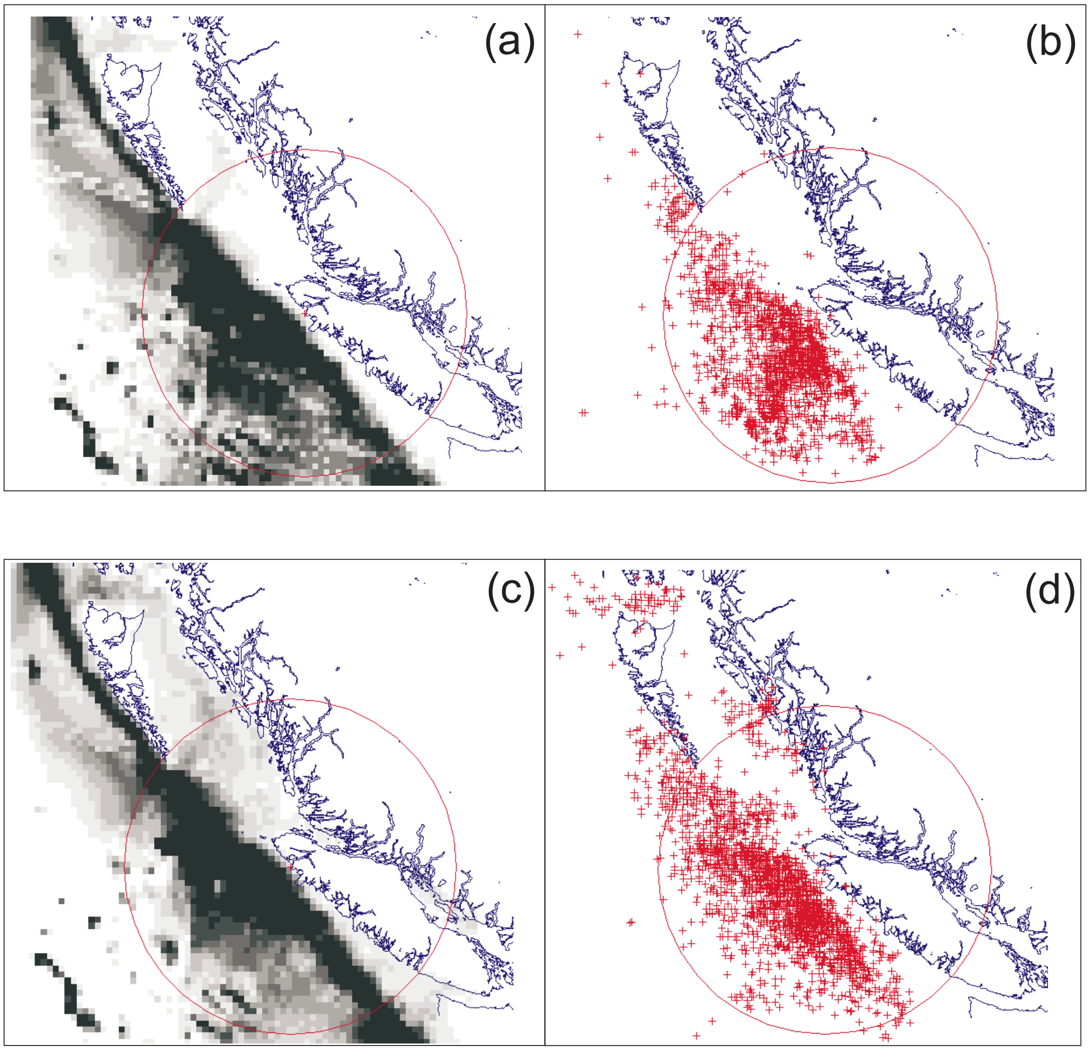
Species	Model						R^2_{L}	df
Sei	*m*	+ *slope*	+ *zClass*	$+ z + z^2$	$+ m/T$	$+ S + S^2$	0.39	9006
	0.116	0.012	0.147	0.098	0.009	0.010		
Fin	*m*	+ *slope*	+ *zClass*	$+ z + z^2$	$+ T$	$+ S + S^2$	0.39	9011
	0.025	0.016	0.085	0.162	0.002	0.011		
Humpback	*m*	+ *slope*	+ *zClass*	$+ z + z^2$	$+ T$	$+ zClass/(S + S^2)$	0.24	9007
	0.058	0.064	0.025	0.012	0.046	0.031		
Male sperm	*m*	+ *slope*	+ *zClass*	$+ z + z^2$	$+ m/T$	$+ zClass/S$	0.24	9005
	0.004	0.098	0.048	0.055	0.004	0.032		
Female sperm	*m*	*slope*		$+ z + z^2$		S	0.30	9015
	0.165	0.006		0.132		0.001		

Note: The contribution of the terms to the R^2_{L} is shown below each term. A slash denotes an interaction between categorical and continuous predictors. Degrees of freedom are based on the number of grid cells in the analysis (n = 9029) and are uncorrected for spatial or temporal autocorrelation.

the migratory movement of these species and provided predictions of seasonal peaks. Humpback and male sperm whales had the most complicated models at both annual and monthly time scales.

The apparent importance of the shelf break and the habitat patch was persistent at both the annual and the monthly time scales. The increased predicted probability in the southwest corner of the study area corresponds to a group of seamounts

Fig. 5. Annual probability predictions and kill locations for (*a* and *b*) sei whales (*n* = 2716) and (*c* and *d*) fin whales (*n* = 3233). Dark areas represent a high probability of whale occurrence and white areas represent a low probability. The circle shows the 150-nmi (275-km) search area used to select the data for the regression analysis.



well offshore and is largely a function of the depth and slope predictors. These results support the trends observed in the preliminary analysis, confirming that in almost all cases, each of the six predictor variables played some role in defining the probability distribution of these species.

A number of the predictors that we used have been examined in previous studies, and the results are broadly similar. Bottom floor topography appears to be correlated with odontocetes (Hui 1985; Tynan 1996) and fin whales (Woodley and Gaskin 1996), while depth and temperature have been used as predictors of right whale distributions (Moses and Finn 1997). Temperature has also been cited as affecting the distribution of baleen species (Nasu 1966; Woodley and Gaskin 1996) and sperm whales (Smith and Whitehead 1993). However, the majority of work relates cetacean distributions to chlorophyll concentrations (i.e., Smith et al. 1986; Jaquet et al. 1996). Given that the relative importance of the predictors to each species is complicated by scale and by the building of the predictive models, a detailed interpretation of these results is beyond the scope of this paper. Further discussion is limited to the predictive power of our models and to the broad ecological implications of our predictions.

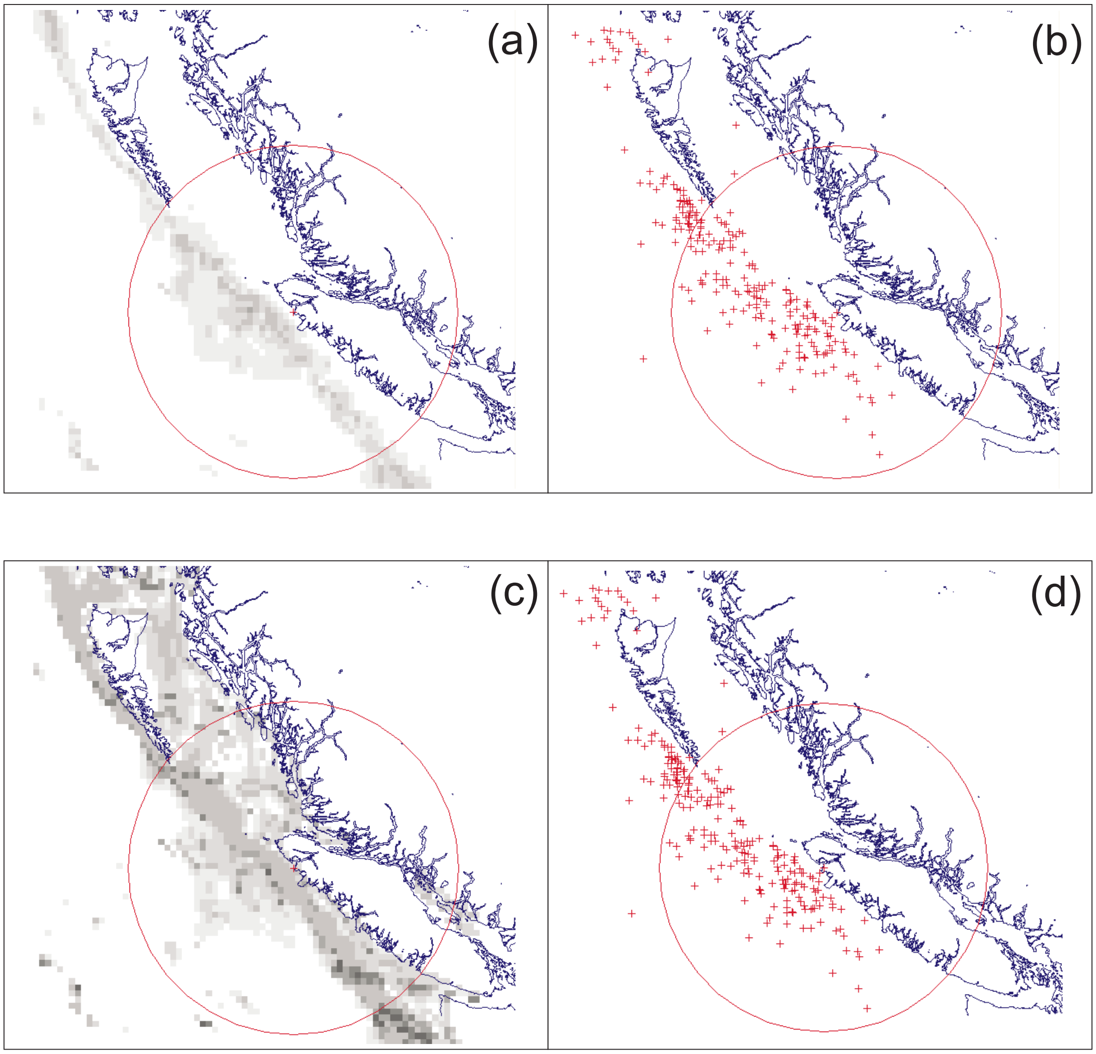
Sei whales

The annual model predicted a high probability for sei whales to be in deep water, while the monthly model showed strong seasonal effects. This is supported by the significant effects of depth class and month on the presence–absence of this species. The large amount of variance explained by the sei whale model suggests that this species may be closely tied to oceanographic conditions.

Fin whales

The annual habitat prediction for fin whales is consistent with Pike and MacAskie's (1969) observation that this species occurred mostly offshore but frequently entered exposed coastal seas such as Hecate Strait and Queen Charlotte Sound. The monthly predictions show how the movement of fin whales into these coastal seas is a seasonal effect (strongest in July and August). These monthly predictions support

Fig. 6. Annual probability predictions and kill locations for (*a* and *b*) blue whales (n = 249) and (*c* and *d*) humpback whales (n = 598). Dark areas represent a high probability of whale occurrence and white areas represent a low probability. The circle shows the 150-nmi (275-km) search area used to select the data for the regression analysis.



the interpretation that fin whales returned to feeding grounds off the British Columbia coast (Gregr et al. 2000). The amount of variance explained rivals that of the sei whale models, implying that the historic distributions of fin whales also had a close relationship with the predictor variables. The similarity in monthly predictions between the fin and sei whale models suggests that these two species respond in a similar way to the predictor variables. However, the inability of the monthly fin whale model to capture much of the on-shelf data suggests that either the contribution of the individual predictors is unequal or a significant predictor is missing from the model.

Humpback whales

The strong affinity of humpback whales for coastal waters is confirmed by the annual model. The model predictions are consistent with reports of humpback whales in the Strait of Georgia and Barkley Sound (Webb 1988) and show a high probability of humpback whales being over the entire shelf area, including enclosed straits and inlets.

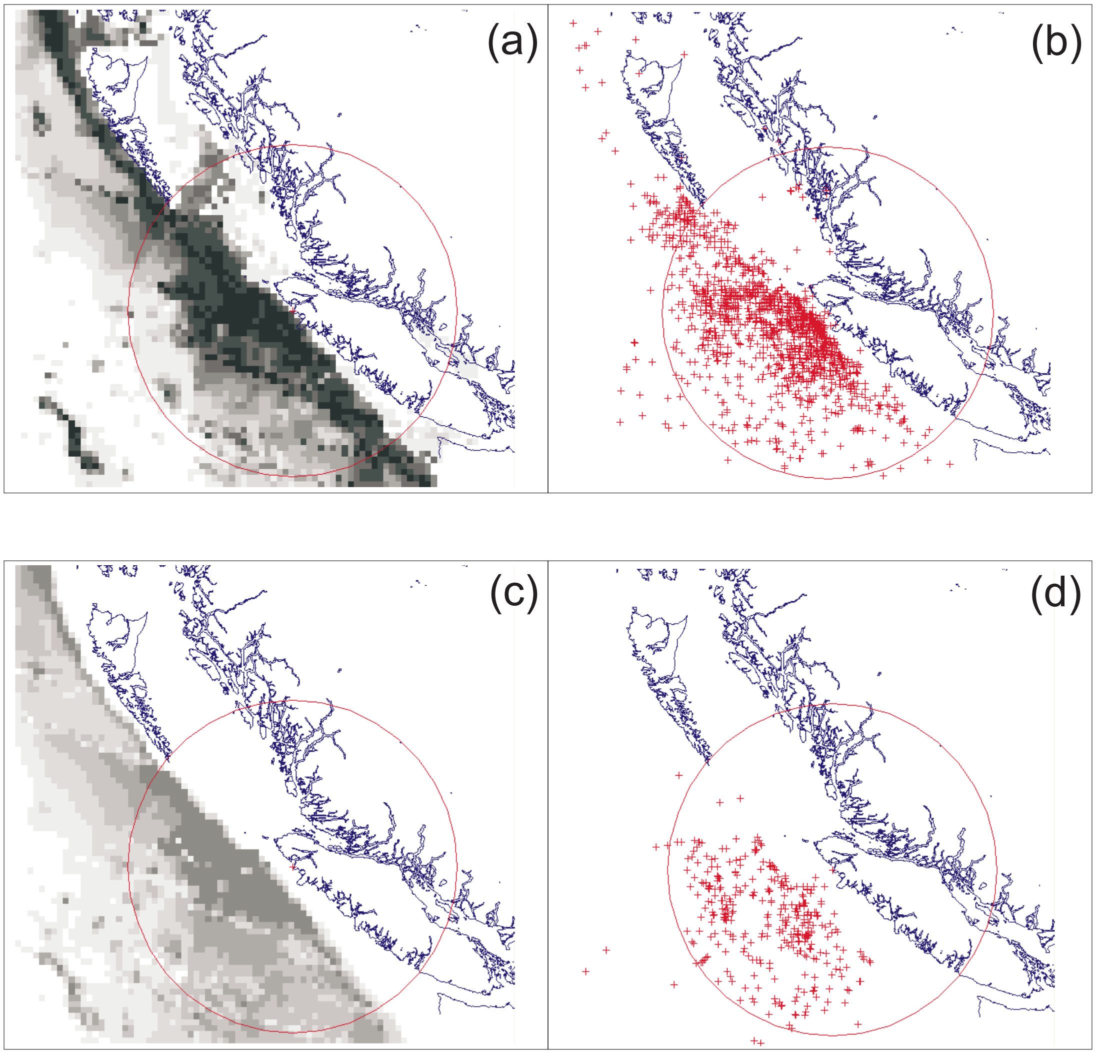
The strong interaction between depth class and salinity could be interpreted as a change in the behaviour of these animals as they move from deep water (migration), where they are relatively indifferent to salinity, to slope and shelf areas (feeding), where higher salinity may be an indication of prey abundance.

The humpback whale models (annual and monthly) explain less variance than the sei or fin whale models. This is also evident from the probability plots, which show lower probabilities for humpback whales. The low correlation coefficients of these humpback whale models are due in part to the small sample of whales killed and the partitioning of this sample into a monthly time scale. However, it may also imply that the association with the predictor variables is relatively weak and that other factors are better predictors of humpback whale habitat.

Blue whales

Given the small sample size available for this species, it is not surprising that the annual prediction shows little contrast. However, the fact that the model predicts blue whale use of the same habitat patch as sei and fin whales may be

Fig. 7. Annual probability predictions and kill locations for (*a* and *b*) male sperm whales (*n* = 1800) and (*c* and *d*) female sperm whales (*n* = 612). Dark areas represent a high probability of whale occurrence and white areas represent a low probability. The circle shows the 150-nmi (275-km) search area used to select the data for the regression analysis.



significant. Given that blue whales are believed to migrate away from coastlines (Mizroch et al. 1984) and feed in eastern Pacific coastal areas (Fiedler et al. 1998), it is possible that the smaller, younger blue whales that dominated the Coal Harbour catch (Gregr et al. 2000) frequented the habitat patch off northern Vancouver Island. This is indirectly supported by our preliminary analysis, which showed the mean depth for this species to be less than that observed for the fin and sei whales.

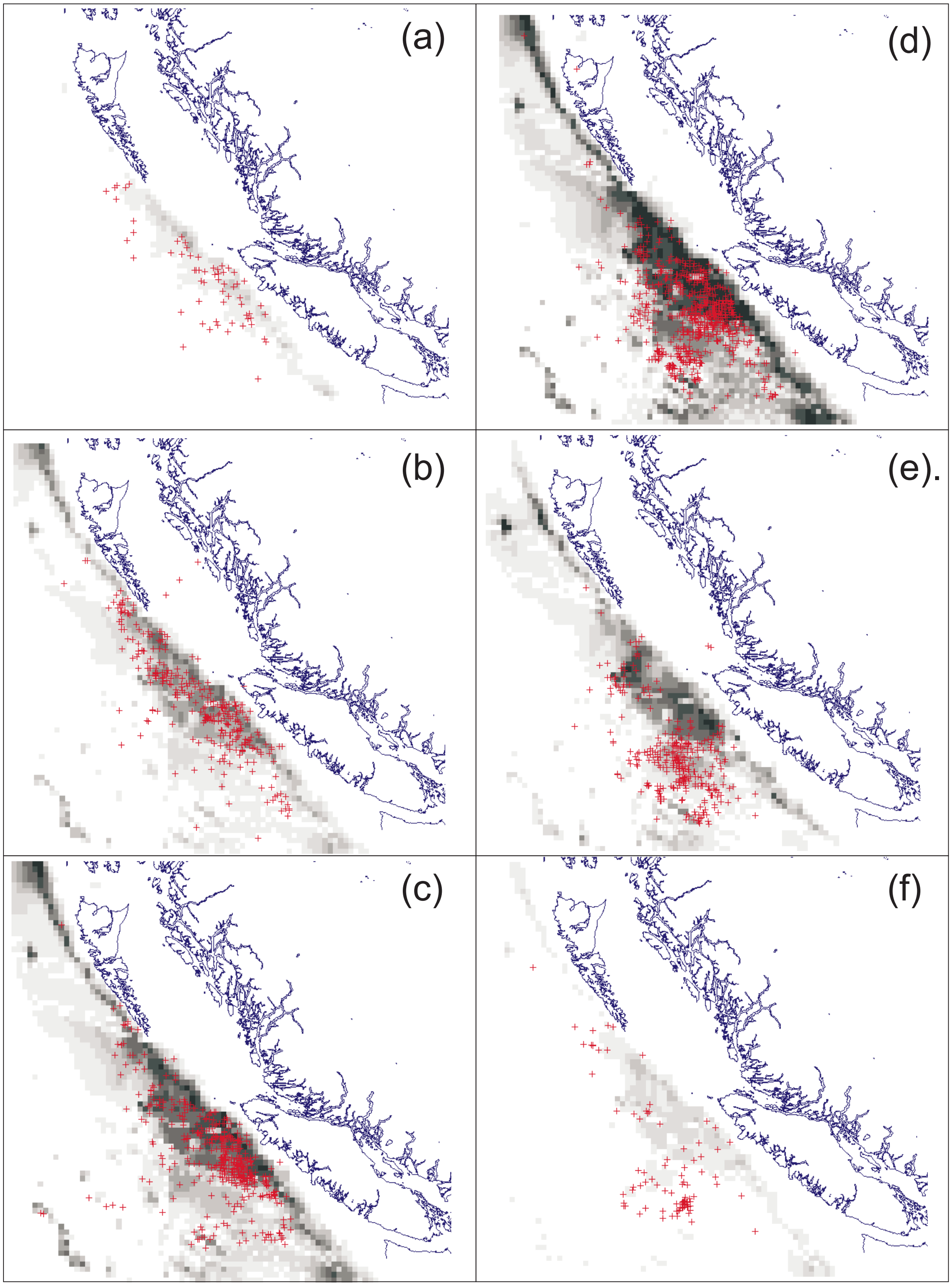
Sperm whales

The annual model predicted a narrower distribution for male sperm whales than for the baleen species and one that is more closely associated with the shelf break. This is consistent with the strong correlation between slope and male sperm whale presence. An apparent month effect on the preferred depth of male sperm whales shows movement into shallower water after May. This is supported by the spatial shift evident in the monthly probability plot.

The annual probability plot for female sperm whales predicts a virtually uniform distribution throughout the deeper waters, although the habitat patch is shown with a slightly higher probability. The monthly predictions serve only to distribute this annual prediction between April and May. This is consistent with the observed effects of depth class and month on the presence of female sperm whales. The lack of temperature and salinity predictors in the annual model and the inclusion of a simple, linear salinity component in the monthly model explain why there is little variance in the predictions. The fact that the monthly female sperm whale model, fitted with a sample one third the size of the male model, explained more of the variance than did the monthly male model (0.30 versus 0.24) is likely due to the limited temporal distribution of female catches.

The model suggests that female sperm whales were relatively uninterested in their surrounding oceanography and supports the hypothesis proposed in Gregr et al. (2000) that sperm whale mating occurred in British Columbia waters during April and May. Given that males are spatially segregated by size, with larger males at higher latitudes (Best 1979), a reasonable hypothesis is that breeding schools travel north to increase their encounter rates with stronger,

Fig. 8. Sei whale monthly probability predictions overlaid with the positions of whale kills: (*a*) April (*n* = 67); (*b*) May (359); (*c*) June (613); (*d*) July (1056); (*e*) August (495); (*f*) September (126). Dark areas represent a high probability of whale occurrence and white areas represent a low probability.

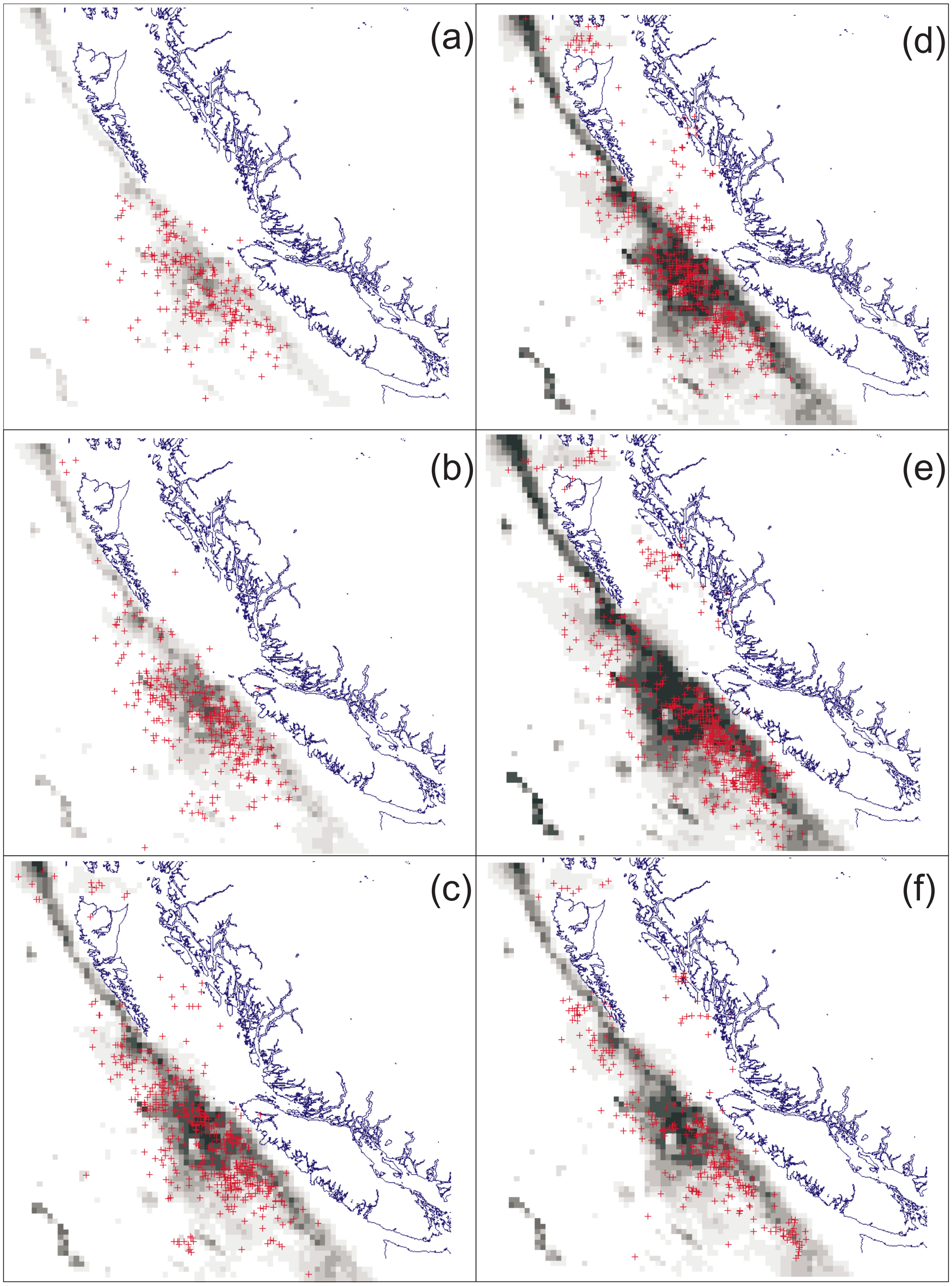


more mature males. Alternatively, given that the waters off Vancouver Island represent the northern boundary for female sperm whales (Reeves and Whitehead 1997), which apparently exhibit a strong degree of natal philopatry (Lyrholm 1998), this area may represent the breeding ground for a subpopulation of females. This mating hypothesis would help explain the presence of small numbers of females in the catch during all months.

Underlying processes

The processes responsible for the patterns that we observed are likely a function of oceanographic effects, which

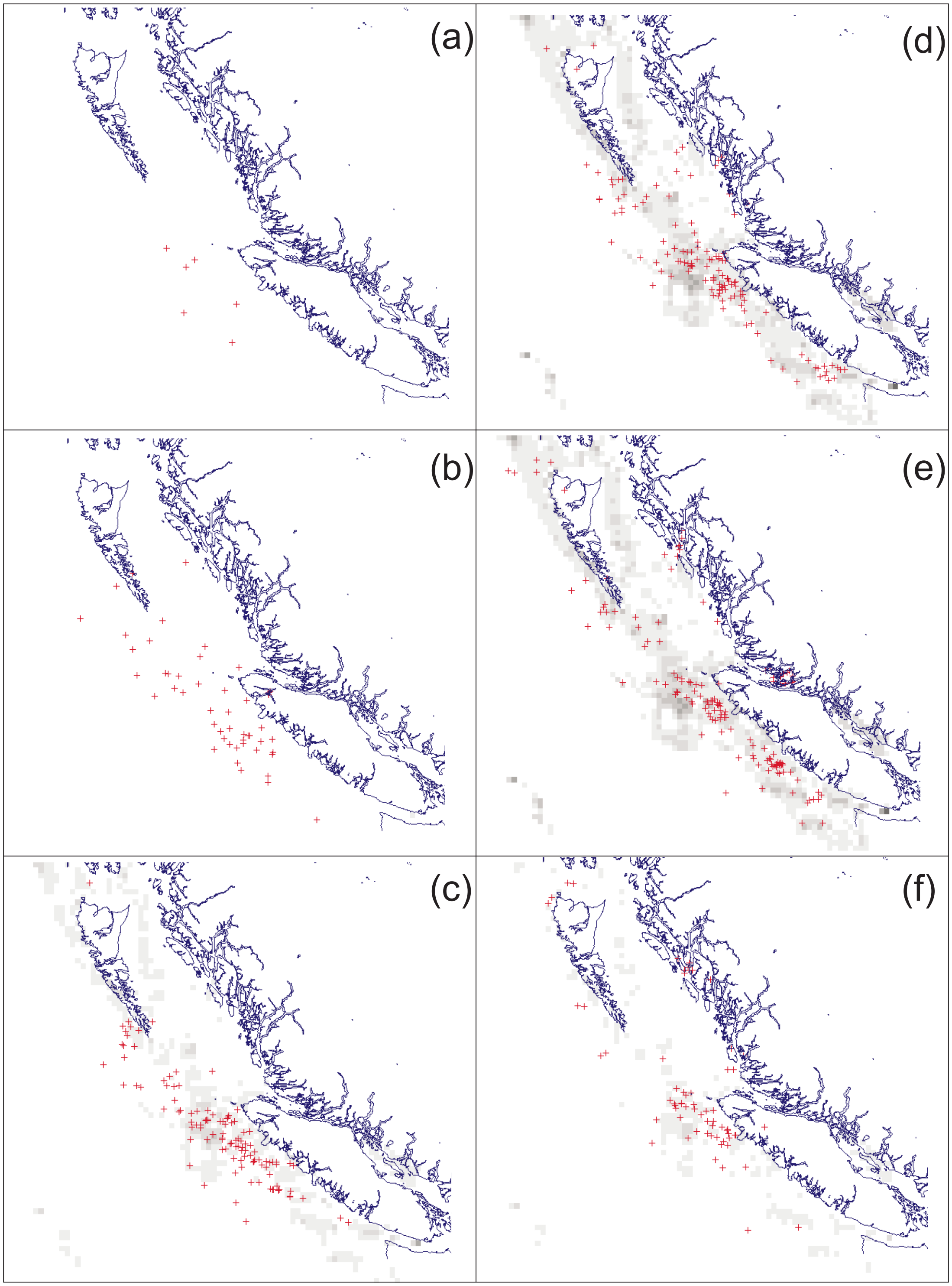
Fig. 9. Fin whale monthly probability predictions overlaid with the positions of whale kills: (*a*) April (*n* = 244); (*b*) May (404); (*c*) June (620); (*d*) July (727); (*e*) August (828); (*f*) September (410). Dark areas represent a high probability of whale occurrence and white areas represent a low probability.



result in enhanced productivity and (or) entrainment of prey, primarily zooplankton. Given the temporal (and spatial) lags between primary production and the development of grazing zooplankton populations, conditions that concentrate plankton may create a more suitable whale habitat than conditions that promote plankton growth.

A number of currents converge at the north end of Vancouver Island, including the Vancouver Island Coastal Current, which brings nutrient-rich, upwelled waters to the region from the southeast (Thomson 1981). This region is a highly productive area during the summer months and supports well-nourished resident zooplankton populations from spring through the fall (Mackas and Galbraith 1992). Summer circulations appear to cause a high washout rate of sur-

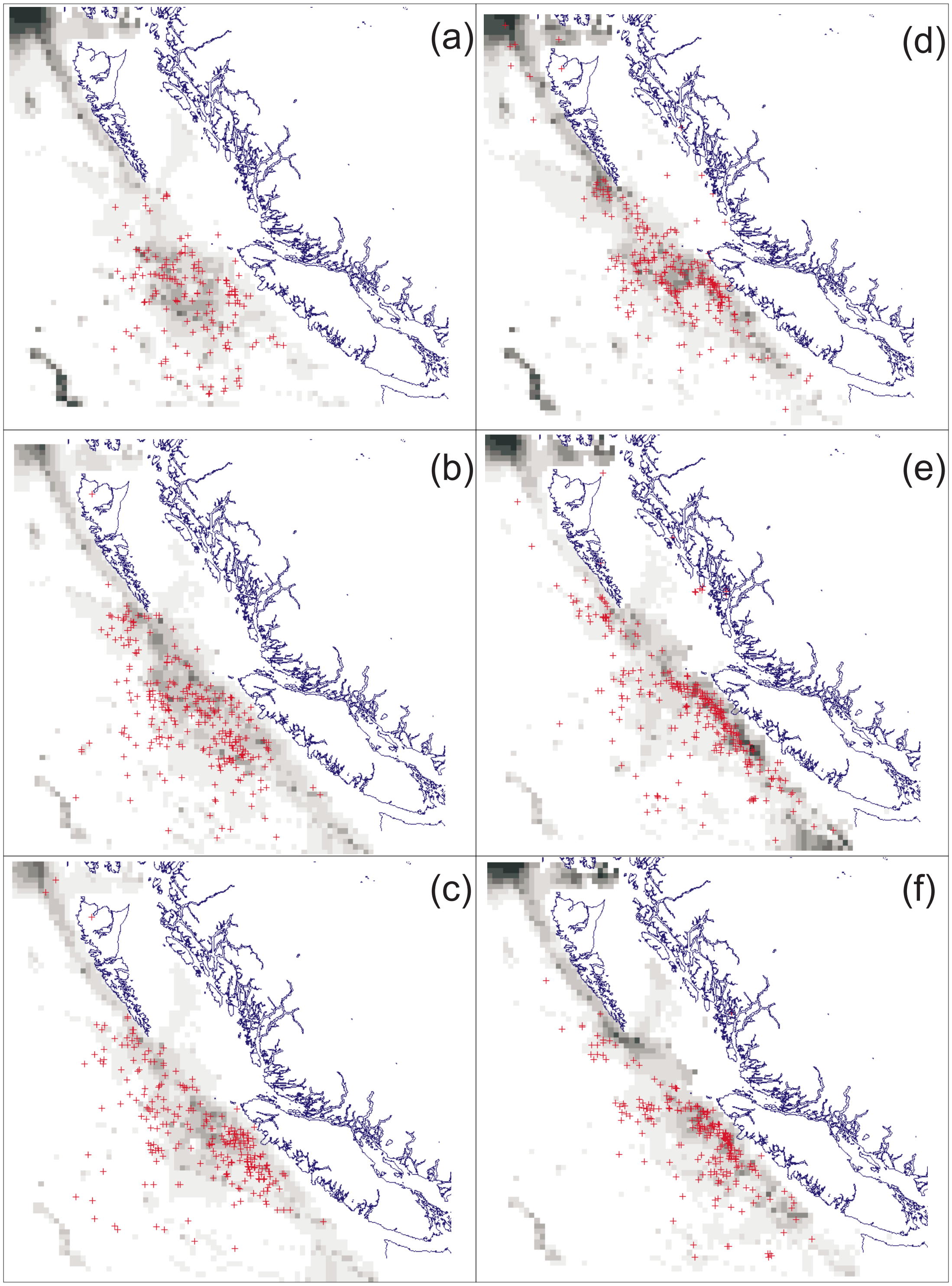
Fig. 10. Humpback whale monthly probability predictions overlaid with the positions of whale kills: (*a*) April (*n* = 6); (*b*) May (54); (*c*) June (133); (*d*) July (162); (*e*) August (170); (*f*) September (73). Dark areas represent a high probability of whale occurrence and white areas represent a low probability.



face zooplankton from on-shelf waters into offshore areas (Mackas 1992), where summer circulations are variable due to the bifurcation of the Kuroshio Current into the Alaskan and Californian currents (Thomson 1981). Thus, oceanographic conditions may combine to create an environment where nearshore primary production is translated into zooplankton concentrations offshore. The habitats identified by our study may be characterized by mesoscale fronts and eddies, produced by a number of converging currents, entraining both primary production and zooplankton.

The distributions of sperm whales, which feed primarily on cephalopods (Kawakami 1980), are unlikely to be influenced by the distribution of zooplankton. Rather, the data suggest that male sperm whale occurence is more closely re-

Fig. 11. Male sperm whale monthly probability predictions overlaid with the positions of whale kills: (*a*) April (*n* = 226); (*b*) May (402); (*c*) June (363); (*d*) July (388); (*e*) August (438); (*f*) September (340). Dark areas represent a high probability of whale occurrence and white areas represent a low probability.

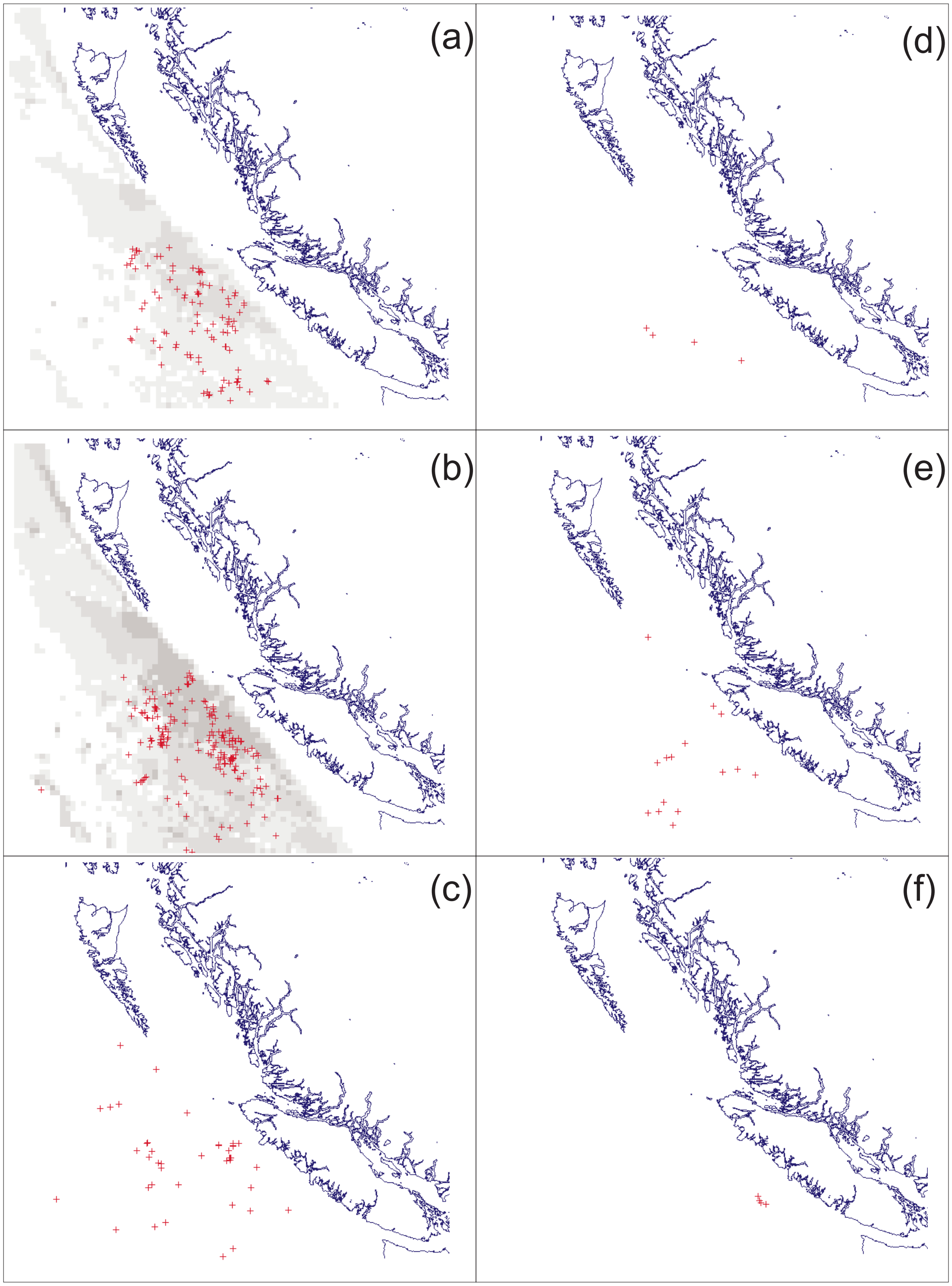


lated to depth and slope. Sperm whale associations with bottom topography have also been observed in the tropical Pacific (Jaquet and Whitehead 1999) and in the northeast Atlantic (Whitehead et al. 1992). The habitat patch proposed off northern Vancouver Island overlays the Dellwood Seamounts, a region of high relief. This would explain why the critical habitat predicted for male sperm whales overlaps with that predicted for the baleen species.

Model test results

Predictive efficiencies, calculated using classification tables, are most commonly applied to dependent data that have

Fig. 12. Female sperm whale monthly probability predictions overlaid with the positions of whale kills: (*a*) April (n = 186); (*b*) May (328); (*c*) June (88); (*d*) July (12); (*e*) August (21); (*f*) September (4). Dark areas represent a high probability of whale occurrence and white areas represent a low probability.



no spatial component (i.e., probability of disease, probability of failure, etc.). Although we are unaware of anyone using this method to evaluate dependent data with spatial characteristics, we are also unaware of any more suitable tests of spatial predictions. Experimenting with different values for the cutoff (i.e., the value that classified a prediction as a positive or a negative outcome) showed that the calculated predictive efficiency was highly sensitive to this value. The classification tables were also sensitive to the spatial distribution of the data, since the "presence" cells were highly autocorrelated. Therefore, the composition of the (randomly generated) prediction and testing samples strongly affected the results. These results highlight the need for spatially explicit quantitative methods to test the spatial predictions of this and other models of habitat.

The sensitivity of our model predictions to the oceanographic data showed that while the different predictor data sets (i.e., all, hot, and other) generated statistically different predictions, the resulting probability plots were almost identical. This can be interpreted in a number of ways.

The simplest explanation is that the sample size (19 375 grid cells) is so large that any small differences between the two predictions would be statistically significant. The validity of the test is also a concern, since the grid cells are likely autocorrelated, violating a key assumption of the *t* test. This highlights the need for more sophisticated statistical methods and procedures to ensure that statistical methods are correctly applied and that spurious statistical significance is not interpreted as biological significance.

However, if we assume that El Niño events do change the spatial location of critical habitats, it may be that the relationships represented by our habitat models do not accurately capture the response to variations in temperature. It may also be that our study is at the wrong spatial scale to detect a shift in habitat as a function of these predictors. A more detailed oceanographic model, perhaps containing depth profiles, combined with concurrent biological data, would address this and other similar questions about the relative importance of all of the predictor variables.

Model biases

The habitat probability plots depict the combination of predictors that best describe where the whales were found within the study area. These “oceanographic recipes” can be considered descriptions of suitable, or perhaps even critical, habitat for these species. However, a number of complicating factors — specifically, data independence, whaling effort, TIN interpolation, and the lack of concurrency between the dependent and independent variables — must be considered when interpreting the habitat plots.

Data independence

Although we did not directly address the issues of autocorrelation (the dependence of a particular measurement on its immediate neighbors, either in space or in time) or colinearity (the effects of one variable on another), the consequences of these effects for our analysis should be considered. Autocorrelation in the dependent data can be assumed to exist at both very fine and very coarse space–time scales due to certain accepted behaviour patterns. For example, the well-documented migration of baleen species implies temporal autocorrelation at monthly time scales and spatial autocorrelation at scales on the order of hundreds or even thousands of kilometres. Similarly, the congregation of whales in areas of high food abundance implies strong spatial and temporal autocorrelation on a scale of metres and minutes. Autocorrelation at these finer scales is further implied for all species in our study by the biological data, which provide numerous examples of multiple kills of a particular species at the same time and location. Thus, the commonly asked question about point data, whether or not the observed distribution patterns are random, is of little interest in our case. Rather, the two questions that need answering are at what temporal and spatial scales are whales correlated and what are the processes responsible? While we do not attempt to answer the first question, the question of processes is central to our study.

The lack of independence, both within and among predictors, complicates the interpretation of our habitat models. Since our sampling unit is a grid cell, spatial autocorrelation will exist for all the independent variables that we considered (i.e., the value at a particular grid cell will not be independent of the values of its neighbours). While methods exist to extract the spatial scales of these autocorrelations (e.g., variograms), it is not clear how identifying the spatial scales of these autocorrelations would help to identify the processes and relationships of interest. Similarly, while slope and depth may be correlated to some degree, quantifying this relationship using some form of categorical analysis (i.e., principal components analysis) does not provide any additional insight into what defines whale habitat and may, in fact, complicate the analysis by introducing abstract component terms.

We accept that there is a significant lack of independence in both the dependent and the predictor data sets, and we have not attempted to correct for these effects. Consequently, the degrees of freedom reported for the results are artificially high. To some extent, this lack of independence is offset by the large sample size and the use of generalized linear models and is more a cause for debating the relative strength and scale of the proposed processes rather than a reason for dismissing the hypotheses out of hand.

Effort assumption

The assumption of equal whaling effort throughout the 150-nmi search area warrants detailed consideration, as it is central to the analysis. Based on information available on the British Columbia coastal whaling industry, whalers traveled up to 200 nmi from shore and remained at sea for several days (Pike and MacAskie 1969; Webb 1988). Captured whales were marked and floated for later recovery while the vessels pursued additional animals. Evidence for the annual movement of whaling effort further and further offshore was provided by Gregr et al. (2000) who showed that the annual mean distance from shore for animals killed changed significantly between 1948 and 1967. Thus, the whalers clearly had to move through areas that were closer to Coal Harbour with greater frequency than through areas further away. It is therefore unlikely that equal effort was expended on all 1507 grid cells within the 150-nmi area. If the monthly time scale is included, the likelihood of equal effort over all 9029 monthly grid cells becomes very small indeed. Given that the change in effort with distance could be estimated, as could the relative monthly effort, it is theoretically possible to develop a technique for weighting the contribution of individual cells based on time and space. However, this additional research and analysis was beyond the scope of our study.

Fortunately, the behaviour of the whalers likely mitigated the effect of unequal effort in both time and space. Given the practices described above, it is likely that animals of any species encountered in nearshore areas were killed prior to the whalers proceeding further offshore. This effectively eliminated any significant monthly bias towards particular species, leaving legal lengths as the only remaining bias

(Gregr et al. 2000). Spatially, it can be assumed that the whalers operated with a fairly detailed knowledge of where whales were commonly found. The whaling captains operating from Coal Harbour had years of experience to draw upon. They were also provided with incentives to whale cooperatively and in later years relied on aerial reconnaissance (Webb 1988). Thus, it is likely that regions with few kills did in fact contain very few whales, even though they may not have been heavily searched.

Any effects of nonrandom sampling on our results would bias the predictions towards certain values of the predictor variables or cause the contributions of the individual predictors to the overall model fit to be incorrectly calculated. This is most apparent at the monthly time scale, where it can safely be assumed that equal effort was not expended in all months. While this monthly effort bias would be a serious concern if our study addressed animal abundance, limiting our interest to animal occurrence reduces its effects. Given the nature of the data, it is unlikely that this bias could be disentangled from the real process of whale migration.

Nonrandom spatial sampling (i.e., the preferential searching by whalers of some areas over others) would bias our habitat predictions towards the oceanographic conditions found in the more commonly searched areas. Since cells closer to Coal Harbour were searched with greater effort than those at a distance, by treating all cells equally, our predictions are biased to some degree towards oceanographic conditions at the more distant cells.

TIN interpolation

TINs are a standard method of representing point data. They are built by connecting data points into a series of triangles based on Delauney triangulation (Burrough and McDonnell 1998). The triangles are then used to interpolate missing values. The greater the density of point data, the smaller the triangles that are created. The accuracy of the interpolation increases with the density of the point data. Interpolations done across larger geographic areas (where point data are sparse) may fail to capture smaller scale regions of variation.

In our study, additional biases were likely introduced by edge effects and extrapolation. The outermost triangles of the TIN surface were artifacts of masking, which set the region outside the study area to zero. This made the interpolated predictor values inaccurate at the edges. In addition, a number of areas in the study area (British Columbia coast) required the predictors to be extrapolated outside the range used to define the models (i.e., within the 150-nmi radius). These extrapolations represent another type of edge effect: at the boundaries of the sampled data.

Concurrency of biological and oceanographic data

The whaling data (1948–1967) did not overlap temporally with the independent oceanographic data (pooled over the years 1980–1998). Although it is clearly more desirable to have dependent and independent measurements made concurrently, the spatial coverage of the oceanographic point data for years prior to 1967 is very poor. We therefore chose data density over data currency.

We have shown that this lack of temporal currency between the dependent and independent variables has statistically significant effects on the habitat predictions using a 10-km grid size. However, at larger spatial scales, we would expect this significance to decrease as localized differences in temperature are pooled and averaged. A more sophisticated oceanographic model is needed to explore how scale mediates the effects of changes in ocean temperature and salinity.

Despite the foregoing, areas of predicted high probability likely represent some aspect of whale habitat. The potential problems associated with the biases discussed only raise the question of the relative importance of the habitats described and do not invalidate our findings. While we may debate whether the habitats described here are “critical” or “important” or simply “suitable,” the areas identified should be acknowledged as having some level of importance to these species.

Future work

Our habitat predictions could be refined through field studies and through a multiscale analysis of the predictor effects at other combinations of spatial and temporal scales. Field tests of the habitat predictions would provide some essential validation of the predictions, while tracking and long-term monitoring of these relatively depleted populations would provide contemporaneous sighting and predictor data. Conducting multiscale analyses would provide valuable information on the scale and relative strength of the predictors, leading to a better understanding of the scales over which the proposed processes operate. Other predictors (i.e., primary production, depth of mixed layer, distance to frontal features, etc.) should also be considered if they can be consistently collected concurrently with the sighting data. The fit of the model could also be improved by addressing the problems of searching effort and autocorrelation. Cells in the study grid could be weighted based on assumptions about the distribution of effort, while an analysis of the correlations within and between the variables would improve the independence of the grid cells. Applying the approach to a larger geographic area, either by adding oceanographic data from California, Washington, Oregon, and Alaska or by constructing new models using positional data from other whale fisheries in the North Pacific (i.e., the pelagic fishery), would provide valuable comparisons of scale and process.

Our work extends previous studies that have been limited to correlation analysis between whale species and various oceanographic features. We treated a suite of independent oceanographic measures as predictor variables in a generalized linear model and compared the relationships at mean annual and monthly time scales. Our study shows that, even in the presence of nontrivial spatial and temporal autocorrelation, unequal sampling effort, and a lack of concurrency between the independent and dependent variables, reasonable hypotheses can be generated using this type of retrospective analysis. Our methods provide a novel approach for generating habitat predictions based on measurements of the physical environment. The software that we developed facilitates the integration of diverse spatial data sets and provides a powerful framework for exploring and presenting the predictions of critical habitat. The ability to quickly generate and view predictions at various spatial and temporal scales is useful to the investigation of scale effects and the linkages between pattern and process. Our study can therefore be considered as both a preliminary set of habitat predictions for five whale species that frequent British Columbian waters and a method for constructing and exploring habitat models.

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Appendix. Regression coefficients

Coefficients are shown for the annual and monthly models. The coefficients are for Poisson regressions. To convert to probabilities, the result is transformed according to

$$\text{(A1)} \quad \Pr(\text{Wh}) = 1 - e^{-u}$$

where u is the Poisson prediction.

The categorical variables slope, depth class, and month have a coefficient for each level, with the value for the first level = 0 (not tabulated). The coefficients for the continuous predictors are multiplied by the predictor value. Where interactions between the categorical and continuous predictors occur, there is a continuous coefficient for each level of the categorical predictor.

Table A1. Annual regression model coefficients for whale species.

	SW	FW	HW	BW	SPW-M	SPW-F
intercept	–1.98	–1660	–1.59	–2340	–2430	–8.03
slope1	–0.35	–0.308	–0.00195		–0.114	–0.297
slope2	–0.934	–0.407	0.488		–0.077	–0.138
slope3	–1.59	–0.741	0.347		–0.16	–0.61
slope4	–1.12	–0.398	0.773		0.768	–0.388
slope5	–0.931	–0.7	0.804		0.372	–1.15
slope6	–0.851	–0.371	0.679		0.817	–0.584
dclass2	1.91	0.336	0.073	2.78	2.1	
dclass3	2.64	1.15	1.22	3.52	2.84	
depth	–0.00561	–0.00498	–0.00279	–0.00382	–0.00208	–0.0074
temp	–0.516				0.459	
temp^2	0.0226				–0.022	
salt		105		149	154	
salt^2		–1.67		–2.36	–2.43	

Note: SW, sei whale; FW, fin whale; HW, humpback whale; BW, blue whale; SPW-M, male sperm whale; SPW-F, female sperm whale.

Table A2. Monthly regression model coefficients for whale species.

	SW[a]	FW	HW[b]	SPW-M[a,b]	SPW-F
intercept	–505	–877	–1310	–28.9	–21.2
month5	8.36	0.548	2.1	–5.28	0.558
month6	7.82	1.23	3.55	–5.42	–0.991
month7	6.11	1.6	4.12	–0.532	–2.71
month8	–4.18	1.85	4.18	–1.09	–2.12
month9	3.63	1.17	3.38	–1.64	–3.81
slope1	–0.296	–0.294	–0.191	–0.19	–0.313
slope2	–0.879	–0.38	0.355	–0.171	–0.142
slope3	–1.54	–0.717	0.311	–0.222	–0.632
slope4	–1.07	–0.327	0.758	0.76	–0.41
slope5	–0.809	–0.651	0.689	0.293	–1.15
slope6	–0.809	–0.355	0.479	0.741	–0.554
dclass2	1.99	0.398	–104	40.5	–0.0072
dclass3	2.66	1.15	–785	70.6	0
depth	–0.00535	–0.00506	–0.00231	–0.00243	
salt	31.8	55.8	80.7	1.01	0.385
			89	–0.198	
			134	–1.12	
salt^2	–0.514	–0.89	–1.25		
			–1.41		
			–2.13		
temp	0.717	–0.172	–0.299	–0.924	
	–0.0662			–0.239	
	0.0425			–0.206	
	0.194			–0.525	
	0.77			–0.44	
	0.198			–0.417	

Note: SW, sei whale; FW, fin whale; HW, humpback whale; SPW-M, male sperm whale; SPW-F, female sperm whale.

[a] Interaction between temperature and month.

[b] Interaction between salinity and depth class.