

**AN ANALYSIS OF HISTORIC (1908-1967) WHALING RECORDS FROM
BRITISH COLUMBIA, CANADA**

by

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Abstract

Analysis of data recorded from 24,862 whales killed by British Columbia coastal whaling stations between 1908 and 1967 revealed trends in the abundance, sex ratios, age structure and the distance from shore of sperm (*Physeter macrocephalus*), sei (*Balaenoptera borealis*), fin (*Balaenoptera physalus*), humpback (*Megaptera novaeangliae*) and blue (*Balaenoptera musculus*) whales. Trends in the relationships between records of where the whales were killed (n=10,275) and a simple oceanographic mode I were used to build generalized linear models, from which predictions of whale habitat were generated.

The catch data were analyzed using annual and monthly mean values. Monthly and annual variation in whaling effort was deduced from accounts of the history of British Columbia coastal whaling, and biases arising from changes in effort were considered in the interpretation of the results. Predictive habitat models were produced at annual and monthly time scales based on an initial analysis of the univariate relationships between whale presence-absence and six independent predictor variables (depth, slope, depth class, sea surface temperature and salinity, and month).

During the later years of whaling (1948 to 1967), the mean lengths of captured whales declined significantly in all five species and pregnancy rates dropped to near zero in fin, sei and blue whales. Monthly patterns in numbers killed revealed a summer migration of sei and blue whales past Vancouver Island, and confirms anecdotal suggestions that local populations of fin and humpback whales once spent extended periods in the coastal waters of British Columbia. Furthermore, the data strongly suggest that sperm whales mated (April-May) and calved (July-August) in British Columbia's offshore waters.

The habitat models showed that the continental slope and a large area off the northwest coast Vancouver Island may represent critical habitat for sei, fin and male sperm whales. Female sperm whales, blue and humpback whales appeared less sensitive to the predictor variables, however, the sample size for these groups was significantly smaller than for the other species. The habitat predictions lend support to the hypotheses regarding sperm whale breeding and predict humpback whale habitat in sheltered bays and straits throughout coastal British Columbia. The habitat models also generated hypotheses about the relationships and processes that link these whale species to their environment.

The historic whaling records reveal much about the migratory behaviour and distribution of the large whales species as they once were, and may continue to be, in the Northeast Pacific. Verifying the persistence of these trends in the remnant populations is a necessary and logical next step.

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Forward

This work is an analysis of historic whaling records from British Columbia, Canada. From 1908 to 1967 the whaling industry sought sei (*Balaenoptera borealis*), fin (*Balaenoptera physalus*), humpback (*Megaptera novaeangliae*), blue (*Balaenoptera musculus*) and sperm (*Physeter macrocephalus*) whales. They took over 24,000 whales during this period and recorded a number of variables for each capture such as species, length, sex and date of kill. A large portion of the records (n=8,164 whales) also include the location of the kill. This rich database has never before been explored in any detail, yet contains valuable information about the natural history (e.g. timing of migration, seasonal distribution) of these whale species and the effects of whaling (e.g. reduced reproduction, local extirpation) on the populations that frequented the coastal waters of British Columbia. The data also provide insights into where the great whales were once found, and a means to describe and identify regions of potentially critical habitat.

The goal of my study was to develop a predictive model of whale distributions and use it to identify whale habitat for the five species that dominated the British Columbia catch record. I also wanted to identify any seasonal and annual trends which would help describe the seasonal movements and long term population level effects of whaling on each of these species.

Chapter One addresses the trends in the whaling records and examines the biases due to non-systematic data collection. Attention is paid to disentangling the biological significance from the regulatory, socioeconomic and technological factors that may bias the interpretation. I relate the monthly trends to existing literature, providing insight into the migration patterns and population structure of the great whales in the Northeast Pacific Ocean.

I present the habitat models in Chapter Two, along with a new methodology and software tool developed to support the model building. The methods required a detailed analysis of the relationship between the species under investigation and six potential predictor variables (depth,

slope, depth class, temperature, salinity and month). This resulted in three, multi-panel figures for each species, totaling 165 panels contained in 15 figures. While these figures are fundamental to the model development, they are presented in *Appendix A: Presence-Absence Scatter Plots* to improve the readability of the text.

After exploring the relationships between the predictor variables and each individual species, I generated probability distributions for each species in the study using generalized linear models. These probabilities, which I interpreted as habitat preferences, allowed me to propose some hypotheses about why these predicted habitats might be attractive to the great whales that once frequented British Columbia waters.

Chapter 1 - Seasonal migration patterns and annual changes in population structures

Introduction

Historic whaling records from Alaskan and Californian whaling stations have provided much information on the seasonal distributions of the great whale species and on the impact of whaling on the whale populations. Reeves *et al.* (1985) summarized the catch records for 6,188 whale kills from two stations in Alaska between 1912 and 1939. They reported a decline in the availability of blue whales (*Balaenoptera musculus*) and a predominance of males in the catch of sperm whales (*Physeter macrocephalus*). Brueggeman *et al.* (1985) used the same data to elaborate on the abundance, distribution and population characteristics of blue whales. Clapham *et al.* (1997) summarized stomach content and body length data from 2,111 animals, mostly humpback whales (*Megaptera novaeangliae*), killed by two stations operating in northern California between 1919 and 1926. They reported sex ratios close to 1:1 in the catch of humpback, fin (*Balaenoptera physalus*) and sei (*Balaenoptera borealis*) whales.

These studies of whaling data from operations in Alaska and California did not demonstrate any seasonal migration or variation in the sex ratios for the species considered, nor did they relate the catch records to existing hypotheses about the stock structure in the North Pacific. The migration and population structure of these five species can be examined by analyzing the data from 24,862 whales killed from British Columbian whaling stations during a 60 year period (1908-1967).

The size and completeness of the British Columbia (BC) catch data present a unique opportunity to identify seasonal abundance trends that were not apparent in previous studies of historic whaling records. My objective was to identify the movements and structure of the seasonal migrations of sperm, sei, fin, humpback and blue whales and to relate the catches to what is currently known about the population structure of these great whale species that once frequented

British Columbian waters.

I begin with an overview of whaling in BC, and then describe the methods used to identify significant annual and monthly trends. Significant findings are outlined in the results, and the subsequent discussion provides an interpretation of the trends, taking into account the biases due to non-systematic data collection. Attention is paid to disentangling the biological significance from the regulatory, socioeconomic and technological factors that may bias the interpretation. The monthly trends are related to existing literature, providing insights into the migration patterns and population structure of the great whales in the Northeast Pacific Ocean.

Whaling in British Columbia

Figure 1.1 shows the locations of the coastal whaling stations that operated in Washington, BC and Alaska during the 1900s. The stations responsible for the majority of the kills operated in BC between 1905 and 1967. Data collected from the BC stations can be divided into two eras based on years of operation. The first era, from 1905 to 1945, includes data from the Vancouver Island stations of Sechart (1905 to 1917) and Kyuquot (1907 to 1925), and the Queen Charlotte Islands stations of Rose Harbour (1910 to 1943) and Naden Harbour (1910 to 1941). The Coal Harbour station (1948 to 1967) was the only BC station to operate after the Second World War. Data collected at this station comprise the second era.

Between 1908 and 1967, the BC stations killed at least 24,862 whales that included fin (n=7,605), sperm (n=6,158), humpback (n=5,638), sei (n=4,002), and blue (n=1,398) whales.

The distribution of these major target species among the stations (Figure 1.2) shows the change in catch composition over time. Data on species, sex, length, location and date of capture were recorded, although not all information was collected for the same time period or with the same degree of accuracy. The catch also contained a number of other species including Baird's beaked

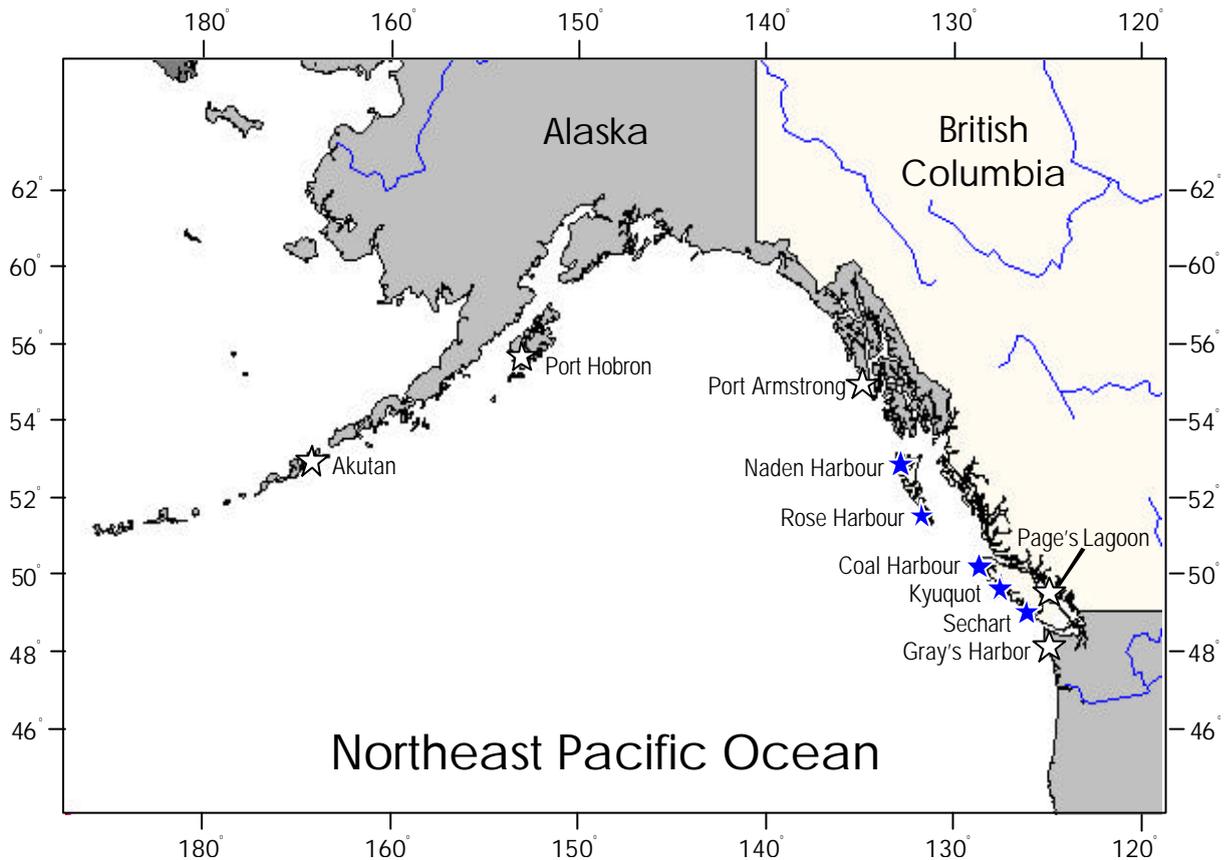


Figure 1.1: Locations of coastal whaling stations (1905 to 1967) in the Northeast Pacific Ocean. Stations included in this study are shown in black, stations not analyzed are shown in white.

whales (*Berardius bairdii*, n=41), minke whales (*Balaenoptera acutorostrata*, n=1) and right whales (*Balaena glacialis*, n=8). Eleven gray whales (*Eschrichtius robustus*) were taken at Coal Harbour in 1953 under a research permit. These species were caught in low numbers because of earlier heavy exploitation (during the 1800's for gray and right whales) and low commercial value due to their small size (i.e. Baird's and minke whales). Detailed morphometric measurements, which were collected between 1962 and 1967 at the Coal Harbour station, were not analyzed as part of my study.

Modern, shore-based, commercial whaling in the eastern North Pacific started in 1905 with the latest available technology. This included exploding harpoons and steam powered "catcher"

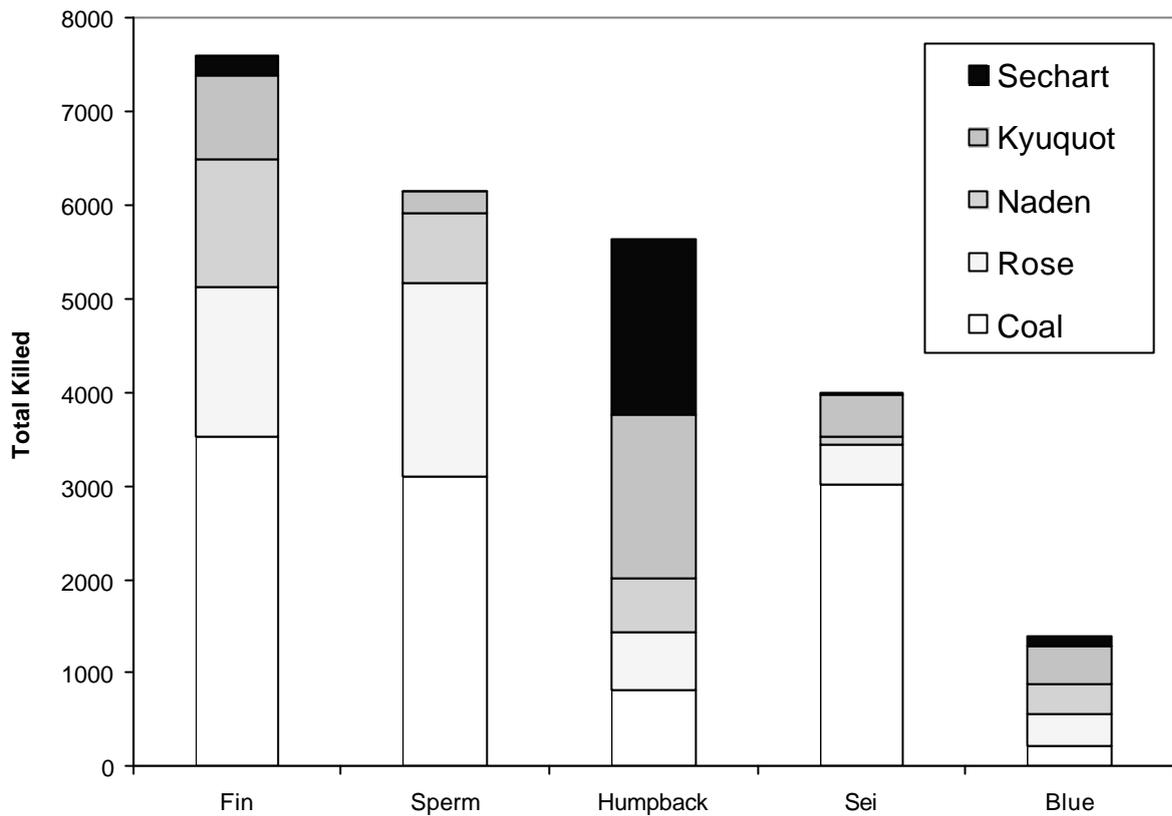


Figure 1.2: Distribution of the five major target species among the five British Columbia whaling stations. The bars are ordered from top to bottom in the order that the stations operated, giving an idea of the temporal distribution of the catch.

vessels which allowed the exploitation of whale species that were previously too fast and too strong to hunt (i.e. fin and blue whales). Further technological improvements included wireless telegraphy (1920s) and the use of spotting planes (1919) to track whale migrations (Rose Harbour and Naden Harbour, Tonnessen & Johnsen 1982). These advances dramatically improved the searching efficiency of the whalers. The adoption of sonar (1950s) further increased their efficiency. Advances in whale processing improved the profitability of the whaling industry. Reduction techniques (1900) allowed the complete whale to be processed, while refinement of the hydrogenation process (1912) removed the odor from whale oil. These techniques increased the demand for whale oil and resulted in a relatively stable climb in whale

oil prices from 1900 through to 1920 (Webb 1988). Afterwards, prices fluctuated dramatically in response to global market conditions.

During the second era of coastal whaling (1948 to 1967), operations at Coal Harbour were affected by a number of social factors including a changing workforce and marketing strategy. Unlike the previous era (1908 to 1941), the fleet at Coal Harbour was constantly upgraded and bonus schedules were designed to encourage cooperation among the fleet (Webb 1988). A 1962 agreement (Webb 1988) between BC Packers Ltd. and a Japanese firm to ship frozen sei whale meat to Japan dramatically improved the skill of the workforce and made the sei whale the preferred target species. The sei whale remained the target species until the depletion of animals and competition from vegetable oils ended commercial whaling in BC in 1967.

Methods for Data Analysis

I analyzed records archived from five of the six BC whaling stations: Sechart, Naden Harbour, Rose Harbour, Kyuquot and Coal Harbour. No records from the station at Page's Lagoon, or for the years prior to 1908, were found and are presumed lost. The surviving records include company processing logs, catcher logbooks, data sheets and reports to the International Whaling Commission (IWC) (Table 1). The quality of the information recorded for each whale killed increased over time. Data from 1908 to 1943 were available from company records only, but regulations adopted in 1935 helped to standardize the data collection. Data reliability was further improved when whaling resumed in 1948 as additional regulations were imposed and radar improved positional accuracy.

I analyzed the data for species where over 100 animals were killed (sperm, sei, fin, humpback and blue whales) to maximize the power of these analyses. The sample sizes for the remaining species (right, gray, minke and Baird's beaked whales) were too low. Annual catch composition

was determined using the entire catch of these five species (n=24,801). Sex ratios were calculated for all sex specific data (n=12,428), which were not collected prior to 1924 and were collected consistently only at Coal Harbour. Sex ratios were calculated as the proportion of males in the catch. I examined available data for seasonal and long-term trends in body lengths (n=12,158) and sex ratios. Only data collected at Coal Harbour were used to test annual trends for significance due to the temporal and technological differences between the Coal Harbour station (1948 to 1967) and the earlier stations (1905 to 1941). The data from all stations were pooled for the seasonal analysis after visual inspection of the monthly trends confirmed that they did not differ between the two eras. Lengths were compared to age at sexual maturity estimates (Leatherwood and Reeves 1983) and the proportion of mature animals compared on an annual and monthly basis.

Exploration of reproductive data included an examination of monthly and annual trends in pregnancy proportion and an analysis of the timing of mating and calving using a scatter plot of fetus lengths against day of capture (n=721).

Distance to shore measurements (i.e. to the nearest coastline) were calculated using positional data recorded for 8,553 kills within 200 nautical miles (370 km) from Coal Harbour. Positional data from the first era, and for the years 1949 to 1951 were omitted from this analysis because of poor precision and accuracy. Mean distances were examined by species and sex to evaluate monthly and annual variation in the distance from shore.

All values are reported as either annual or monthly means and are plotted with standard errors. Sex ratios were calculated as proportion of males, and are shown with 95% confidence intervals. Deviations from equal sex ratios were tested for significance using the deviance test (chi-square

Table 1.1: Sources of data for Coal Harbour (1948-1967), Sechart (1908-1917), Kyuquout (1910-1925), Rose Harbour (1910-1943) and Naden Harbour (1911-1941).

Source ¹	Years	Stations ²	Data Description
IWC database	1948-1959	C	date, species, sex, length, foetuses and location of capture
plant tally books	1952-1955, 1963-1967	C	date, species, sex, length, foetus sex and foetus length of whales processed (1963 to 1967 have location of capture)
catch slips	1958-1962	C	date, time, species, location of capture
data sheets & cards	1962-1967	C	stomach contents, blubber thickness, foetus length, sex and testis or ovary weight
catcher logs	1963-1966	C	date, location, species, number of whales seen, number of whales killed, sea conditions and water temperature
Consolidated Whaling Corp.	1908-1923	N,R,K,S,B,A	Accounts of the daily, weekly and monthly catch by station, species and often by boat
Consolidated Whaling Corp.	1908-1923	N,R,K,S,B,A	Catch records. Daily and monthly totals by species, boat and station.
Consolidated Whaling Corp.	1916-1924	K	Analysis of whaling operations by year. Monthly totals, boat days, whaling and non-whaling days, oil and fertilizer produced.
Consolidated Whaling Corp.	1917, 1929-1943	N,R	Pilot logbooks, Chief Officers logbooks and Engineers logbooks. Descriptive accounts of where whales were caught.
Consolidated Whaling Corp.	1920-1943	N,R,K	Weekly catch report of whales caught and oil production.
Consolidated Whaling Corp.	1924-1943	N,R,K	Catch records. Daily records of species, length, sex and location of capture (for some years).
Consolidated Whaling Corp.	1928-1942	N,R	Gunners reports. Descriptive accounts of where whales were caught.

¹ Data for Sechart, Kyuquout, Rose Harbour and Naden Harbour were obtained from the Pacific Biological Station, Nanaimo, British Columbia, the British Columbia Provincial Archives, Victoria, British Columbia and the W. Lagen Collection, Suzzallo Library, University of Washington, Seattle, Washington. Data for Coal Harbour were obtained from the Pacific Biological Station, Nanaimo, British Columbia.

² Stations: C=Coal Harbour, K=Kyuquout, N=Naden Harbour, R=Rose Harbour, S=Sechart, B=Bay City, A=Akutan. Bay City and Akutan stations operated in the states of Washington and Alaska respectively. Sechart opened in 1905, but no surviving records were found for 1905, 1906 or 1907. Kyuquout opened in 1908 but no surviving records were found for 1908 and 1909.

test) on logistic regression models. Trends in means were tested for significance using a single factor ANOVA (F test) on polynomial regressions. Polynomial regression was conducted according to the forward selection method outlined in Zar (1996). All regressions were weighted with sample size to compensate for any lack of homogeneity in the variances. Mean values were removed from the analyses if their contribution to the total sample was less than one percent.

Results

Annual Catch Composition

The first era of modern, shore-based whaling in BC (1908 to 1945) focused on humpback, blue and fin whales (Figs. 1.2 and 1.3a). Early catches of blue and humpback whales were high, but numbers dropped by 1915. The majority of the humpback whales were caught from the Vancouver Island stations of Kyuquot and Sechart between 1908 and 1913 (Fig. 1.2). The majority of blue whales were caught during the same period, with Kyuquot and Rose Harbour responsible for most of these kills (Fig. 1.2). Fin whales were caught with roughly equal success by all stations, with their contribution to the catch declining during the first era from a peak in 1912 to a low in 1941 (Fig. 1.3a). In contrast to the decline of these three species, the catches of sperm whales increased at roughly the same pace as the catch of fin whales declined. The Queen Charlotte stations of Naden Harbour and Rose Harbour caught most of the sperm whales during the first era (Fig. 1.2). Sei whales, the last species to be heavily exploited, were caught in relatively small numbers during the first era. Their contribution to the catch during this period shows no apparent trend.

The second era of commercial whaling (1948 to 1967) focused primarily on fin, sperm and sei whales (Fig. 1.2) and was conducted entirely from Coal Harbour, on Vancouver Island. This period shows a dramatic rise and fall in the number of fin whales caught, peaking in 1958 with 573 animals. This is followed by a similar pattern in the sei whale catch (Fig. 1.3a), which peaked in 1964 with 613 animals. The catch of sperm whales during this period was substantial and appears to have been fairly constant. A small peak is evident for blue whales, but neither these, nor humpback whales, ever made a notable contribution to the total catch after the high takes during the beginning of the first era.

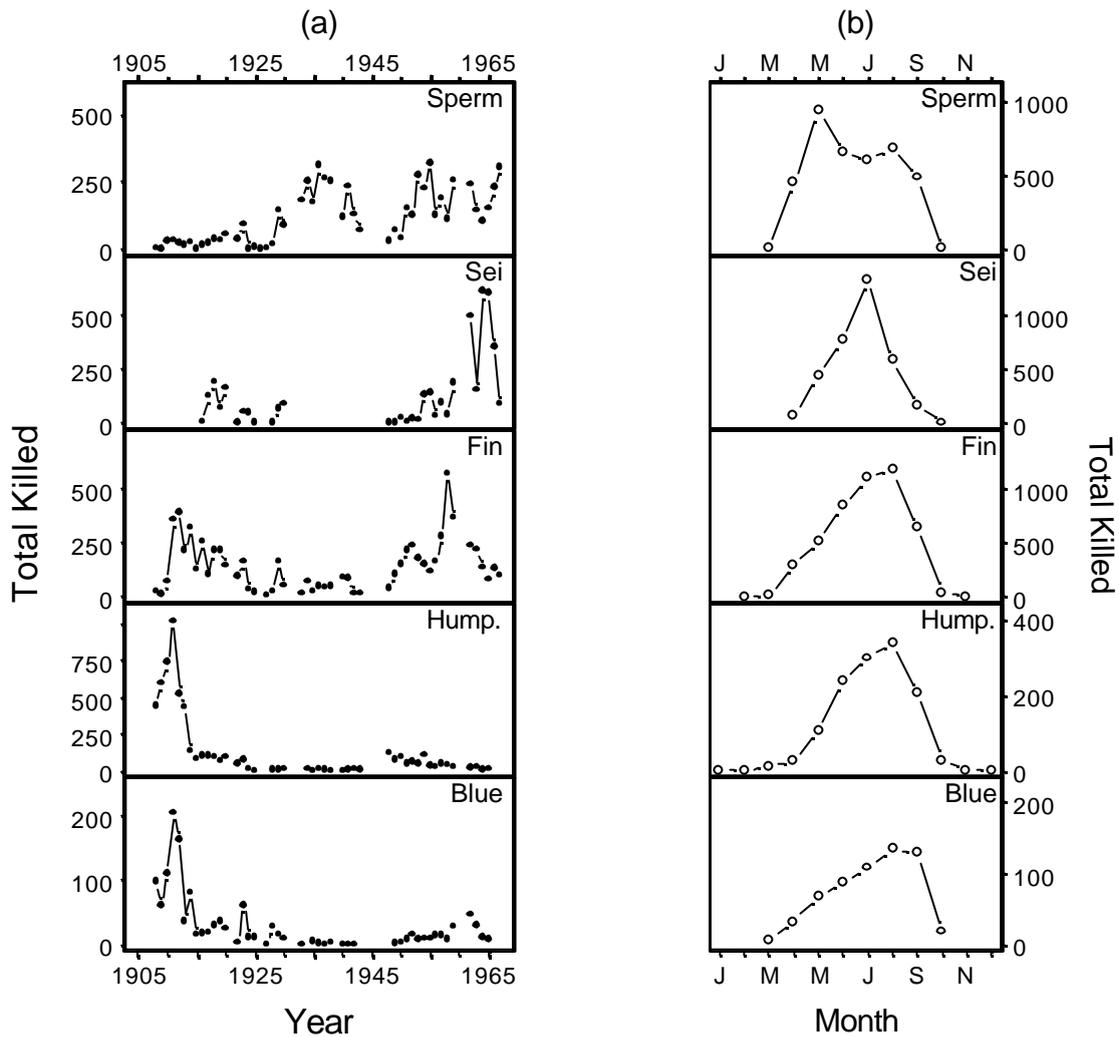


Figure 1.3: Total number of animals killed shown annually (a) and monthly (b), by species, for all British Columbia whaling stations.

The annual proportion of males in the catch of fin and humpback whales was close to 50% in all years where sex data were collected (Fig. 1.4a). For sei whales, the proportion of males varied significantly from year to year, ranging from a high of 77% to a low of 20%. The proportion of males in the blue whale catch was consistently less than 50%, however the sample size for this species was relatively small (Fig. 1.2). The sperm whale was the only species to show a significant decline in sex ratio from close to 100% males to less than 50% males during the second era of whaling ($\chi^2_{(13)} = 494.79$, $p < 0.001$).

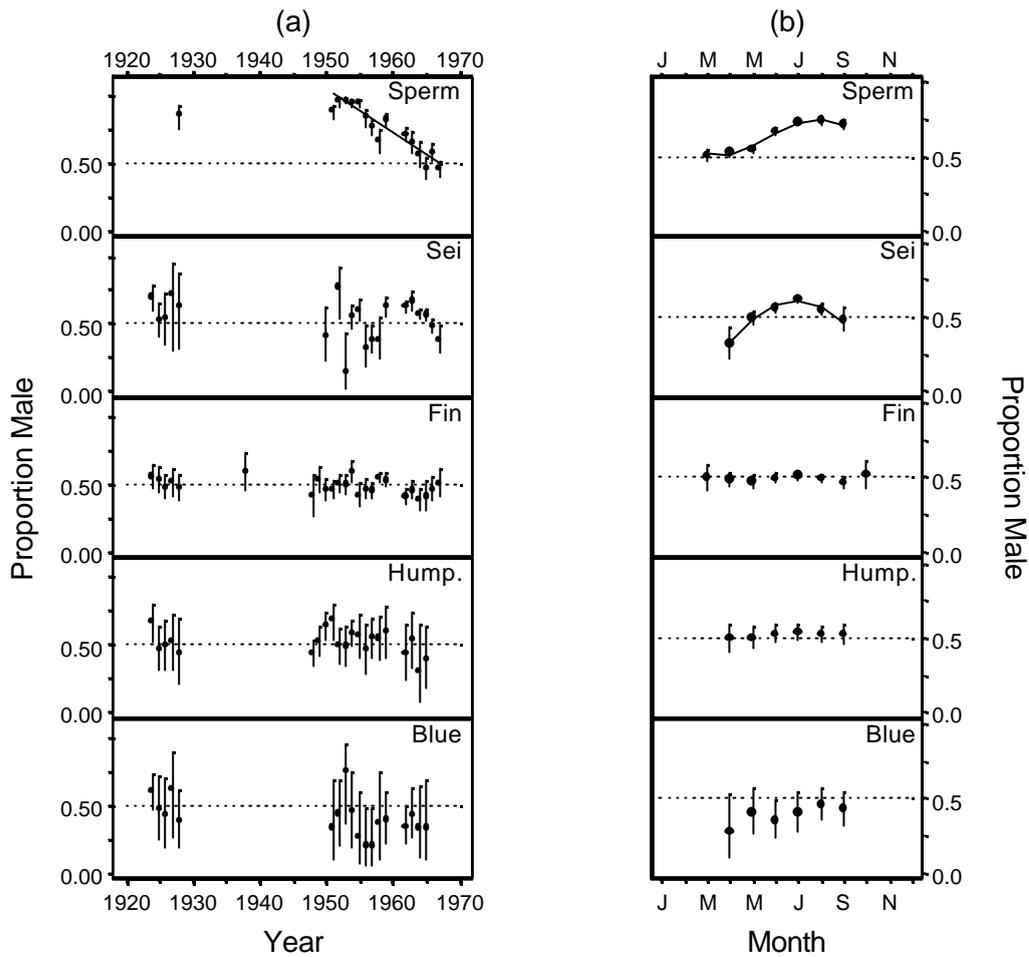


Figure 1.4: Proportion of males in the total catch shown annually (a) and monthly (b), for data pooled from all British Columbia whaling stations. The dashed horizontal lines denote a proportion of 0.50. The results are shown with 95% confidence intervals calculated for proportional data, using an expected value of 0.50. Statistically significant trends, based on logistic regression analysis ($\alpha = 0.05$), are shown as trend lines.

Monthly Catch Composition

In general, the number of whales killed for all species increased from spring to summer, and decreased as summer turned to fall (Fig. 1.3b). However there appeared to be species-specific differences in the timing of peak catches. Sperm whales were taken in large numbers in April, with a peak occurring in May. This was followed by a peak in the number of sei whales in July and in the number of fin, humpback and blue whales in August.

The proportion of males in the catch of humpback and fin whales remained fairly constant at 52% and 49% respectively throughout the season (Fig. 1.4b). The proportion of male blue whales remained below 50% (monthly average was 39%) but appeared to increase slightly over the course of the season. The male proportion in the sperm whale catch rose from an average of 53% (March to May) to an average of 72% (June to September). This change in the sperm whale sex ratio was a direct result of the disappearance of females from the catch (n=569 for March to May, n=148 for June to September). Sei whales also showed considerable variability in monthly sex ratio rising from 32% (April) to a peak of 62% (July) before dropping to 48% late in the season (September). Logistic polynomial regressions fitted to the monthly proportion of male sperm and sei whales showed that these monthly changes in sex ratio were significantly nonlinear (sperm: $\chi^2_{(5)} = 223.40$, $p < 0.001$; sei: $\chi^2_{(4)} = 7.18$, $p = 0.007$).

Mean Lengths

Between 1948 and 1967, significant declines took place in the mean annual lengths of male sperm whales ($F_{1,16} = 28.78$, $p < 0.001$, $r^2 = 0.643$) and female sei whales ($F_{1,16} = 11.99$, $p = 0.003$, $r^2 = 0.444$). There was no significant trends in the mean annual lengths of fin, blue or humpback whales (Fig. 1.5a).

Seasonal changes in mean lengths were examined by combining length data for all years, at all stations. Changes in mean monthly lengths are apparent for each of the species killed in BC, though these were not always statistically significant, and varied between the sexes (Fig. 1.5b).

The mean length of male sperm whales caught increased significantly between May and June, and remained high for the rest of the season ($F_{2,3} = 10.71$, $p = 0.043$, $r^2 = 0.877$). Lengths of female sperm whales showed little variation over the course of the season. Mean lengths of both sexes were consistently above the estimated length at sexual maturity.

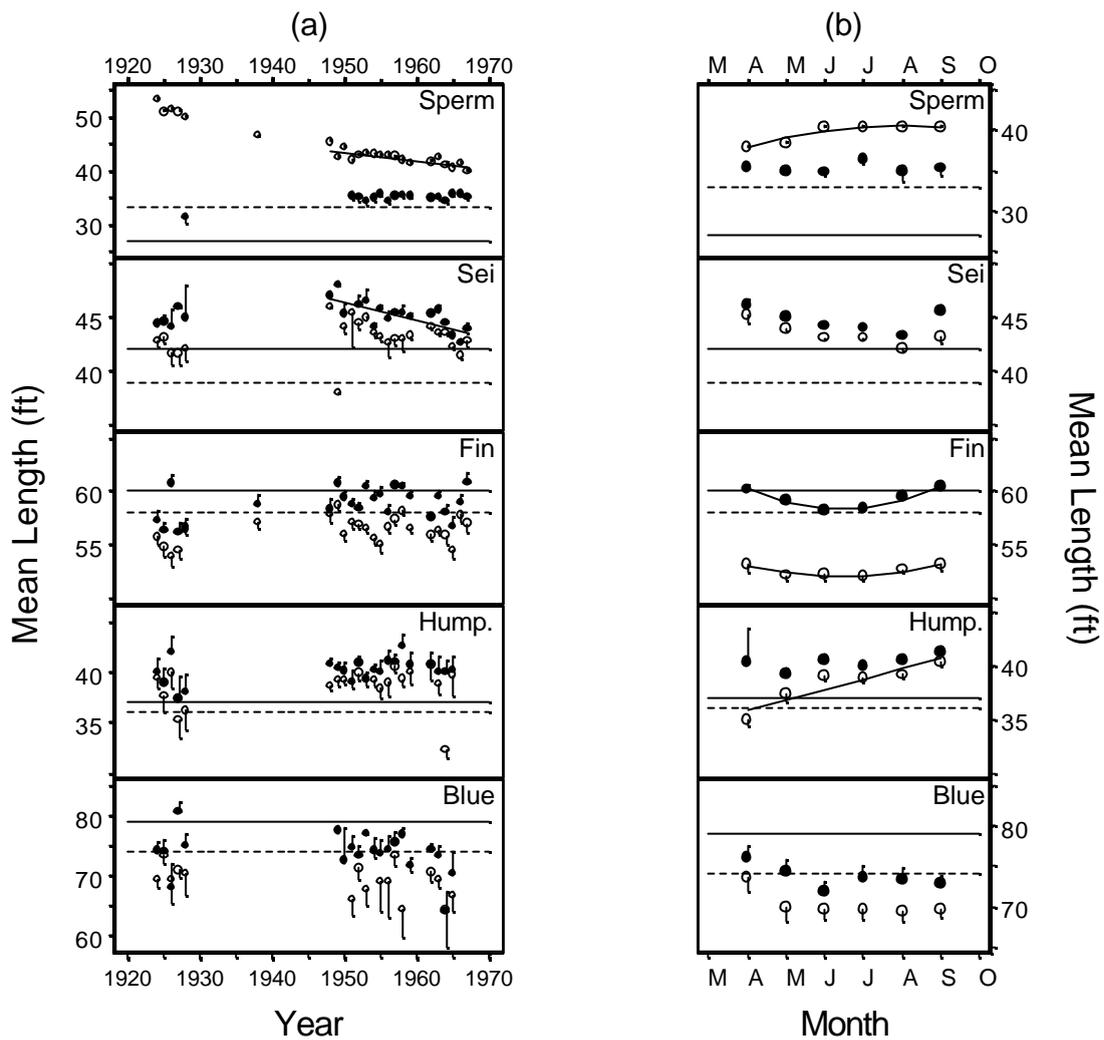


Figure 1.5: Mean lengths for males (○) and females (●), shown annually (a) and monthly (b), for data pooled from all British Columbia stations. Horizontal lines represent estimated lengths at sexual maturity for males (- - - -) and females (———). The results are shown with standard error bars, in one direction only, for clarity. Statistically significant trends, based on polynomial regression analysis ($\alpha = 0.05$), are shown as trend lines.

The mean lengths of fin whales caught showed a concave distribution with the shortest animals taken in June and August respectively. This change was significant for both sexes (male: $F_{2,3} = 11.92$, $p = 0.037$, $r^2 = 0.888$; female: $F_{2,3} = 29.15$, $p = 0.011$, $r^2 = 0.951$). Both monthly and annual fin whale lengths were generally below the estimated length at sexual maturity.

For the remaining three species, the monthly trends in sei whale lengths were not significant and the mean lengths of both sexes were above the length at sexual maturity. For humpback whales, males showed a significant increase in mean length over the course of the season ($F_{1,4} = 8.26$, $p = 0.045$, $r^2 = 0.674$), and both sexes were above the estimated maturity length in all years and all months (except for males in April). Finally, mean lengths for blue whales of both sexes were below the estimated length at sexual maturity for all months and all years, with no significant trend in monthly mean lengths.

Reproduction

The annual proportion of females that were pregnant decreased significantly for sperm, sei and fin whales (Fig. 1.6a) (sperm: $\chi^2_{(16)} = 16.54$, $p < 0.001$; sei: $\chi^2_{(16)} = 176.30$, $p < 0.001$; fin: $\chi^2_{(16)} = 72.00$, $p < 0.001$). For sei and blue whales, pregnant females were virtually absent from the catch by the 1960s. Only sei whales showed a significant decrease in the monthly pregnancy rate ($\chi^2_{(4)} = 43.97$, $p < 0.001$). The monthly proportion of female sperm whales in the catch that were pregnant increased until July, then dropped to near zero. In contrast, a fairly constant proportion of female fin whales were pregnant throughout the season (Fig. 1.6b).

Fetus lengths (Fig. 1.7) increased steadily for all the baleen species over the summer months, but sperm whale fetuses appeared to be near term in April through June. In contrast, fin and sei whales appeared to be near term in late September, while humpback and blue whale fetuses were approximately half the estimated birth length at the end of the whaling season (late September).

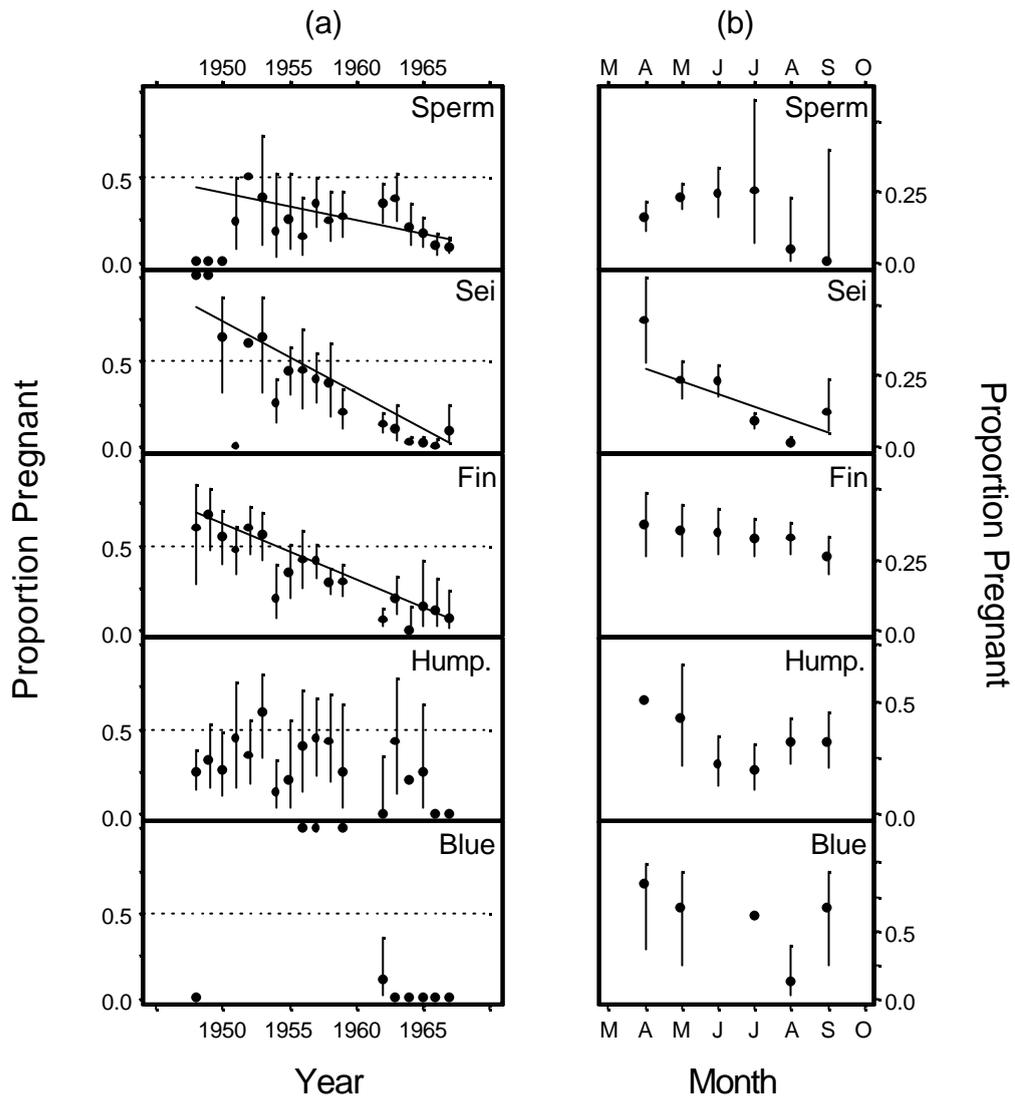


Figure 1.6: The proportion of pregnant females in the catch, calculated as the number of fetuses divided by the catch of females, shown annually (a) and monthly (b). The horizontal lines on (a) denote a proportion of 0.50. Results are shown with 95% confidence intervals calculated for proportions using an expected value of 0.50. Statistically significant trends, based on logistic regression analysis ($\alpha = 0.05$), are shown as trend lines.

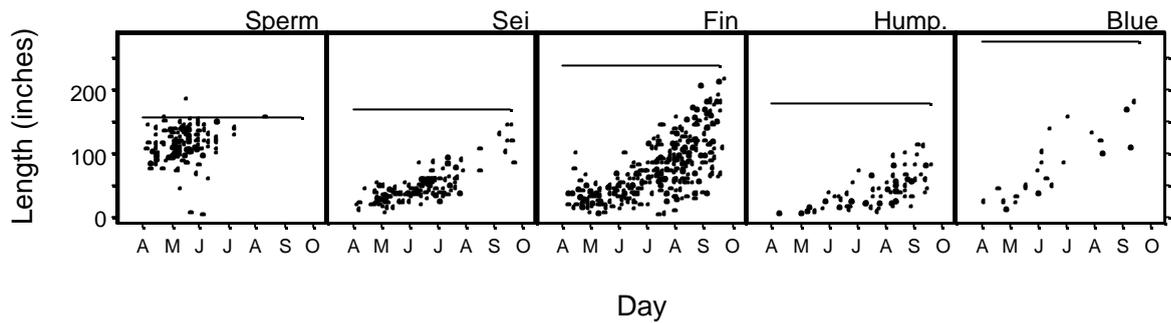


Figure 1.7: The lengths of measured fetuses vs. the day of capture, by species. Horizontal lines represent estimated lengths at birth.

Distance from Shore

The distance between the locations where the whales were captured and the nearest coastline increased significantly over time (1948 to 1967) for both sexes of all species except for blue whales (Fig. 1.8a). On a monthly basis, the distance from shore changed significantly for female sei and fin whales and for male sperm, sei and humpback whales (Fig. 1.8b). Annual distance from Coal Harbour changed significantly for females of all species except humpback whales. The statistics are summarized in Table 1.2.

Effort

Reliable effort data were available only from the Coal Harbour station (Fig. 1.9). Effort was examined by comparing the mean number of days that boats spent looking for whales monthly (average for all years) and annually (average for all months). Weighted regression analysis showed a significant increase in annual effort ($F_{2,14} = 17.38$, $p < 0.001$, $r^2 = 0.713$) from 1948 to 1967. However the change in monthly effort (March to September) was not statistically significant ($F_{2,4} = 5.653$, $p = 0.068$, $r^2 = 0.739$). March was removed from the analysis of all Coal Harbour data because whaling occurred in that month only once over the 17 year period.

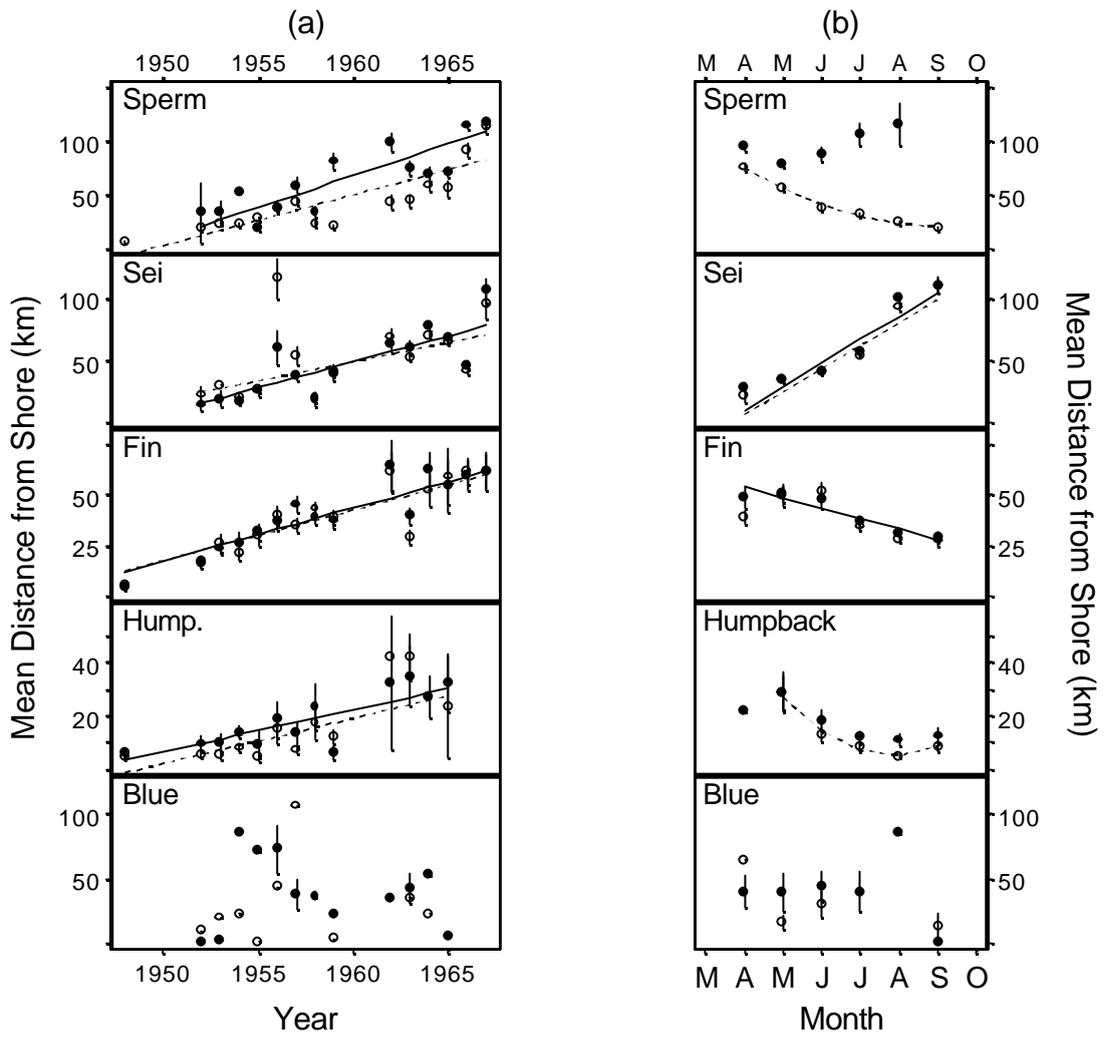


Figure 1.8: Mean distance from shore for males (○) and females (●) shown annually (a) and monthly (b) for the Coal Harbour catch data only (1948-1967). The data are shown with standard error bars. Statistically significant trends, based on regression analysis ($\alpha = 0.05$), are shown as trend lines.

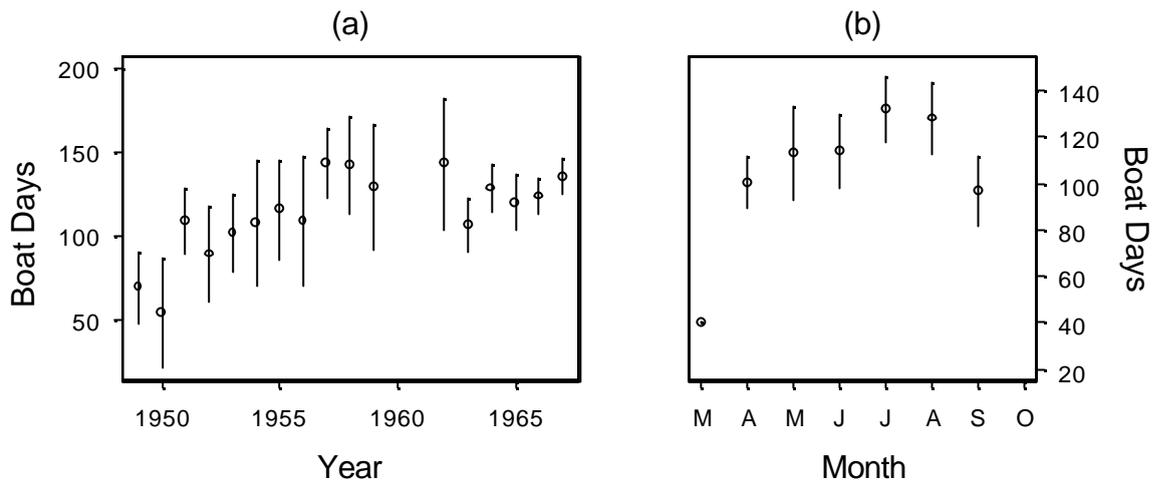


Figure 1.9: Mean annual (a) and monthly (b) whaling effort, measured as the mean number of days that boats spent searching for whales from Coal Harbour (1948 to 1967). The results are shown with 95% confidence intervals.

Table 1.2: Summary of significant ($\alpha = 0.05$) regression analysis results for annual and monthly mean distance from shore calculations by species and by sex.

Species	Sex	Annual Distance from Shore				Monthly Distance from Shore			
		D.F.	F	R squared	p	D.F.	F	R squared	p
SPW	M	(1,13)	32.93	0.717	< 0.001	(2,3)	152.40	0.99	0.001
SPW	F	(1,12)	26.62	0.689	< 0.001				
SW	M	(1,12)	8.85	0.424	0.012	(1,4)	21.59	0.844	0.010
SW	F	(1,12)	18.10	0.601	0.001	(1,4)	23.16	0.853	0.009
FW	M	(1,13)	25.39	0.661	< 0.001				
FW	F	(1,13)	42.53	0.766	< 0.001	(1,4)	34.00	0.872	0.002
HW	M	(1,10)	12.90	0.563	0.005	(2,2)	28.08	0.966	0.034
HW	F	(1,11)	32.88	0.749	< 0.001				

Discussion

Annual trends in the numbers of whales killed by BC coastal stations are consistent with patterns of over-exploitation of these whale species in other regions of the world. For example, Clark and Lamberson (1982) describe the progressive movement of exploitation moving from blue to fin to sei whales in the Antarctic, and Pike (1968) outlines the successive depletion of humpback, blue, fin and sei whales in the entire North Pacific, citing exploitation by both coastal and pelagic whalers. The serial depletion of BC whale populations between 1908 and 1967, moving from humpback and blue whales, to fin, sperm and finally to sei whales, was largely a function of the relative profitability and ease of capture of these species. However significant technological and socioeconomic changes also affected the species preference, search distance and search efficiency of the whalers.

In spite of the potential biases introduced by shifts in whaling effort, the annual trends in sex ratios and body lengths allow interpretations that contribute to our understanding of population structure and the population effects of exploitation. The monthly trends, although somewhat confounded by the pooling of data over many years and several sites, are strongly supported by large sample sizes. Pooling the large numbers of whales killed over a broad temporal and geographical range reduces inter-annual variability, and emphasizes the commonalities reflective of the species' biology rather than the effects of technological change. The significant seasonal and annual trends identified in this study have implications for our understanding of the migration, population structure and social behaviour of the great whales that were once commonly found in BC coastal waters.

Population Structure in the North Pacific

Traditionally, interest in the structure of whale populations in oceanic basins was based on improving the success of whaling expeditions. Once it became clear that whale populations were being depleted, the objective changed to maximizing sustainable yield and refining harvesting plans (IWC 1950). Consequently, this work adopted many aspects of fisheries management, particularly the concept of exploitable stocks. However this traditional fisheries concept of a stock, which is generally taken to mean a geographically isolated population, is insufficient when describing the structure of humpback whale populations (Baker *et al.* 1986) and may be inadequate for other species as well. For example, Reeves and Whitehead (1997) suggest that sperm whales in the North Pacific may occupy ranges rather than being divided into discrete stocks. To add to the confusion, the term stock has been used in the literature to represent various types of animal aggregations (i.e. geographic stocks, genetic stocks, breeding stocks). To clarify this and subsequent discussions, I propose that the term “population” be used to describe a group of animals in relative reproductive isolation, and the term subpopulation be applied to groups of animals believed to be geographically isolated at some point in their use of habitat.

Annual Catch Composition

Humpback and blue whales, respectively the easiest and most lucrative to catch, dominated the early years of the first era (1908 to 1913). Humpback whales, with their coastal distribution (Johnson and Wolman 1984), were the easiest targets for the coastal whalers. The exploitation of blue whales, followed by fin and sei whales, can be explained in large part by the preferential harvest of larger, more valuable, animals. This strong bias towards larger animals is a major and consistent bias in these whaling data. A clear switch in target species from humpback and blue whales to fin whales is evident from the catch proportions recorded at Kyuquot, where the proportion of fin whales in the catch increased as the proportion of humpback and blue whales declined. A switch from humpback to fin whales was also reported by Clapham *et al.* (1997) for

the California data. At Rose Harbour and Naden Harbour, the fin whale catch decreased steadily from a peak in 1911, but still made up a significant proportion of the total catch every year until the 1930s.

The catch of sperm whales during the first era (1908 to 1941) rose as the fin whale catch declined (Fig. 3a) and can be partially explained by the depletion of humpback and blue whale populations. A worldwide switch to sperm whales from fin whales began in the mid-1920's as the price of whale oil dropped steadily from a peak in 1919 to the lowest levels recorded in 1931 and 1932 when there was an oversupply of whale oil (Tonnessen & Johnsen 1982). This oversupply of oil caused the BC stations to close in those years. Whaling resumed in BC in 1933 with a new bonus structure required under the Geneva Convention – the first international agreement to impose restrictions on whaling - ratified by Canada in 1933. The revised bonuses for the 1933 season were set at \$5.25 or \$5.75 for fin whales, depending on length, and \$10.00 for sperm whales. The previous bonus schedule paid whalers approximately \$3.00 per whale (Webb 1988). This shift to sperm whales likely granted the remaining fin whale population a brief reprieve until the second era of whaling began in 1948, when larger and faster vessels operated out of Coal Harbour, and an increased Japanese and Russian pelagic fishery in the North Pacific focused on the remaining animals of all species. The number of fin whales caught and their proportion in the catch dropped after 1958. A 1962 agreement to ship frozen sei whale meat to Japan sustained the whaling industry until its final collapse following the 1967 season. The BC sperm whale catch never peaked and declined in the same way as the catches of the four baleen species. However during the modern era, worldwide catches of sperm whales peaked in 1966-67 (Gosho *et al.* 1984), and showed a decline only after the BC stations had been closed. Thus the consistently high catch of sperm whales at Coal Harbour were likely due to some combination of a lower pelagic (Russian and Japanese) effort, a larger pre-exploitation

population size, and possibly a behavioural component that continued to make sperm whales available to the Coal Harbour station even as their total numbers were being reduced.

Mean Annual Lengths

Understanding the sequence and intensity of exploitation is helpful when considering annual changes in the mean lengths of animals caught. During the second era, humpback, blue and fin whales were taken from previously exploited populations, while sei and sperm whales were harvested from populations that had previously remained largely unaffected by whaling (Fig. 1.2). The increased pressure on fin, sei and sperm whales during this second era (Fig. 1.3) explains some of the trends in the length data, which were collected consistently only at Coal Harbour.

The significant decline in the mean annual lengths of male sperm whales and female sei whales during the second era of whaling is attributed to their increased exploitation during this period (Fig. 1.5a). A significant decrease in the proportion of male sperm whales (Fig. 1.4a) shows how the depletion of large males led to an increase in the number of females caught. This bias towards male animals is explained by significant sexual dimorphism in this species which makes males more valuable commercially. Maximum sperm whale lengths (Table 1.3) are 65 feet (19.8 m) for males and 40 feet (12.2 m) for females. A restriction on taking nursing females (IWC 1950) also contributed to this male bias. No decline in the mean length of female sperm whales was observed, likely due to the 35 foot (10.7 m) minimum length limit imposed in 1949 (Table 1.3). This effectively limited the catch to all but the largest females. The mean length of female sei whales in the Coal Harbour catch declined, presumably because their maximum length was well above the minimum legal limit imposed in 1949 (Table 1.3).

In contrast to the declines in mean lengths observed in sperm and sei whales, the previously

exploited species (humpback, blue and fin) showed no significant change in mean length during the second whaling era. All three of these species were protected with minimum length limits by 1949 (Table 1.3). As with female sperm whales, a comparison of the mean catch lengths of blue and fin whales to the legal limits (Table 1.3) suggests that the stability of the mean lengths was a result of the length restrictions.

In humpback whales, mean annual lengths for both sexes (during both eras) were consistently above the estimated length of sexual maturity (Fig. 1.5a) with the mean length caught approximately 3 feet longer than the maturity estimate (Table 1.3). This suggests that mature animals were regularly within reach of the whalers. Since the mean lengths in the catch were consistently around 40 feet, it is unlikely the length restriction (35 feet) prevented a decline in mean lengths for this species.

The mean lengths of fin whales caught (both sexes) were below the estimated length at sexual maturity for most years but above the legal limit (Table 1.3, Fig. 1.5a, b). Since the whalers were strongly biased towards larger animals, this suggests that fin whales may have been segregated based on size, with mature animals out of range of the station either temporally or spatially. An alternative explanation is that the population from which the fin whales were taken was shorter than the populations on which the maturity estimates were based. The catch of blue whales (both sexes) also showed mean annual lengths consistently below the estimated length at maturity, with mean male lengths slightly below the legal limit and mean female lengths above (Table 1.3). This suggests the possibility of spatial or temporal segregation based on length as is suggested for other rorqual (sei and fin whale) migrations. However, given the previous exploitation history of this species, it is perhaps more likely that no large animals remained.

Table 1.3: Length summary table showing results from this study and length estimates from the literature. Results include counts (n), mean and maximum measured lengths. Estimates are shown for length at birth, length at sexual maturity (mat), maximum lengths (est. max) and imposed legal limits, by sex, for all species.

		n	mean	meas. max	birth ^a	mat	est. max ^a	legal ^{a,b}
Sperm ^c	M	3001	43.7	64	13	33	65	35
	F	717	35.1	49		27	40	
Sei ^d	M	1822	43.0	56	14	39	60	40
	F	1400	44.3	54		42		
Fin ^e	M	2034	56.7	82	20	58	88	55
	F	2106	59.1	82		60		
Hump. ^f	M	516	39.1	51	15	36	51	35
	F	444	40.4	56		37		
Blue ^g	M	141	69.8	79	23	74	80	70
	F	200	73.3	86		79		

^a Estimates for birth and length at maturity, and legal length limits are for both sexes unless separate values are specified. Sources of species estimates are:

^b IWC 1950; ^c Gosho *et al.* 1984; ^d Mizroch *et al.* 1984c; ^e Mizroch *et al.* 1984b; ^f Leatherwood and Reeves 1983; ^g Mizroch *et al.* 1984a.

Reproduction and Distance from Shore

The significant decreases in the annual pregnant proportions in the catch of sperm, sei and fin whales (Fig. 1.6a) is the strongest evidence of population level effects. By the early 1960's, the number of pregnant females was reduced to near zero for sei and fin whales, while blue whales contained very few pregnancies throughout the period. Potential causes of this reduction include a disruption of the breeding patterns of these species due to harvesting, or simply the removal of virtually all reproductive female animals.

Annual mean distance from shore data (Fig. 1.8a) show that whales of all species (except blue

whales) were caught further from shore over time. While this could be interpreted as learned whale behaviour, the weight of evidence showing large scale depletion of these species is sufficient to explain their disappearance from nearshore waters.

The monthly trends in pregnancy proportions and the distance from shore help to interpret the migratory behaviour of these species. When combined with the monthly trends in male proportions and mean lengths, the species specific stories begin to emerge.

Sperm Whales

The locations of the sperm whale catches show a spatial segregation of males and females (Fig. 1.8a, b). Females were generally found further from shore than males, and the distance between the sexes increased through July and August as females moved progressively further offshore and males moved progressively further onshore (Fig. 1.8b). Males were caught throughout the season (April – September). Changes in the monthly sex ratios (Fig. 1.4b) show that the onshore movement by males made them increasingly accessible to whalers from Coal Harbour. The sharp drop in the proportion of pregnant animals in August (Fig. 1.6b) and the prevalence of near term fetuses in May through June (Fig. 1.7) imply that calving occurred off the coast of BC sometime in July and August. The movement patterns of males and females and the evidence for calving in July and August strongly suggest that breeding occurred in BC waters in late spring (April-May), before the females moved away from the BC coast to calve. It is not clear from the BC catch records whether males left the coastal area during winter months.

It is understood that sperm whales form a number of distinct schools based on sex and maturity (Ohsumi 1971). Gosho *et al.* (1984) described breeding schools (females of all ages and juvenile males) and bachelor schools (young, non-breeding males), and noted that older, mature males are often solitary and frequent higher latitudes. Interactions between mature males and the breeding

schools have been examined in subtropical waters (Best 1979 and Best *et al.* 1984) and the composition of breeding and bachelor schools has been intensively studied in tropical waters by Whitehead and colleagues (for example Whitehead *et al.* 1998, Christal *et al.* 1998). However no studies have examined sperm whale interactions at higher latitudes, and all recent references to sperm whale migration assume that it is sufficiently described by Best (1979), who concluded that, in the southern hemisphere, male sperm whales migrate to tropical latitudes to breed and return to higher latitudes at the end of the breeding season.

My study represents the first time sperm whale breeding has been suggested to occur at temperate latitudes (50° N). Central to supporting this hypothesis is work by Ohsumi (1965) who studied the reproduction of North Pacific sperm whales in detail. Ohsumi (1965) concluded that the modal breeding month was April, with a gestation period of 16.4 months, a mean length at birth of 13.3 feet (4.0 m), and calving occurring between June and October. These reproductive details add to the interpretation of the trends uncovered in my study.

The mean monthly distance to shore (Fig. 1.8b) combined with the monthly sex ratios (Fig. 1.6b) showed a spatial separation of the sexes beginning in June. Comparing fetus lengths to the mean length at birth (Fig. 1.7) suggests that calving occurred for these females in July and August, and that it likely occurred in BC waters. This hypothesis is further supported by the monthly pregnancy proportions (Fig. 1.6b) which showed an increasing proportion of pregnant females until July, after which the proportion, along with the number of females in the catch, dropped to low values. This is consistent Pike and MacAskie (1968) who suggested that calving occurred off the BC coast.

The possibility of breeding in BC waters is suggested by the relative proximity of males and females in April and May (Fig. 1.8b), and the subsequent separation of the sexes, with mixed

schools (i.e. mature females) moving offshore and large males moving closer to shore. A gestation period of 16 months (Ohsumi 1965) necessitates breeding in April and May if calving occurred in July and August. In addition, Pike (1965) observed that in April and May, female schools outnumbered male schools by more than 10:1 and that during these months, large bulls were mostly found associated with the female schools. The combination of these historic observations and the trends identified as part of this report provide convincing evidence for breeding prior to calving in BC waters.

Sperm whale breeding in BC waters also has implications for our understanding of the population structure of this species in the North Pacific, studies of which have remained inconclusive (Reeves and Whitehead 1997). Reeves and Whitehead (1997) suggested that groups of females and individual males may have ranges, with no other clear geographic structure to the populations. If breeding occurs at temperate as well as at tropical latitudes, then the number of potential ranges that may be occupied increases substantially. Three North Pacific stocks, suggested by Kasuya and Miyashita (1988) may, in fact, represent three ranges in the temperate North Pacific.

Sei Whales

Trends in monthly sex ratios, mean lengths and proportion of females pregnant (Figs. 1.4b, 1.5b and 1.6b) suggest that mature (pregnant) females tended to migrate past Vancouver Island ahead of non-pregnant females beginning in May. Mean monthly length and distance from shore data (Figs. 1.5b, 1.8b) further suggest that males and females of the same age migrated together. The peak of the migration passed Vancouver Island between June and August (Fig. 1.3b). However it is not clear from these data whether the subsequent migratory path was northward towards Alaska or offshore towards the open ocean. Evidence of strong offshore movement (Fig. 1.8b), combined with a lack of sei whales caught by contemporary stations in northern BC and Alaska,

suggests a northern limit for this sei whale population of 55°N. Length and pregnancy data (Figs. 1.5b and 1.6b) suggest that the southward migration to calving areas started in September.

Pregnant females are believed to lead the migration to and from northern feeding grounds (Mizroch *et al.* 1984c). Substantial segregation by age and sex is also reported by Horwood (1987) for the Antarctic pelagic catches of sei whales. Segregation by age in the BC catch is apparent from the decreasing mean monthly length of sei whales caught from May to August (Fig. 1.5b) and by the significant decrease in pregnant proportion over the course of the season (Fig. 1.6b), confirming that the pregnant females leading the migration were also the longest. However the catch records show no evidence of segregation by sex. Rather, trends in the mean lengths (Fig. 1.5b) and in the mean distance from shore (Fig. 1.8b) show very similar trends for both sexes. The most logical explanation is that both males and females staged their migration based on maturity, and that larger animals of both sexes migrated further north. This counters the suggestion by Mizroch *et al.* (1984c) that pregnant females may migrate to higher latitudes than other members of the species. The presence of both sexes at higher latitudes is indicated by the high proportion of males caught near Rose Harbour (52°N; male proportion: 0.70, n=122) and Naden Harbour (54°N; male proportion: 0.50, n=6).

The pattern of seasonal abundance is markedly different from the other baleen species in the catch record (Fig. 1.3b), suggesting that sei whales were intercepted as they migrated past Coal Harbour to feeding grounds elsewhere. The peak of this northward migration appears to have passed Coal Harbour in July, showing significant offshore movement (Fig. 1.8b). The apparent reappearance of mature sei whales in the catch in September (Fig. 1.5b), including mature females (Figs. 1.4b, 1.6b and 1.7), suggests that the return migration to southern waters was underway in September.

Fin Whales

The monthly length data (Fig. 1.5b) suggest an age structured migration with larger fin whales arriving in BC waters ahead of smaller ones. The monthly proportion of pregnant females (Fig. 1.6b) remained fairly constant throughout the season, implying that pregnant females stayed within reach of the coastal stations. Animals of both sexes were caught at similar distances from shore (Fig. 1.8b) indicating no evidence of spatial segregation by sex. The stable pregnancy rate from April to September (Fig. 1.6b), the sigmoid rise in the number of whales killed (Fig. 1.3b), combined with the monthly decrease in distance from shore (Fig. 1.8b), all suggest that these animals returned to BC waters to feed. Annual and monthly mean lengths (Figs. 1.5a, b) were consistently below the commonly reported values for length at sexual maturity, but well above the legal limit. Since there is no apparent decrease in mean lengths between 1948 and 1967 (Fig. 1.5a), it appears that the BC subpopulation was generally shorter than the populations on which the estimates for length at maturity are based. Fetal growth is well represented in all months, until females approached term in late September (Fig. 1.7). The sudden drop in fin whale catches in September (Fig. 1.3b) is presumably due to the majority of females leaving the area to give birth in more southerly waters. This suggests that the southward migration may have been more synchronous than the northern one.

A comparison of the numbers of fin whales killed by the BC and Alaskan stations provides no evidence that fin whales were limited in their distribution in the eastern North Pacific. Fin whales represented about one third of the kills at the BC stations, which is comparable to their proportion in the catch from Alaskan stations during the same period.

According to Pike & MacAskie (1968), the BC catch contained both migrating animals and some shorter animals thought to feed in BC waters. Fujino (1964) suggested an isolated stock off BC in addition to eastern and western North Pacific stocks. The trends in my study, which show an

increasing availability over the course of the season (Fig. 1.3b) and the presence of mature females throughout the season (Fig. 1.6b), support the suggestion of a local BC population.

Humpback Whales

The large catches of humpback whales by the BC stations between 1908 and 1917 (Fig. 1.3a) appear to have depleted a subpopulation that was distinct from the ones subsequently exploited in California (1919 to 1926) and western Alaska (1912 to 1939) and suggest the possibility of at least three historic subpopulations in the northeast Pacific. The parallel decline in humpback whale catches at all of the operating BC stations (Sechart, Kyuquot, Rose Harbour and Naden Harbour, Table 1.2) shows that the BC subpopulation reached at least 54°N. A seasonal increase in the proportion of mature animals and pregnant females (Figs. 1.5b and 1.6b) suggests an age structured migration, where immature animals appeared on the feeding grounds before the mature animals. Based on the early accounts of BC whaling, humpback whales appear to have frequented feeding grounds in both Barkley Sound and the Strait of Georgia during winter months. The animals using these grounds were extirpated in the early years of coastal whaling and have not yet returned.

The suggestion that at least 3 distinct subpopulations once frequented the eastern North Pacific is based on the timing of peak catches from the three different regions. Catches of humpback whales in BC peaked in 1911 when 1,022 animals were taken, and dropped to low levels by 1917. Clapham *et al.* (1997) found that the population of humpback whales off California was severely depleted by whaling in later years (1919 and 1926) and suggested that these catches came from a single stock extending from California to Washington State. Reeves *et al.* (1985) summarized whaling records from two stations in the western Gulf of Alaska where catches of humpback whale peaked in 1925, with significant numbers still caught in the 1930s. While these successive peaks in humpback whale catches could be due to shifts in the distribution of a single

population, I believe it is more likely that the exploitation affected subpopulations that were segregated spatially during at least part of the year.

Recent work also supports the separation of the northeast Pacific humpback whales into subpopulations. Baker *et al.* (1986) proposed that the eastern North Pacific stock is composed of “feeding herds” which frequent different coastal regions during the summer months.

Calambokidis *et al.* (1996) confirmed the existence of a single, intermixing feeding aggregation ranging from California to Washington State with a low exchange rate with BC and no exchange with Alaska. However assessing the degree of exchange among feeding areas in western Alaska is currently impossible, given the size and remoteness of the area (Calambokidis *et al.* 1997).

Consequently, assessing the current rate of exchange between southeast Alaska and western Alaska is also difficult.

A significant degree of exchange is currently observed between BC and southeast Alaska (Straley and Ellis unpublished data). This suggests that the southeast Alaska population is slowly dispersing to fill available feeding areas in BC. Whether historically the BC feeding grounds supported a subpopulation discrete from that in southeast Alaska, or whether a single subpopulation ranged from southern BC to southeast Alaska is not clear, and may never be known.

The proportion of mature humpbacks of both sexes increased as the season progressed (Fig. 1.5b) with the largest animals available at the end of the season. This suggests an age structured migration, with immature animals of both sexes appearing on the feeding grounds before the older and larger animals. Two recent studies on sex-based segregation of humpback whales (Brown *et al.* 1995, Craig and Herman 1997) demonstrate that males are more likely to complete the migration between feeding grounds and wintering grounds, and that females may remain on

the feeding grounds or make an incomplete migration. This is not apparent from the BC catch record, which shows a sex ratio very close to 50% both monthly and annually (Figs. 1.4a, b).

Evidence (from the whaling data) of age structure in the migration supports the idea of a staggered migration as proposed by Straley (1990), who observed some animals remaining in southeast Alaska until early winter, while others arrived in late winter. However, recent observations fail to confirm that the animals observed at the tails of the migration are mostly immature (J. Straley personal communication). Alternatively, the observation of some animals leaving a feeding ground late and others arriving early could be due to individual differences in foraging patterns. Pregnant and immature animals would appear to benefit very little from time spent on the breeding grounds, and may therefore choose to continue foraging, perhaps in a wider geographic range, during the winter months. Evidence for historic widespread winter foraging by humpback whales in BC waters is provided by accounts of coastal whaling operations in the Strait of Georgia between 1866 and 1873 (Merilees 1985) when a minimum of 81 whales were taken, mostly between November and February. Later operations by the modern coastal whalers from Page's Lagoon (Fig. 1), located in the Strait of Georgia, operated between November 1907 and January 1908 and took 97 animals in those three months (Merilees 1985). This station closed after a single season, presumably because no more whales could be found. Similarly, the station at Sechart in Barkley Sound, occasionally extended its season to take advantage of the humpback whales apparently found in the winter months in the sheltered waters near the station.

Blue Whales

Comparing the pattern of depletion between the BC and Alaska stations suggests that there may have been discrete subpopulations of blue whales feeding in the Aleutian Islands and off the northern BC coast. The seasonal timing of the catches from these two stations suggests that the

two subpopulations arrived at their respective feeding grounds at different times. The annual predominance of immature animals in the BC catch (Fig. 1.5a) suggests that the mature animals had either passed by the stations prior to the whaling season, or were too far offshore for the coastal stations to reach. Declines in the maturity of the catch over the course of the season (Figs. 1.5b and 1.6b) supports the hypothesis of an age structured migration, led by mature animals, to feeding grounds beyond the reach of the coastal stations.

Blue whale catches in BC peaked in 1911 with 205 animals and dropped to low numbers in just a few years. This pattern is repeated six years later in the blue whale catch from the Alaskan station at Akutan, where catches peaked in 1917 with 131 animals (Brueggeman *et al.* 1985). The suggestion that there may have been discrete subpopulations feeding in the Aleutian Islands and off the BC coast is supported by recent work on the population structure of North Pacific blue whales by Reeves *et al.* (1998). They suggest that at least five subpopulations exist in the North Pacific, two of which are thought to be the Aleutian Islands and the eastern Gulf of Alaska. The degree of mixing between these subpopulations is unknown (Reeves *et al.* 1998).

Blue whale catches by the BC stations increased over the course of the season peaking in August (Fig. 1.3b). In contrast, peaks in the catches at the Alaskan stations occurred in June (Brueggeman *et al.* 1985) and were followed by a steady (although not significant) decline. This could be interpreted as two subpopulations, feeding at opposite sides of the Gulf of Alaska, arriving at different times, or simply as a single population moving first to Alaskan (June), and then to British Columbian (August) waters.

Pike and MacAskie (1968) suggested that blue whales were usually found well offshore. The decrease in mean female lengths over the course of the summer (Fig. 1.5b), and a steadily decreasing pregnancy rate (Fig. 1.6b) implies an age-based segregation in the migration similar

to that suggested for fin and sei whales. The general lack of mature animals in the blue whale catch (Figs. 1.5a, b) suggests that mature blue whales were never within reach of the shore stations. As with fin whales, this could be the result of age-based longitudinal separation, or simply a result of the larger animals passing through BC waters prior to the start of the whaling season.

The female bias in the monthly sex ratio (Fig. 1.4b) and in the last part of the second era (Fig. 1.4a) is attributed to a lack of males above the legal length (70 feet), which appear to have only been available in April (Fig. 1.5a). While this could be interpreted as providing support for sex-based spatial segregation in this species, it is more likely due to overexploitation.

Conclusions

Analysis of the BC historic whaling records reveals the effects of over-exploitation of sperm, fin, sei, humpback and blue whales. The removal of large numbers of mature females which led to the declining pregnancy rates in sperm, fin and sei whales may have had effects that persist to this day. The extirpation of local humpback and possibly fin whale populations may have been facilitated by maternal feeding ground philopatry.

The monthly results provide corroborative evidence for structured migrations based on age and sex, and present new information which answers several important questions about the migration and population structure of Northeast Pacific whales.

The data support the contention that resident humpback and fin whales existed in coastal BC waters and show that sei and blue whale migrated past Vancouver Island. The data also suggest that sperm whales once bred in BC waters. This represents the first time sperm whale breeding has been suggested for temperate latitudes. These conclusions, while strictly applicable only to the historic distributions of these animals, may persist today in the remnant populations.

Chapter 2 – Habitat characterization models from historic whaling records

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 (1963) 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, fin, humpback and sei 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 (GIS) 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 features based on these relationships (e.g. Watts and Gaskin 1985, Moses and Finn 1997).

The objective of my study was to identify coastal regions that may be regarded as critical habitat for sperm (*Physeter macrocephalus*), fin (*Balaenoptera physalus*), sei (*Balaenoptera borealis*), blue (*Balaenoptera musculus*) and humpback (*Megaptera novaeangliae*) whales. I 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.

My approach was based on work by Jaquet *et al.* (1996) and by Moses and Finn (1997). Jaquet *et al.* (1996) analysed the correlations between 19th century Yankee sperm whaling records and satellite observations in the tropical Pacific at spatial scales of 220 km² to 1,780 km² 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 km² grid, using concurrent measurements of oceanography (depth and surface temperature) and whale presence-absence.

My study examined the relationship between historic whale positions and six oceanographic predictors. It was based on the relatively fine scale positional data collected as part of the British Columbia coastal whaling industry between 1948 and 1967. The quantity and spatial resolution of these data far exceed that used in any previous study of the pelagic habitat of large whales. I used generalized linear models to predict whale presence-absence based on six oceanographic predictors. The results are discussed in the context of Northeastern Pacific oceanography, whale biology and whale behaviour.

Methods

This analysis builds on the work conducted in Chapter One by investigating the positional data recorded for the whales killed between 1948 and 1967. I produced geographic probability distributions for sei, fin, humpback, blue and sperm whales as a function of depth, temperature, salinity and month. I divided the coastal region of British Columbia into grid cells, and used Cause&Effect software (Facet 1999) to spatially associate the dependent and independent data

with each grid cell. I then generated data sets from this data model for regression analysis in SPlus (MathSoft 1999).

I began the analysis with an exploration of the relationships between the predictor variables and the probability of whale presence and postulated an *a priori* model using these results. This “biological” model defined the terms to be included in the generalized linear models and subjected to stepwise regression techniques. 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. I also tested the sensitivity of the predictions to the predictor variables by comparing predictions from cold years to those from warm years because the temperature and salinity predictors (1980-1998) were not concurrent with the biological data (1948-1967). A separate regression model was generated for each species, at annual and monthly time scales.

Study Scope

The dependent variable consists of position, species, sex and date of capture for whales killed between 1948 and 1967 as part of the British Columbia coastal whaling industry. All the coastal whaling during this period occurred from Coal Harbour, on the west coast of Vancouver Island (Fig. 2.1). A five minute grid of bathymetry, and long term point data on surface temperature and salinity were used as the continuous independent variables. I chose point data for temperature and salinity rather than remotely sensed data because no remote sensing grids were readily available at resolutions better than 2 degrees – 12 times coarser than the resolution of the biological data.

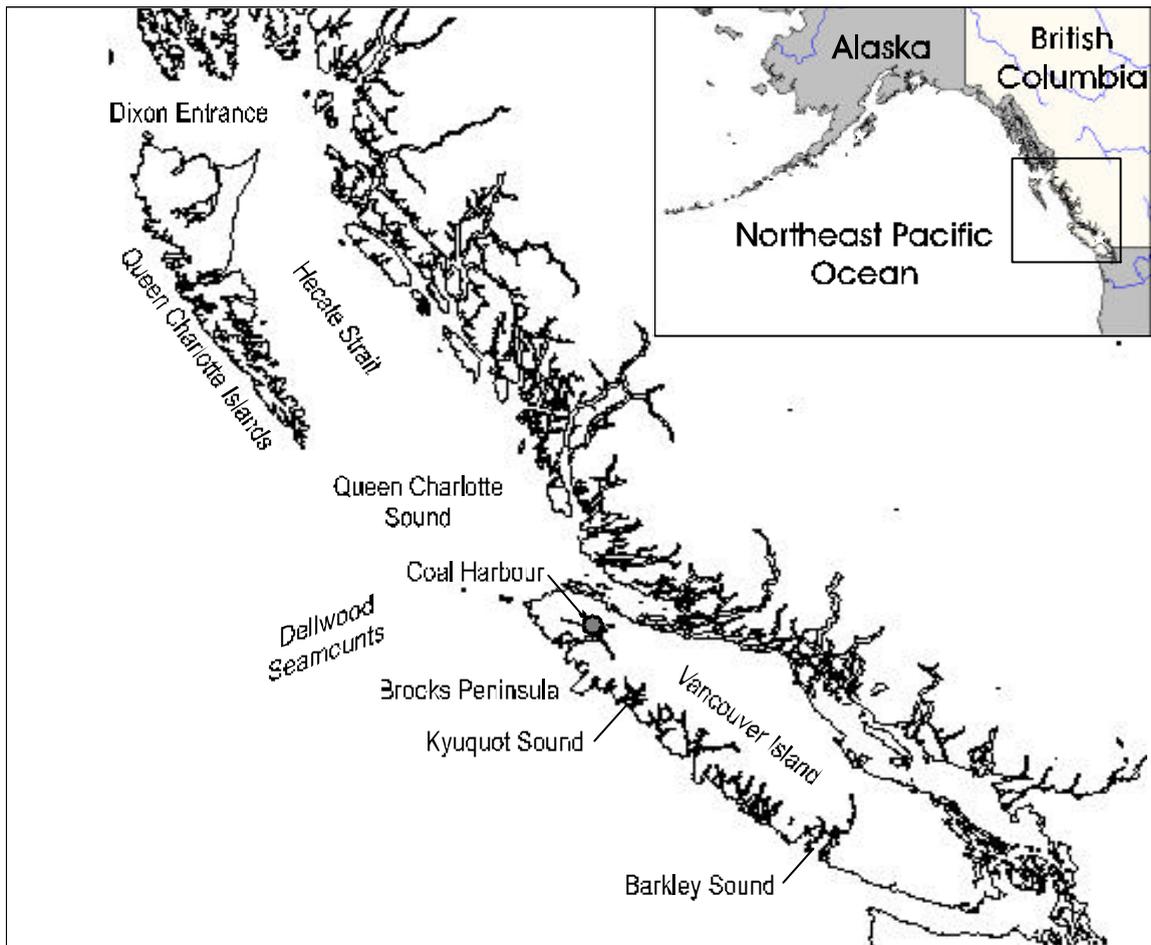


Figure 2.1: Map showing the study area and its location within the Northeast Pacific Ocean, the location of the Coal Harbour whaling station, and the place names mentioned in the text.

The whaling data used in the regression analysis were restricted to an area within 150 nautical miles (nm) of the Coal Harbour whaling station (n=8,164 whales). This represented about 80% of the georeferenced whaling data. 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 nm) (Pike and MacAskie 1968). Areas within 150 nm of the station that had no recorded kills were assumed to be empty of whales. Thus, I assumed that the spatial patterns of whales killed within a 150 nm radius of the station were primarily a function of whale distributions and less a function of concentrated whaling effort. Difficulties with this

assumption and with the consequences of non-random sampling are considered below.

I chose to use a spatial resolution of 10 km by 10 km, corresponding to a grid cell area of 100 km². Months included in this analysis were April through September, when the majority of whaling occurred (Chapter One). I also excluded from the study area regions of extreme oceanographic conditions (i.e. only grid cells with depths greater than 10 m and salinities higher than 30 ppt were included).

Regression Modeling Methods

Generalized linear models apply linear regression techniques to non linear data with heterogeneous variances (Chambers & Hastie 1993). This allows response variables to be modeled as counts or probabilities instead of as linear responses. Counts are modeled using Poisson regression, while binomial values (i.e. presence-absence) are modeled using logistic regression. In order to capture the number of whales in the grid cells, I modeled the data using Poisson regression and used a simple transform to convert the predicted number of whales (generated by the Poisson model) into probabilities. I mapped these probabilities onto the study area to generate the habitat predictions. Details regarding these generalized linear modeling methods, and the transformation of counts into probabilities are presented in Appendix 1.

Independent Variables

To obtain the best spatial resolution and to minimize interannual variability, the most recent 18 years (1980 to 1998) of conductivity (salinity), temperature and depth point data were obtained from the Department of Fisheries and Oceans. I reduced this large (780 MB), multidimensional data set (latitude, longitude, year, day, time, depth, temperature, salinity) to mean monthly surface temperature and salinity values. For each depth profile, I used only the mean of the values in the top 1.5 m of the water column.

To assign temperature and salinity values to the grid cells, I created triangular irregular networks (TINs) for each of these independent variables, for each month of the study (Fig. 2.2). TINs are a standard method of representing point data, where the data points are connected with straight lines, forming a network of triangles. The greater the density of point data, the smaller the triangles that are created. These triangles are then used as the basis for interpolation of missing values. Interpolation was done equally in all directions. I did not correct for any potential spatial autocorrelations.

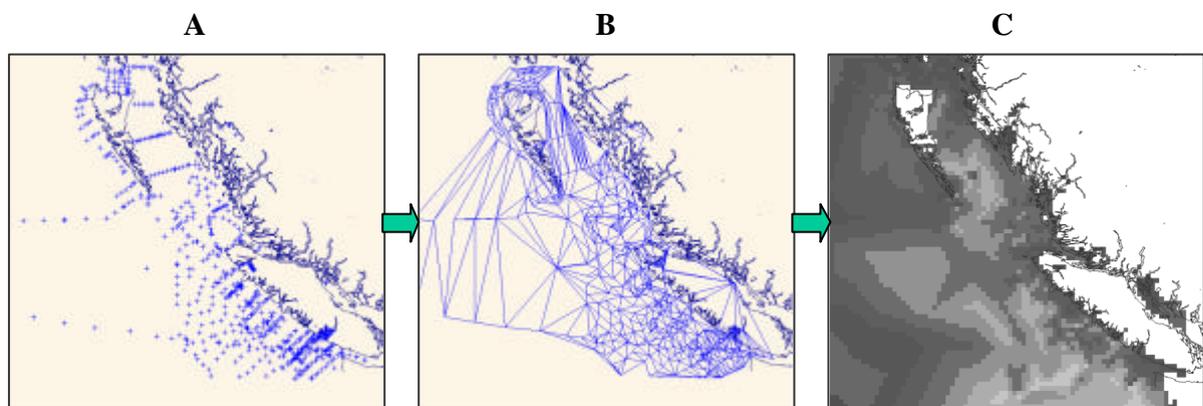


Figure 2.2: An example of how point data were converted to study grids using Triangular Irregular Networks (TINs). Panel A shows point temperature data for July. Panel B shows the TIN used to interpolate temperature to unsampled areas. Panel C shows the temperature grid resulting from the interpolation. This process was used to produce mean monthly and annual temperature and salinity grids for all months. The resolution of the resulting grids is independent of the resolution of the point data.

Temperature and salinity TIN surfaces were created for each of the six months, and used to interpolate any missing grid cell values. All years were treated equally when generating the mean monthly values and no attempt was made to correct for variance in the means. A five minute bathymetric grid was used as a measure of depth. This regular grid of point data was made into a TIN to facilitate the mapping of bathymetry onto the study grid.

In addition to these three continuous, independent variables, I included the categorical variables month, slope and depth class in my analysis. Recent analysis of the whaling data from coastal British Columbia whaling stations (Chapter One) showed significant species-specific monthly changes in the mean distance from shore. This monthly effect (at least partially due to annual migration behaviour), combined with significant monthly changes in the temperature data (Fig. 2.3), suggested that month should be included as a factor in the regression analysis.

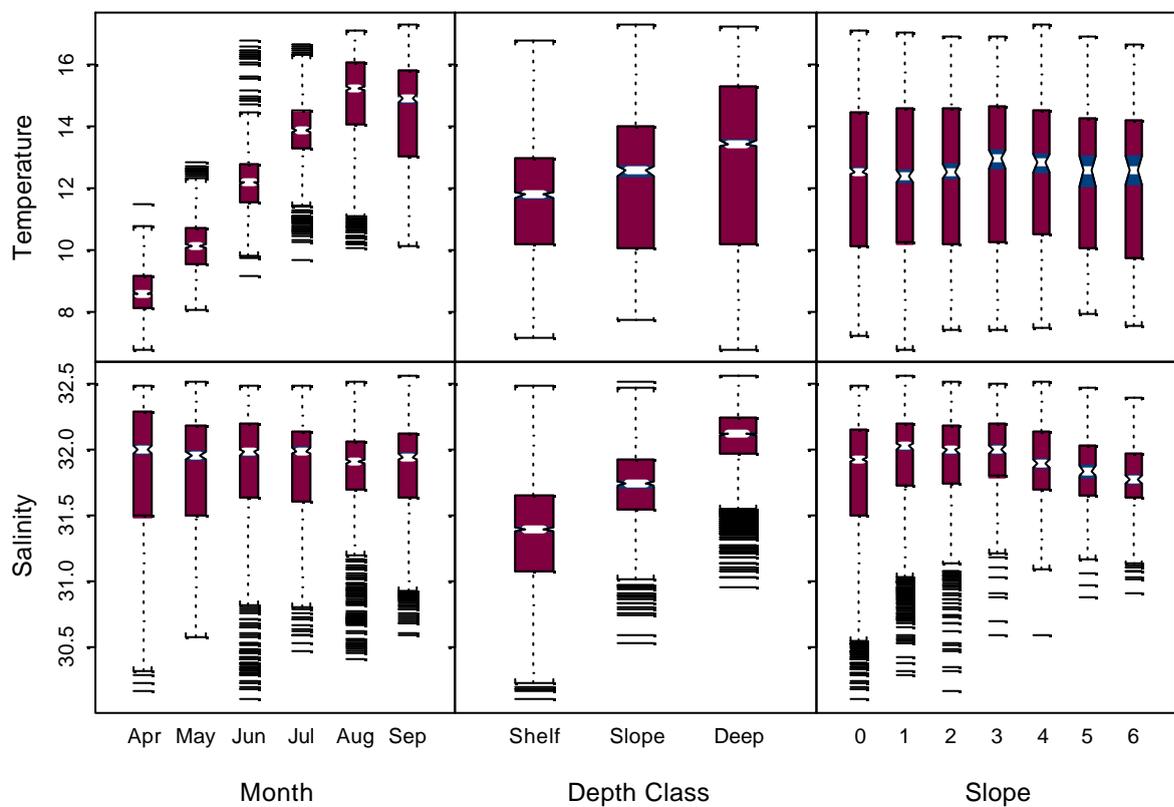


Figure 2.3: Effects of categorical variables “Month”, “Depth Class” and “Slope” on the distribution of the continuous predictor variables Temperature and Salinity. Data (n=9,030) are derived using a 10 km grid on a search area with a radius of 150 nm from the Coal Harbour whaling station.

Slope was included as a measure of undersea topography, since topographic upwelling may play a role in biological productivity (Mann and Lazier 1996). This categorical predictor variable was defined to have slope classes from 0 (flat) to 6 (steepest). Although slope was derived from the

bathymetry data, 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 shelf waters to deep waters.

I created the categorical predictor depth class based on the distribution of the depth variable, which was clearly bimodal (Fig. 2.4). While generalized linear models do not require the independent variables to be normally distributed, normality does yield a better fitting model. I therefore divided the study area into three depth classes: shelf (≤ 200 m), slope (between 200 and 1,800 m) and deep water ($>1,800$ m), with the slope depth class being representative of the shelf break. In addition to creating a more normal distribution of depths at each depth class (Fig. 2.4), this allowed me to test for interactions between these depth classes and the other predictor variables.

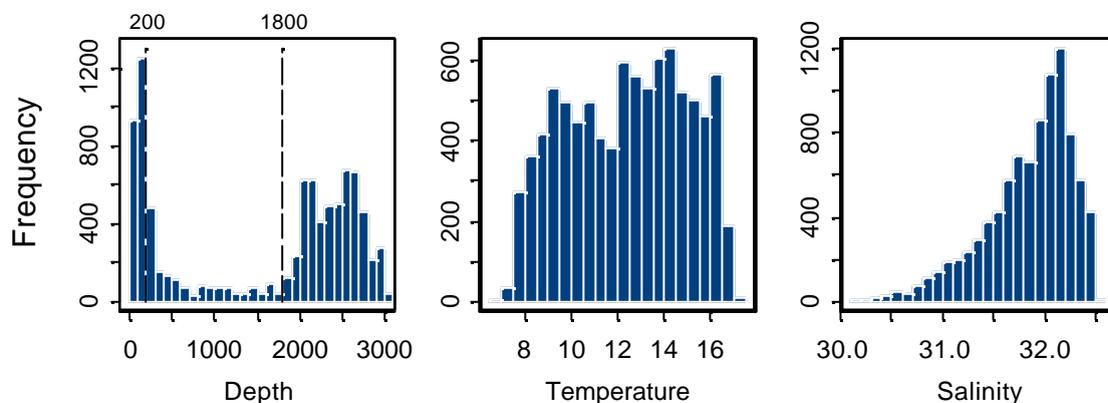


Figure 2.4: Frequency distribution of the continuous predictor variables Depth, Temperature and Salinity for the grid cells within the study area ($n=9,030$). The vertical dashed lines on the depth frequency plot show the three levels of the depth class categorical variable.

All positional data were converted to a regular, Universal Transverse Mercator (UTM) grid for analytical and display purposes. UTM grids, which are measured in metres, are the preferred representation for spatial analysis because latitude and longitude measures do not reflect

consistent distance measures. Data integration, transformation, and preparation for analysis were performed using Cause&Effect software, and the generalized linear modeling was conducted using SPlus.

Model Building

For each of the five species, I began with an exploratory analysis of how each of the continuous variables independently affected the presence of whales. I fit lowess (locally weighted scatterplot smoothing) curves to scatter plots showing the presence or absence of whales versus the independent variables. I examined the mean effects, as well as the effects for each month and for each depth class. I used the results of this analysis to hypothesize a relationship between the presence-absence of whales and the independent variables based on biological significance. I used this *a priori* “Biological Model” to define the upper limit on the complexity of the regression models. I also generated annual predictions using an *a priori* annual model.

To generate the predictive models for each species, I used forward stepwise selection. 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 they explain. Thus, the most significant variables enter the model first. The pool of variables for my study was defined by the biological model. I 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 (see Appendix B for details).

I applied forward stepwise selection to the all the data within the 150 nm radius for each species to select the model terms. I then generated the annual and monthly probability predictions, which I used to produce the habitat maps for entire British Columbia coast, using models whose

coefficients were determined using the data within the 150 nm radius. I tested the models using a cross validation test and conducted a simple analysis of the sensitivity of the predictions to the oceanographic model.

Model Testing

I tested the resulting models for predictive power 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. generate equation coefficients), and the fitted model is then tested against the testing data set. For each species, I used half of the grid cells within 150 nm of Coal Harbour for fitting, and the other half for testing. Since the predictions generated by my models were probabilities, I 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 to predicted model values. In order to evaluate the predictive efficiency of my models, I needed to define a cutoff value which would convert probability into a presence-absence result. I set this cutoff value individually for each model such that the fitted model produced the same number of presences found in data set used for the fitting.

To assess the effects of using mean surface temperature and salinity values from an 19 year period (1980 to 1998) that was not concurrent with the 20 years of whaling data (1948 to 1967), I compared predictions obtained from warm years to 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 Nino Southern Oscillation (ENSO) events. Four of the warmest years since 1895 were associated with strong or

moderate ENSO events (1983, 1987, 1992, 1994). I 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. I 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

Data Preparation and Scale Selection

Frequency plots of all the positional data (Fig. 2.5) show that whalers tended to round the location to the nearest five minute increments of both latitude and longitude. I therefore assumed the precision of the positional data was five minutes, which corresponds to a spatial resolution of approximately 10 km. Because my objective was to develop a model at the finest possible resolution, I chose a grid size of 10 km, corresponding to the resolution of the biological data. The number of whales, the number of grid cells at the annual and monthly scales, and the mean probabilities of finding a whale in a grid cell are summarized in Table 2.1.

Examination of the independent variables showed little collinearity among the independent variables using the 10 km grid. Collinearity can be tested using the tolerance statistic, which is $1 - R^2_x$, where R^2_x is the variance in each independent variable x , explained by the other independent variables. A low tolerance is an indication of collinearity, and Menard (1995) suggests that a tolerance below 0.20 is cause for concern. The tolerances for the independent variables in this study ranged between 0.47 to 0.97 indicating that the amount of collinearity was not significant. While correlation between temperature and salinity might be expected, it may exist at scales (either finer or coarser) other than the one considered here.

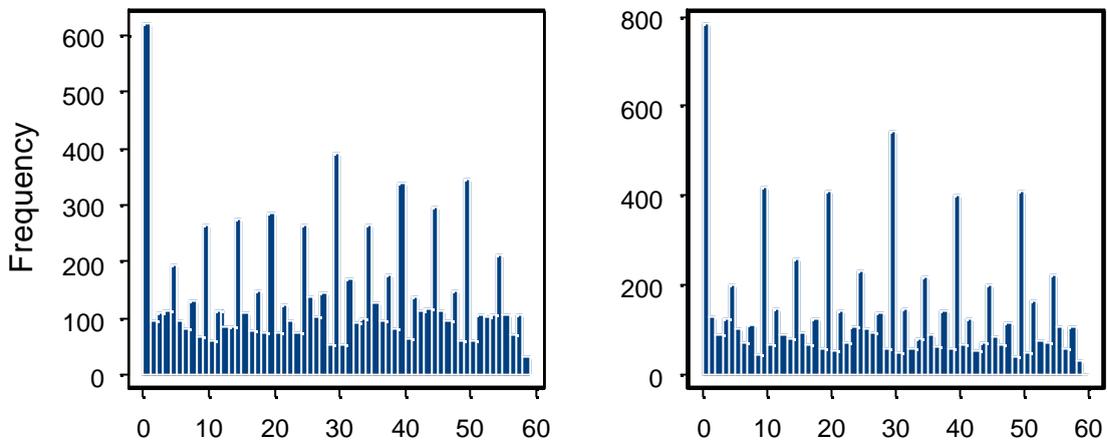


Figure 2.5: Frequency plot of latitude and longitude minutes from positional information recorded for 8,431 whale kills showing clumping at 5 and 10 minute intervals.

Table 2.1: Comparison of sample sizes and probability of whale occurrence ($Pr(Wh)$), for each species at annual and monthly time scales.

Species	Total Whales (within 150 nm)	Annual			Monthly ¹		
		Grid Cells	Presence Cells	Mean $Pr(Wh)$	Grid Cells	Presence Cells	Mean $Pr(Wh)$
Sei	2,560	1,508	574	0.38	9,030	1,004	0.11
Fin	2,613	1,508	680	0.45	9,030	1,409	0.16
Humpback	433	1,508	212	0.14	9,030	288	0.03
Blue	146	1,508	118	0.08	9,030	138	0.02
Sperm – m	1,800	1,508	522	0.35	9,030	909	0.10
Sperm - f	612	1,508	234	0.16	9,030	263	0.03

¹ Monthly values were based on monthly grid cells obtained by extending the grid cells into six months (May through October) and removing those cells where depth > -10 m and salinity < 30.0 (ppt). Whales were redistributed into the grids based on month of capture.

The Biological Model

Scatter plots of presence-absence as a function of each of the independent variables were fitted with lowess curves for each of the species. These plots are shown in Appendix 1, Figs. A.1 through A.18. I examined these plots for potential relationships between the presence of whales and each of the 6 predictors (3 continuous, 3 categorical). The lowess curves, all fitted with a span of $F=2/3$, showed two types of general trends: Increasing trends (i.e. sei whales, temperature and depth class, Fig. A.1), and trends that peaked at a particular value (i.e. sei whales, depth and salinity, Fig. A.1).

I examined both the first order (mean annual) effects of all six predictors on presence-absence (Figs. A.1, A.4, A.7, A.10, A.13 and A.16), and the interactions between each of the continuous variables for each level in month (Figs. A.2, A.5, A.8, A.11, A.14 and A.17), and in depth class (Figs. A.3, A.6, A.9, A.12, A.15 and A.18) because of the apparent interactions between the continuous predictors and the categorical variables month and depth class (Fig. 2.3).

Figures A.1, A.2 and A.3 show that sei whales were most commonly found at a depth of 1800-1900 m, and at a salinity of 32.0 ppt, regardless of the time of year. The mean temperature effect appeared to be linear, but was complicated by the interaction with month (Fig. A.2). Figure A.3 shows that sei whales were found primarily in deep water, as only 5 animals were found on the shelf (depth less than 200 m).

As with sei whales, fin whales were most commonly found at depths of 1800-1900 m, and at a salinity of 32.0 ppt, regardless of month (Figure A.5). However the effect appears to be more diffuse as the peaks are somewhat broader than those for sei whales. Fin whales appear to be distributed at different salinities and temperatures based on depth class (Figure A.6).

Figure A.7 shows that humpback whales were most commonly found at depths of 1100 m to

1300 m and at salinities of approximately 31.7 ppt. The humpback whale was the only baleen species to show a strong response to an optimum temperature with most animals being caught at temperatures of 13⁰ C. Humpback whales showed the strongest interaction between depth class and salinity compared to the other species (Fig. A.9).

The preliminary analysis of blue whale presence-absence (Figs. A.10 to A.12), while based on a small sample size, suggest that the distribution of this species was relatively insensitive to temperature and depth class. Most animals were caught at a depth of 1500 m and a salinity of 31.9 ppt.

Male sperm whales show a strong response to the slope variable, which is also reflected in the preference for the slope depth class (Fig. A.13). However, they appear relatively unresponsive to month. By contrast, female sperm whales show a strong month response, a preference for deep water, and virtually no response to slope (Fig. A.16).

The monthly interaction plots (Figs. A.2, A.5, A.8, A.11, A.14 and A.17) show little effect by month on depth with the exception of male sperm whales which appear to have been caught in shallower water in later months. The temperature month interaction is very similar for all species, showing a decreasing linear effect in early months followed by a quadratic (optimum) effect in later months. Salinity appears to be minimally affected by month and the optimum response appears similar for all species.

Depth class interactions (Figs. A.3, A.6, A.9, A.12, A.15 and A.18) appear to be strongest with depth and salinity. The slope of the salinity response for a number of species (fin, humpback and male sperm whales) actually changes between depth classes. A small depth class temperature interaction also appears for fin and humpback whales, and both sexes of sperm whale.

These plots show that all species were found most commonly 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 (Figs. A.13 and A.16) support independent treatment of the sexes in this species.

Based on this exploratory analysis, I proposed a biological model which encompassed all of the observed effects. I defined the logit (linear component) of this *a priori* biological model as:

$$\Pr(\text{Wh}) \propto f\left[m + \text{slope} + z\text{Class} + \left(z^2 \text{ in } z\text{Class}\right) + \left(S^2 \text{ in } z\text{Class}\right) + \left(T^2 \text{ in } m\right)\right] \quad \text{Equation 1}$$

In Equation 1, the $\Pr(\text{Wh})$ 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 each of the six variables, including the categorical variables month (m), *slope* and depth class ($z\text{Class}$); the quadratic relationships in depth (z^2) and salinity (S^2) nested within $z\text{Class}$; and temperature (T^2) nested in m .

The biological interpretation of this model is simply that whale presence is dependent in some way on the month, slope and the depth class; and that there is an optimum depth and salinity at each depth class, and an optimum temperature in each month.

Model Building

The regression parameters, the amount of variance they explained (R^2_L), and the degrees of freedom for the annual models are summarized in Table 2.2. The variable *slope* was significant for all species except blue whales. *Depth class* was also significant for all species except female sperm whales. As for the remaining variables, *Depth*² was significant for all species, *salinity*² was significant for fin, blue and male sperm whales only, and *temperature*² was significant only for sei and male sperm whales. The humpback whale distribution model was the only annual model to include an interaction term (*depth:depth class*). The amount of variance explained (R^2_L)

ranged from a low of 0.25 (humpback, blue and female sperm whales) to a high of 0.49 (fin whales). Generally, R^2_L values were higher for the groups (sei, fin and male sperm whales) with higher sample sizes (i.e. number of whales killed).

Table 2.2: Annual regression models for each species, the amount of variance explained (R^2_L), and the degrees of freedom (d.f.), when fitted with all the data within 150 nm of Coal Harbour.

Species	Model	R^2_L	d.f.
Sei	$slope + zClass + z^2 + T^2$	0.48	1495
Fin	$slope + zClass + z^2 + S^2$	0.49	1495
Humpback	$slope + zClass + z^2$ in $zClass$	0.25	1493
Blue	$zClass + z^2 + S^2$	0.25	1501
Sperm – m	$slope + zClass + z^2 + T^2 + S^2$	0.38	1493
Sperm – f	$slope + z^2$	0.25	1495

The monthly models (Table 2.3) also showed a high diversity in model terms, but provided marginally lower R^2_L values than their annual counterparts. All three categorical variables were significant for all species with the exception of *depth class* for female sperm whales. *Depth* was significant in all the models, but was nested in *depth class* for humpback whales. *Salinity* was also significant for all the species, and was nested in *depth class* for both humpback and male sperm whales. *Temperature* was omitted only from the female sperm whale model, and was nested in *month* for sei and male sperm whales. R^2_L values ranged from 0.24 (male sperm whales) to 0.39 (sei whales). The model for female sperm whales, fitted with a sample that was only one third the size of the male sperm model, explained more of the variance (0.30 vs. 0.24).

These results support the trends observed in the scatter plots (Appendix A), showing that in almost all cases, each of the six predictor variables played some role in defining the probability distribution of these species. Humpback and male sperm whales had the most complicated models at both annual and monthly time scales.

Table 2.3: Monthly regression models for each species, the amount of variance explained (R^2_L), and the degrees of freedom (d.f.), when fitted with all the data within 150 nm of Coal Harbour.

Species	Model	R^2_L	d.f.
Sei	$m + slope + zClass + z^2 + S^2 + T$ in m	0.39	9006
Fin	$m + slope + zClass + z^2 + S^2 + T$	0.30	9011
Humpback	$m + slope + zClass + z^2$ in $zClass + S^2$ in $zClass + T$	0.25	9003
Sperm – m	$m + slope + zClass + z^2 + S$ in $zClass + T$ in m	0.24	9005
Sperm – f	$m + slope + z^2 + S$	0.30	9015

Model Predictions

The left-hand panels of the annual predictions (Figs. 2.6 to 2.8) 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 nm search radius, which encompasses the data used in building and fitting the models. The positions shown on 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. 2.6 and 2.7) show sei, fin and humpback whale predictions moving progressively onto the shelf, with sei whales in the areas furthest offshore. Predictions for humpback whales are almost exclusively on the shelf, while those for fin whales are in between the sei and humpback whale predictions. Both the sei and fin whale predictions encompass a large area that includes the shelf break, and a large 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 nm (185 km) offshore. This “habitat patch” is also apparent in the mean blue whale prediction. The annual humpback whale prediction includes virtually the entire 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 seasonal predictions (Figs. 2.9 to 2.13) show monthly probability plots overlaid with the

monthly positional data for the species. These predictions not only contain an expected monthly effect, but 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, which have the highest probability of being on-shelf and in sheltered waters in July and August. Both sei and fin whales show an increasing probability of occurrence in the offshore habitat patch described above.

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 observations 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. 2.12 and 2.13). Male sperm whale distributions appear similar to those of the baleen species, while females 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 right through September.

Habitat Prediction Plots

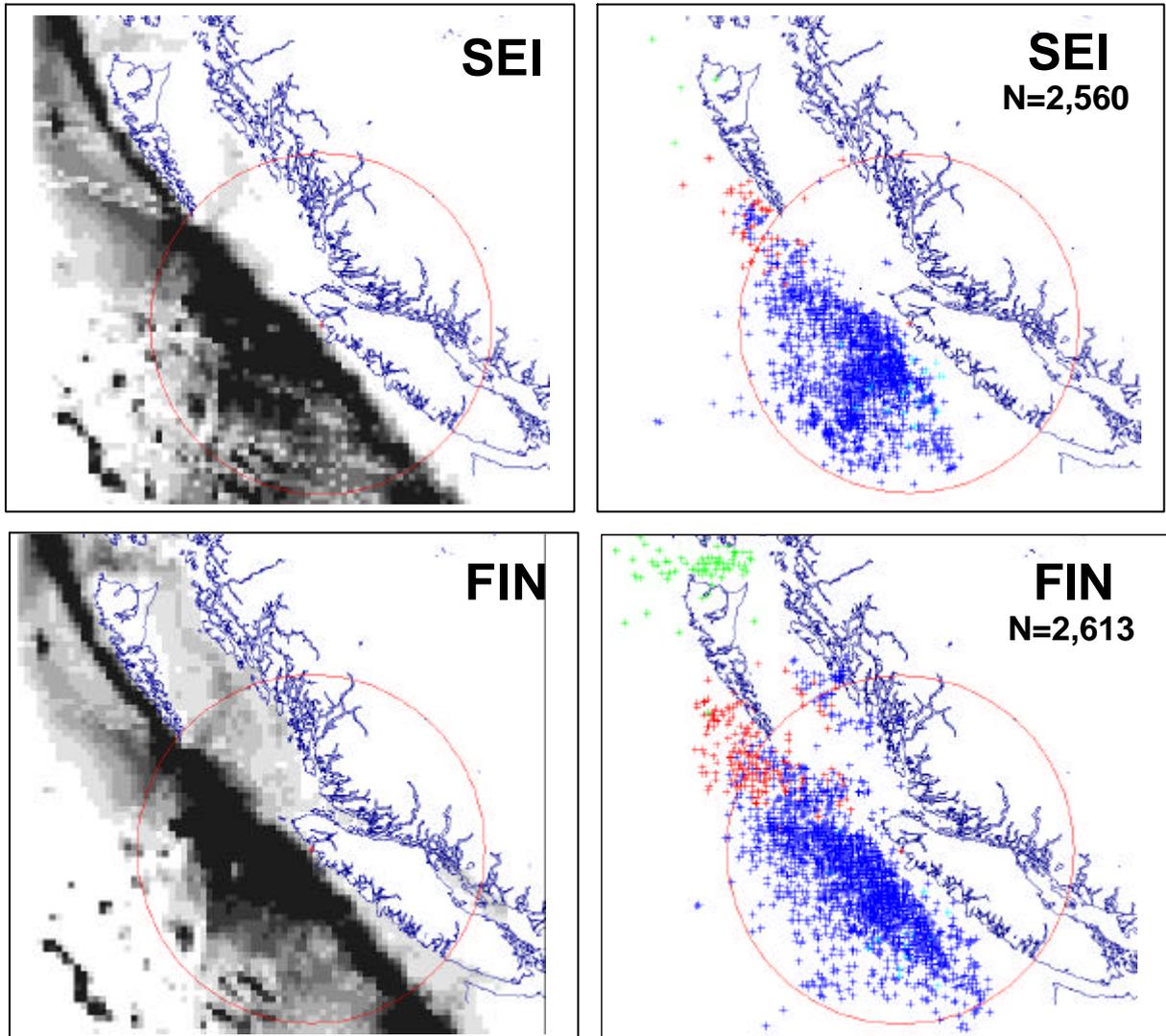


Figure 2.6: Annual probability predictions for sei and fin whales (left hand panels) and the actual positions of whale kills (right hand panel). Dark areas on the probability plots represent areas with a high probability of whale occurrence and white areas represent areas of low probability. The circle represents the 150 nautical mile (275 km) search area which encompasses the data used to calculate the regression coefficients.

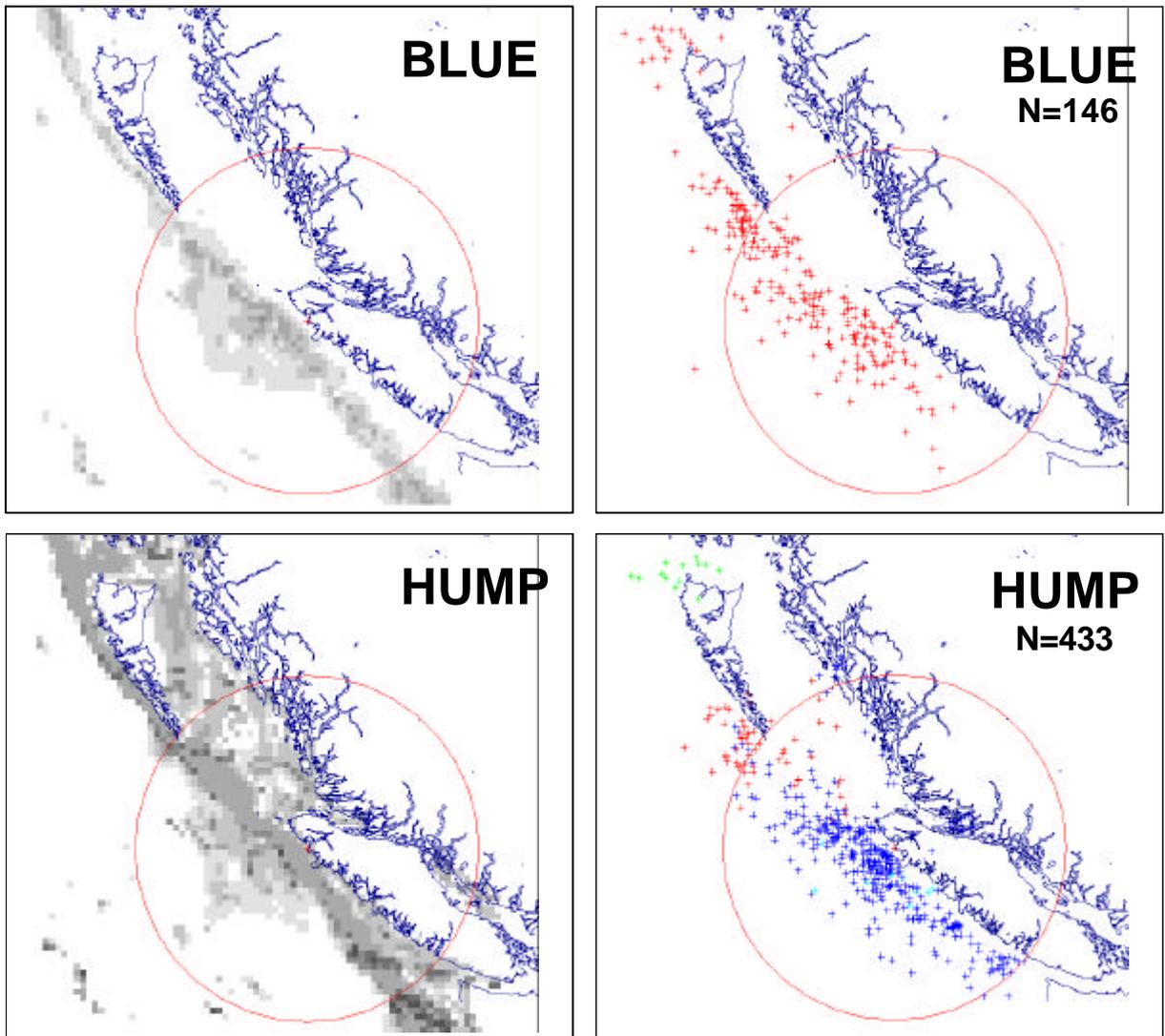


Figure 2.7: Annual probability predictions for blue and humpback whales (left hand panels) and the actual positions of whale kills (right hand panel). Dark areas on the probability plots represent areas with a high probability of whale occurrence and white areas represent areas of low probability. The circle represents the 150 nautical mile (275 km) search area which encompasses the data used to calculate the regression coefficients.

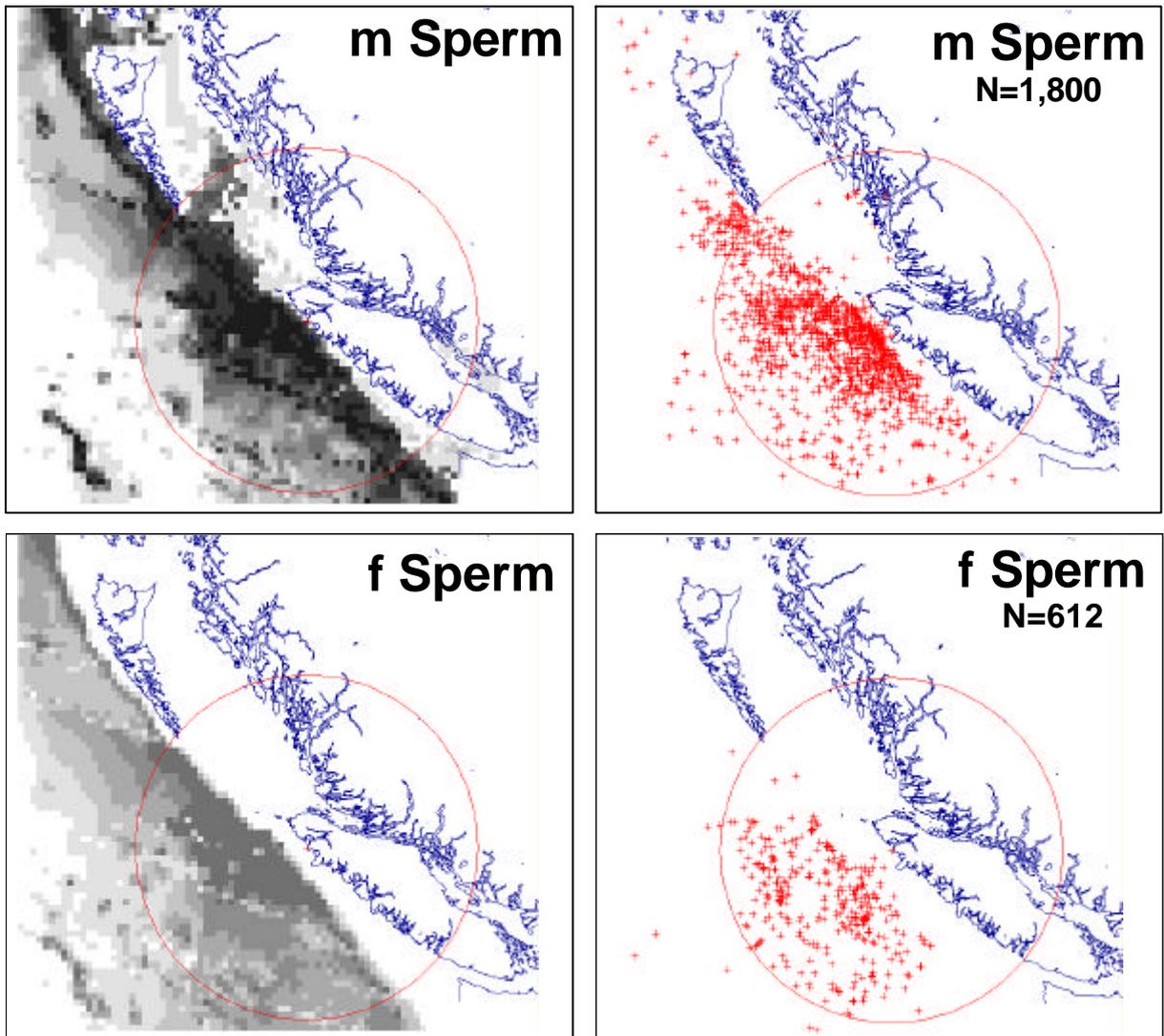


Figure 2.8: Annual probability predictions for male and female sperm whales (left hand panels) and the actual positions of whale kills (right hand panel). Dark areas on the probability plots represent areas with a high probability of whale occurrence and white areas represent areas of low probability. The circle represents the 150 nautical mile (275 km) search area which encompasses the data used to calculate the regression coefficients.

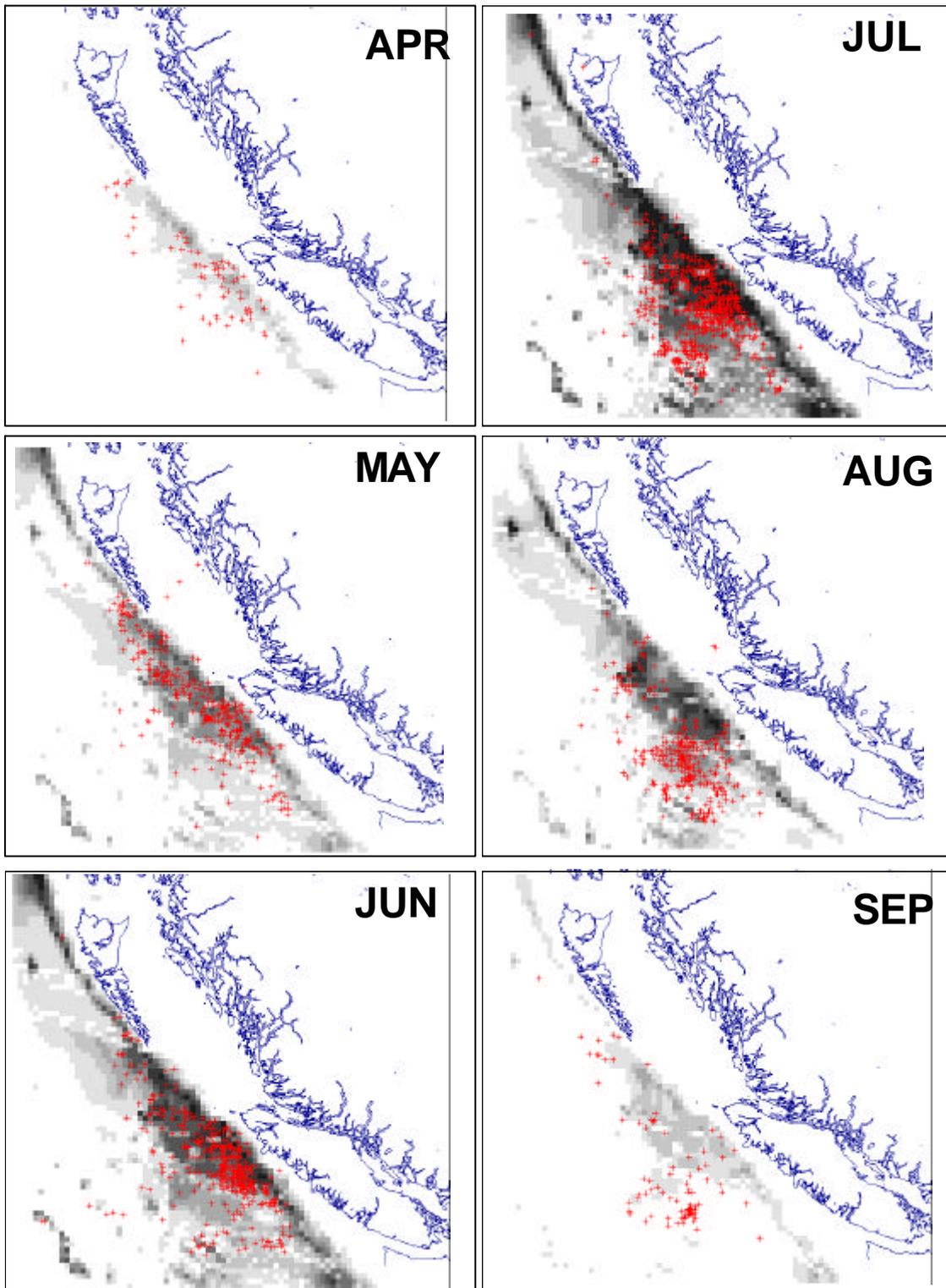


Figure 2.9: Sei Whale: Monthly probability predictions overlaid with the actual positions of whale kills. Dark areas on the probability plots represent areas with a high probability of whale occurrence and white areas represent areas of low probability.

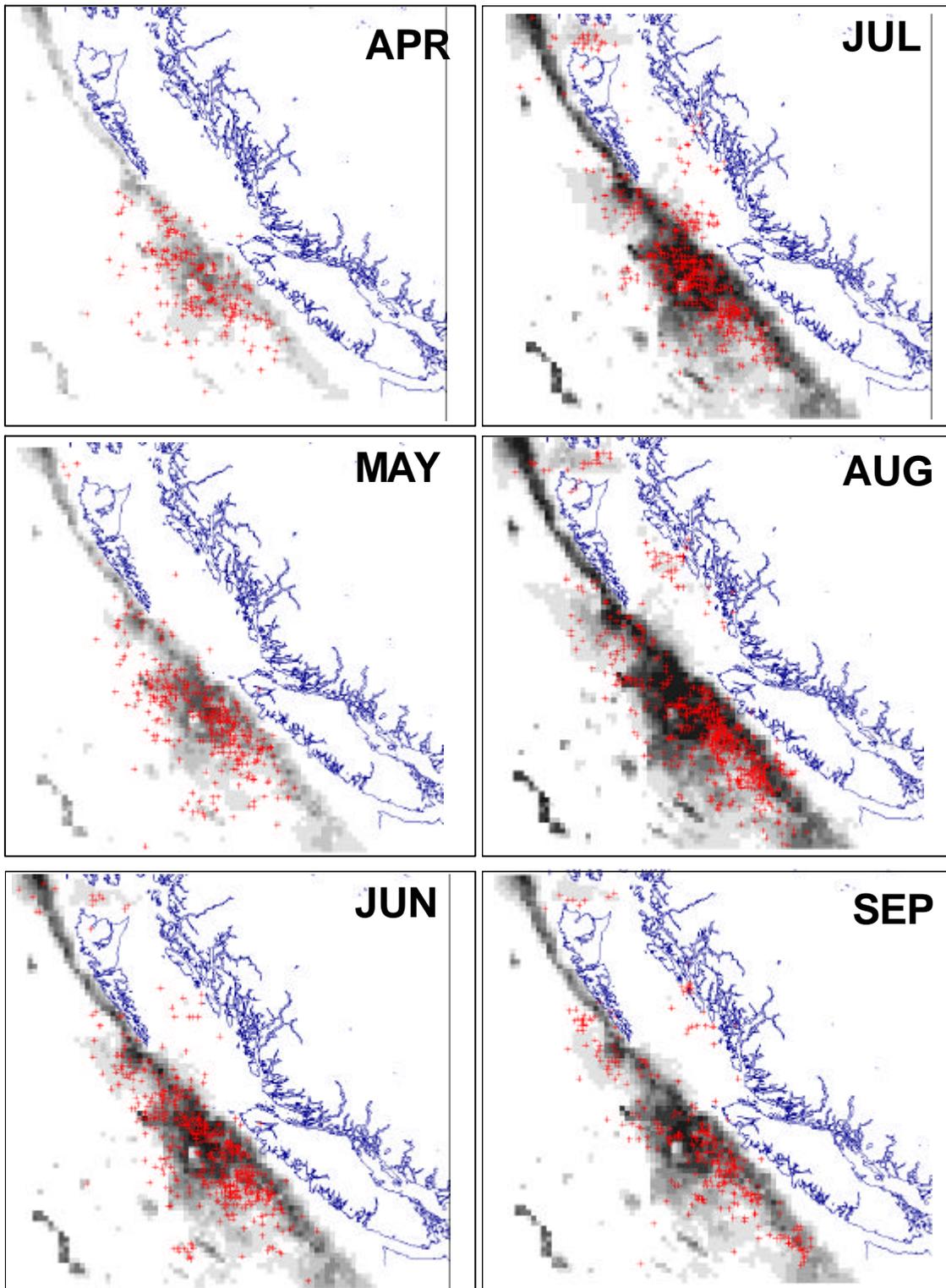


Figure 2.10: Fin Whale: Monthly probability predictions overlaid with the actual positions of whale kills. Dark areas on the probability plots represent areas with a high probability of whale occurrence and white areas represent areas of low probability.

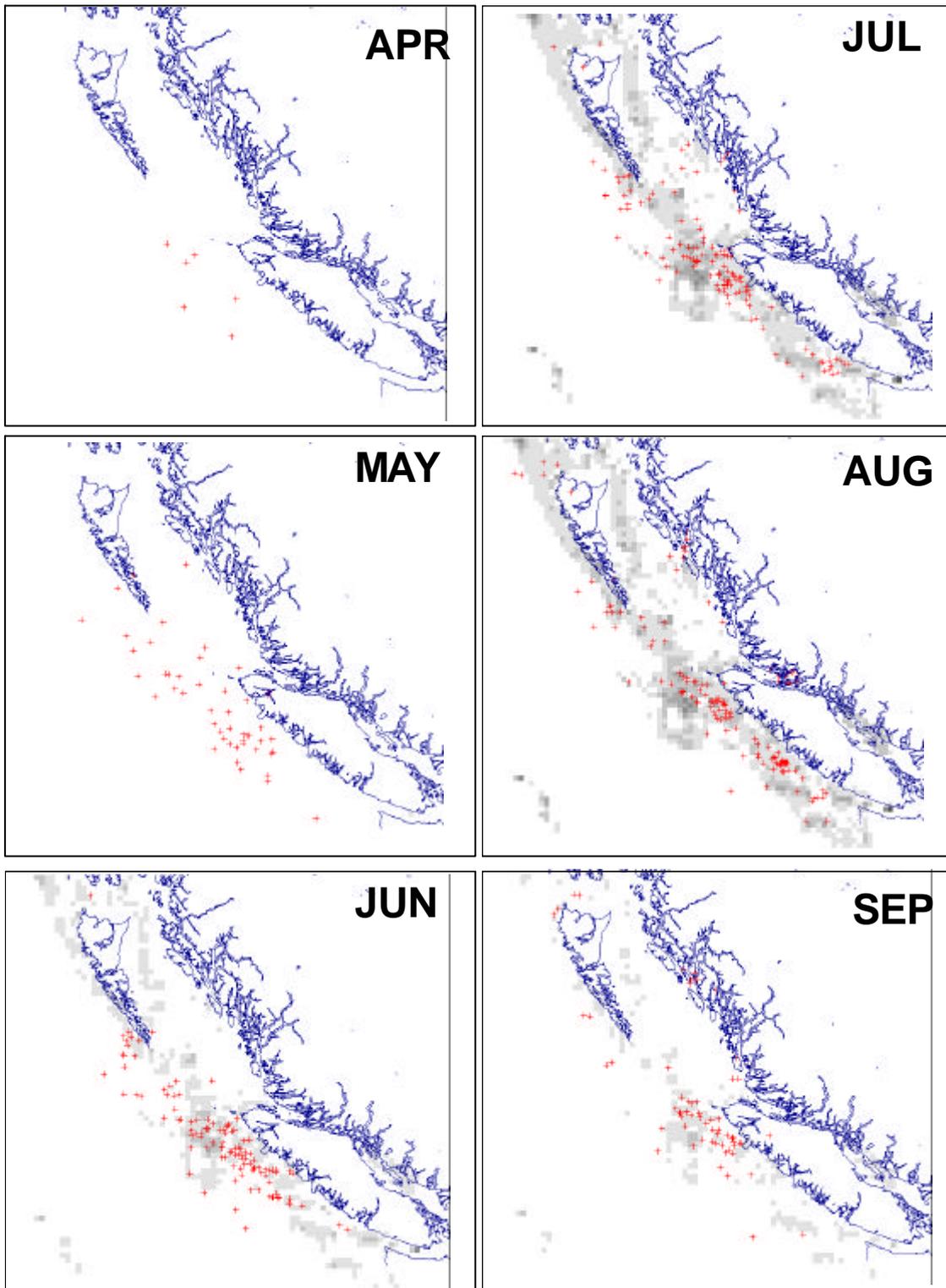


Figure 2.11: Humpback Whale: Monthly probability predictions overlaid with the actual positions of whale kills. Dark areas on the probability plots represent areas with a high probability of whale occurrence and white areas represent areas of low probability.

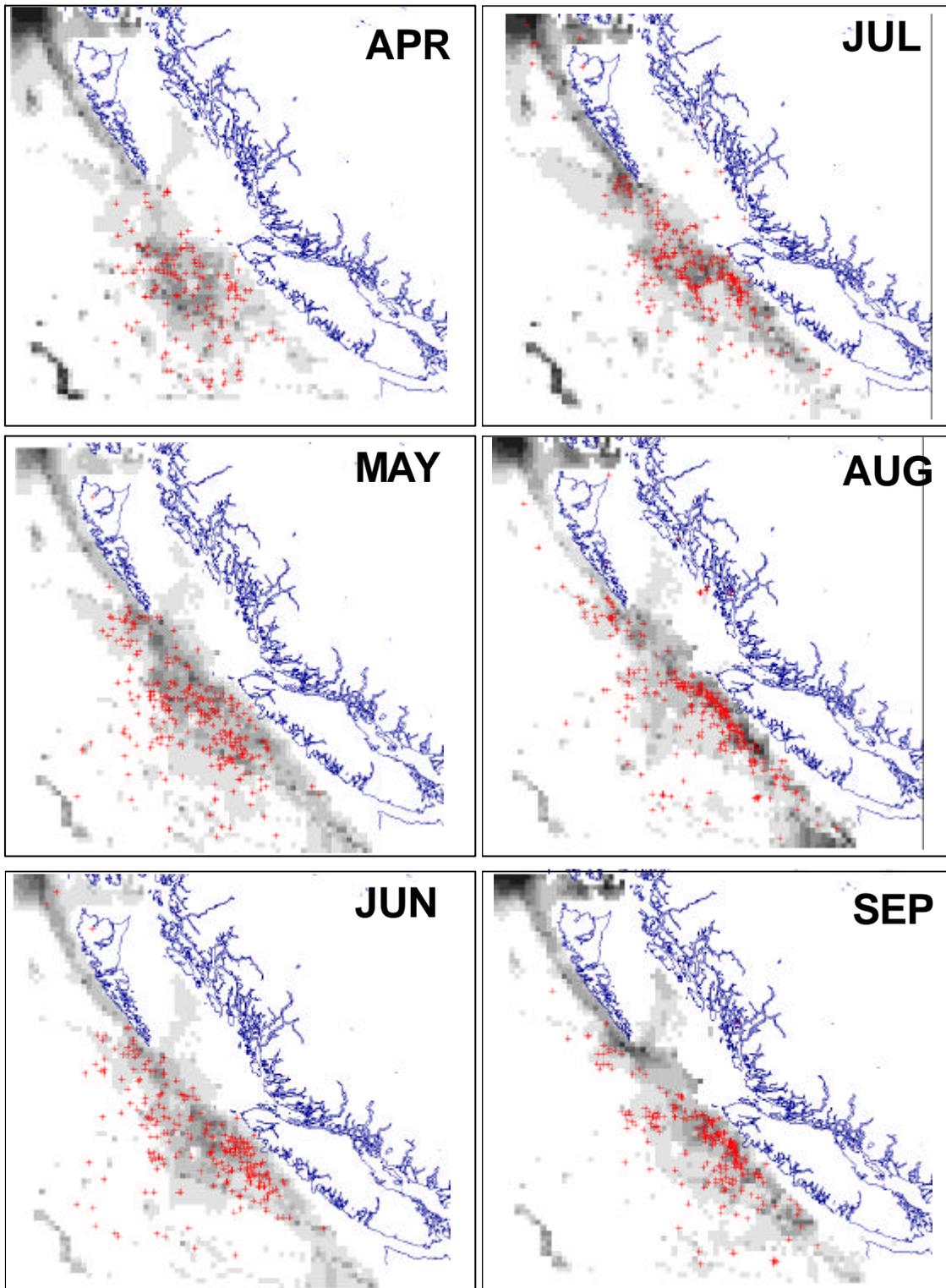


Figure 2.12: Sperm Whale (male): Monthly probability predictions overlaid with the actual positions of whale kills. Dark areas on the probability plots represent areas with a high probability of whale occurrence and white areas represent areas of low probability.

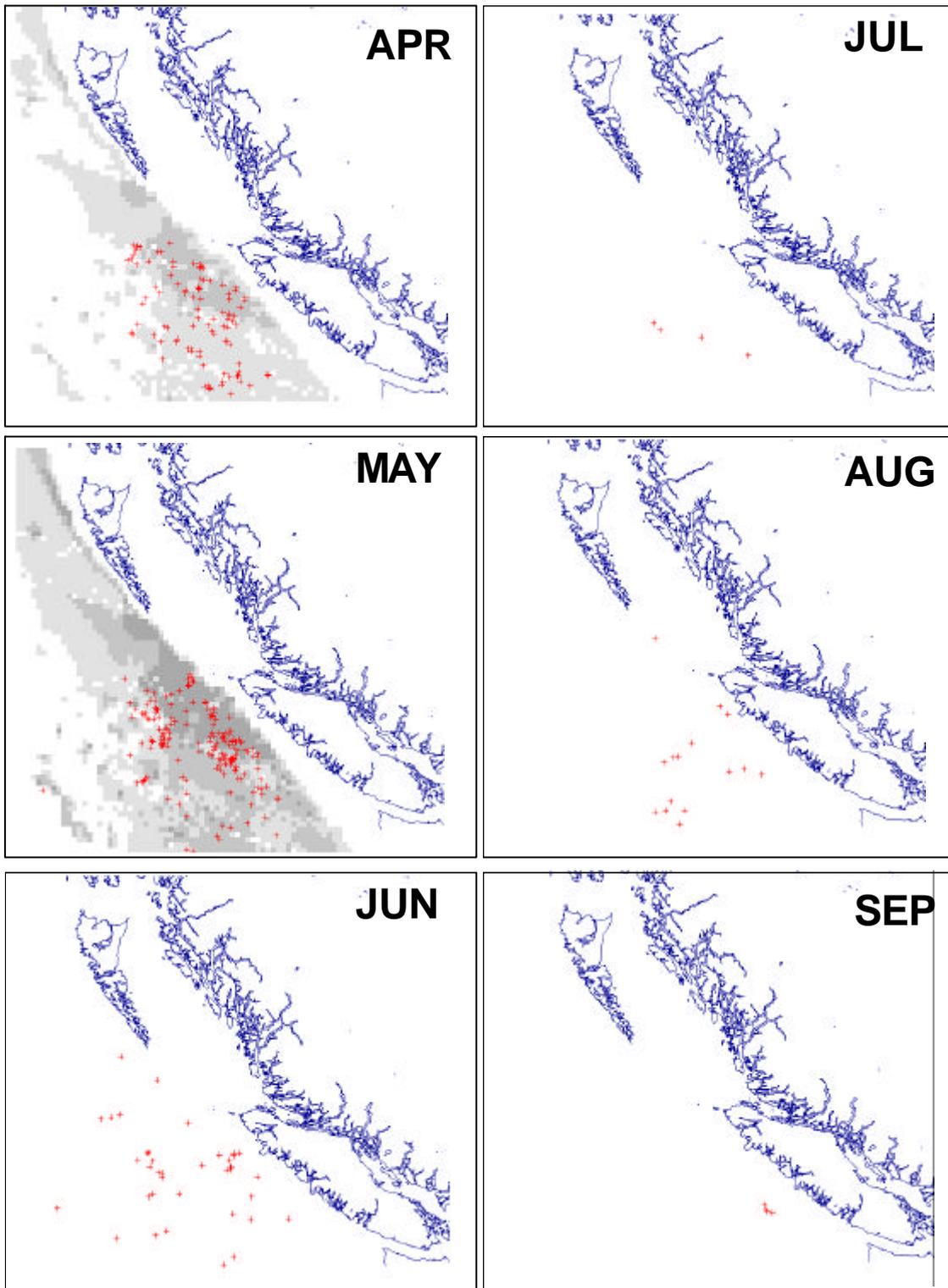


Figure 2.13: Sperm Whale (female): Monthly probability predictions overlaid with the actual positions of whale kills. Dark areas on the probability plots represent areas with a high probability of whale occurrence and white areas represent areas of low probability.

Model Testing

The predictive efficiencies of the species models were defined using classification tables. The cutoff values selected consistently generated classification tables where the presences were predicted with much less efficiency than the absences (Table 2.4). 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).

Table 2.4: Classification table results showing the predictive efficiency (as percent) of the annual and monthly models for predicting presence, absence and overall, for all species.

	SW		FW		HW		BW		SPW m		SPW f	
	Ann.	Mo.	Ann.	Mo.	Ann.	Mo.	Ann.	Mo.	Ann.	Mo.	Ann.	Mo.
Presence	0.70	0.46	0.76	0.48	0.35	0.22	0.22	--	0.61	0.36	0.38	0.25
Absence	0.83	0.93	0.82	0.90	0.90	0.97	0.94	--	0.78	0.92	0.83	0.98
Overall	0.76	0.70	0.79	0.69	0.62	0.60	0.58	--	0.70	0.82	0.60	0.62

For each group, I 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.

To evaluate the difference qualitatively, I compared the annual habitat predictions for all years to predictions generated by models with coefficients calculated using the “hot” and “other” data sets. The resulting probability plots (Fig. 2.14) are virtually identical.

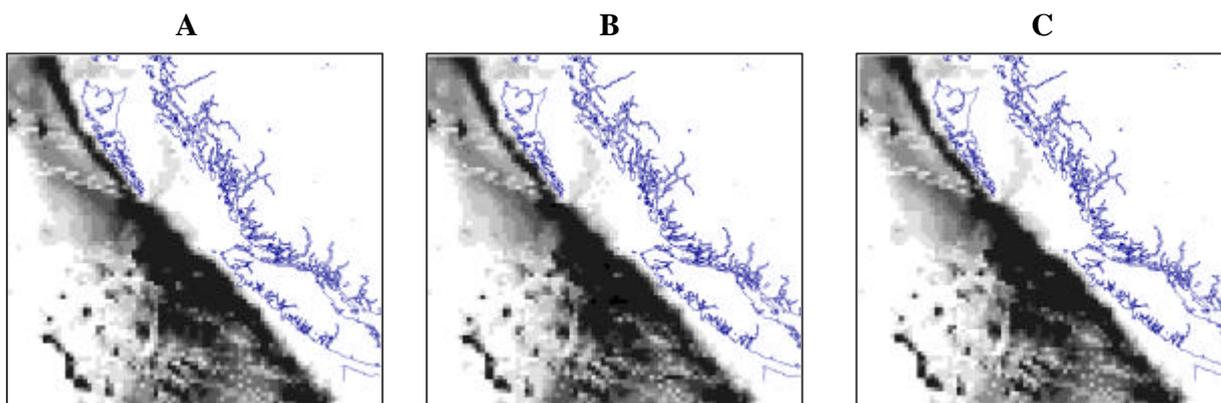


Figure 2.14: Comparison of annual sei whale habitat predictions generated using three different sets of regression coefficients. Panel A coefficients were calculated using the entire 17 year data set of sea surface temperature and salinity measurements. Panel B coefficients were calculated using only data from the five warmest years. Panel C coefficients were calculated using all but the five warmest years.

Discussion

My study focused on defining habitat for five whale species based on oceanographic conditions. I assumed *a priori* that some form of association existed based on the relatively large body of existing literature which, in the Pacific, dates back to Uda (1954, 1962) and Nasu (1963) whose work showed an association between hunted whale species and oceanographic fronts. Examples of specific relationships that have been identified include a significant relationship between two small cetacean species and bottom topography (Hui 1985), and an association between a number of cetacean species and chlorophyll concentrations (Smith *et al.* 1986). However only one study (Moses and Finn 1997) has attempted to explicitly predict cetacean habitat, and this was limited to bathymetry and sea surface temperature.

Underlying all 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 relation of common baleen whale prey species to

oceanographic conditions can take two forms: conditions can be ideal for production and growth (i.e., plankton blooms), or oceanographic conditions can work to concentrate existing prey in specific areas. In the first case, there is likely to be a temporal lag while the prey develop. Due to oceanic transport, this temporal lag can also create a significant spatial lag. For baleen whales feeding on zooplankton, which are trophically close to primary production (trophic levels 2.0-2.3 vs. 1.0 - Trites *et al.* 1999), this lag may be quite short. The lag may be extended considerably for sperm whales (Jaquet 1996, Jaquet *et al.* 1996), where the primary prey items (cephalopods, trophic level 3.7 - Trites *et al.* 1999) are further removed from primary production.

If the relationship is more a function of prey concentration or aggregation, such as oceanographic conditions concentrating plankton through small scale eddies or gyres, very little temporal and no spatial lags would be expected. Similarly, if certain bathymetric features (i.e. areas of high relief) caused prey species to aggregate, lags would also be absent.

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

In this study, I produced patterns at a high spatial resolution at two different time scales because, while generalizations are more likely to be uncovered at broader scales, fine scale studies may provide more information about the biological processes underlying the patterns (Weins 1989).

The annual models predicted that fin, sei and male sperm whales will occur with near certainty, sometime over the course of the summer along the entire shelf break, and in a large area

extending 75 km to 100 km beyond the shelf at the north end of northern Vancouver Island. This offshore region stretches from the continental shelf to approximately 100 nm offshore and ranges from Kyuquot Sound, just south of Brooks Peninsula, to the northwest as far as the Dellwood Seamounts. The models predicted a high probability of sei, fin, blue and male sperm whales in this habitat patch. The models predicted less use of this habitat by humpback and female sperm whales. The apparent importance of the shelf break and the habitat patch was persistent at both the annual and the monthly time scales.

Sei Whales

The annual models (Fig. 2.6) predicted a high probability for sei whales to be in deep water, while the monthly models (Fig. 2.9) showed strong seasonal effects. This is supported by the significant effects of depth class and month on the presence-absence of this species (Fig. A.1). The large amount of variance explained by the sei whale model (Tables 2.2 & 2.3) suggests that sei whales are closely tied to oceanographic conditions.

My interpretation of the sei whale data in Chapter One suggests that sei whales migrated past the Coal Harbour station. Although the monthly predictions do not confirm or contradict this suggestion, the predictions can be interpreted as a migration through the area by some (perhaps larger and more mature) animals, while less mature animals ended their northward movement sooner, remaining in the vicinity of the habitat patch. However this interpretation is far from conclusive, and requires further analysis of the distribution of this species according to age structure.

Fin Whales

The annual habitat prediction for fin whales (Fig. 2.6) is consistent with Pike and MacAskie's (1968) observation that this species occurred mostly offshore, but frequently entered exposed

coastal seas such as Hecate Strait and Queen Charlotte Sound. The monthly predictions (Fig. 2.10) show how the movement of fin whales into these coastal seas is a seasonal effect (strongest in July and August). These monthly predictions support the interpretation in Chapter One that fin whales returned to feeding grounds off the British Columbia coast. 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 that 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 (Fig. 2.7). The model predictions is consistent with reports of humpback whales in the Strait of Georgia and Barkley Sound (Webb 1988) and shows 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 (Fig. A.9) 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 (Tables 2.2 and 2.3). This is also evident from the probability plots (Figs. 2.7 and 2.11) which show lower probabilities for humpback whales. The low correlation coefficient is 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 (Fig. 2.7) shows little contrast. However, the fact that the model predicts blue whale use of the same habitat patch used by the sei and fin whales may be significant. Given that blue whales are believed to migrate away from coastlines (Mizroch *et al.* 1984a), and feed in eastern Pacific coastal areas (Fiedler *et al.* 1998), it is possible that the smaller, younger blue whales which dominated the Coal Harbour catch (see Chapter One) frequented the habitat patch off northern Vancouver Island. This is indirectly supported by the preliminary analysis that showed the mean depth for this species to be less than that observed for the fin and sei whales (Figs. A.1, A.4 and A.10).

Sperm Whales

The annual model predicted a narrower distribution for male sperm whales (Fig. 2.8) 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 (Fig. A.13). An apparent month effect on the preferred depth of male sperm whales (Fig. A.14) shows movement into shallower water after May. This is supported by the spatial shift evident in the monthly probability plot (Fig. 2.12).

The annual probability plot for female sperm whales (Fig. 2.8) predicts a virtually uniform distribution throughout the deeper waters, although the habitat patch is shown with a slightly higher probability. The monthly predictions (Fig. 2.13) 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 (Fig. A.16). 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.

This result, which suggests that female sperm whales were relatively uninterested in their surrounding oceanography, adds support to the hypothesis proposed in Chapter One regarding sperm whale mating during April and May. Given that males are spatially segregated by size, with larger males at higher latitudes (Best 1979), a reasonable hypothesis that supports the data presented here and in Chapter One is that females ready to breed travel north to secure the strongest, most mature mate. While the female may not actually select a specific male (given the suggestion of competition among large males – Best, 1979), by travelling north, she would at least assure herself of stronger, more mature suitors. This mating hypothesis can also explain the presence of small numbers of females during all months (Fig. 2.13) given the possibility of spontaneous or induced ovulation (Best *et al.* 1984) in females. Alternatively, it is possible that ovulation is spontaneous and cyclical, as with other large odontocetes such as killer whales (*Orcas orcinus*) (J. Ford personal communication).

Underlying Processes

Given the assumptions that whales will generally be found where their food is abundant, and that food concentrations are somehow related to oceanographic conditions, some hypotheses about the processes underlying the observed patterns can be made.

Since baleen whales forage primarily on zooplankton, the processes generating the patterns observed in this study are likely related to oceanographic effects that manifest themselves through either enhanced productivity or entrainment of prey. Since temporal (and spatial) lags between primary production and the development of grazing zooplankton populations can be

expected, conditions that concentrate plankton may be a better indication of whale presence than conditions that promote plankton growth.

The outer coast of Vancouver Island is a highly productive area during the summer months, and the resident zooplankton populations are well fed from spring through the fall (Mackas and Galbraith 1992). Summer circulations appear to result in a high washout rate of surface zooplankton from on shelf waters into offshore areas (Mackas 1992).

The north end of Vancouver Island is a region where a number of currents converge. An off-shelf flow in a generally southwest direction out of Queen Charlotte Sound (Thomson 1981) converges with the Vancouver Island Coastal Current from the southeast which brings nutrient rich, upwelled waters to the region. During this period, surface circulations on the shelf near Vancouver Island are dominated by small scale circulations and eddies due to weaker bottom currents (Crawford and Thomson 1991). In addition, summer circulations offshore of northern Vancouver Island were identified as variable by Thomson (1981) due to the bifurcation of the Kuroshio current into the coastal Alaskan and Californian currents.

These oceanographic conditions may combine to create an environment suitable to both increased primary production and entrainment of phytoplankton. This may, in turn, increase zooplankton concentrations. Thus, both the entrainment and increased productivity mechanisms described above may be at work to create the habitats identified by my study.

While this may represent a reasonable description of habitat for the baleen species, it does not provide a direct link to sperm whales, which are believed to feed primarily on giant squid, several trophic levels above zooplankton. This is complicated by the obvious differences in distribution of the sexes, which I have suggested is largely a behavioural effect. Since males were present throughout summer months, and their concentrations on the slope and in other

regions of high relief increase after the departure of the females, I suggest that male sperm whale feeding is more closely related to bathymetric features such as depth and slope. Since in the habitat patch off northern Vancouver Island, these features are coincident with the oceanographic processes discussed above, this would explain why the model predictions for male sperm whales are similar to the baleen species.

Limitations on the interpretation of the probability plots

The probability plots depict a combination of physical conditions, an oceanographic recipe, that best describes where the whales were found within the study area. These oceanographic recipes can be interpreted as descriptions of suitable, or perhaps even critical habitat for these species. However several complicating factors need to be considered.

The effectiveness of the predictions depend on the assumption of equal effort applied throughout the study area. Since this assumption is clearly violated to some degree, the implications of non random sampling (discussed below) should be kept in mind when interpreting the plots.

A further consideration is the unreliability of results predicted at the edges of the study area, caused by the spatial boundaries of the study area. This “edge effect” is caused by both interpolation and extrapolation: The TIN interpolation, which estimates the values for the predictor variables, is inaccurate at the edges of the study area because the masking applied to bound the study area sets the region outside to zero. This can potentially make the outermost triangles in the TINs artifactual, leading to unreliable interpolations. Another type of edge effect is caused by the extrapolation to predictor values (especially depth) outside the range used in the definition of the models. This can lead to unexpected results in regions where the independent variables take on values not considered during the model building.

Model Test Results

Predictive efficiencies, calculated using classification tables, are most commonly applied to dependent data that have no spatial component (i.e. probability of disease, probability of failure, etc.). I found no published articles that used this method to evaluate dependent data with spatial characteristics. Experimenting with different values for the cutoff (the value which classifies a prediction as a positive or a negative outcome) shows that the predictive efficiency is highly sensitive to this value. The classification tables also appear sensitive to the spatial distribution of the data. Since the testing was done using grid cells, and the “presence” cells were highly spatially autocorrelated, the results were strongly affected by the composition of the prediction and testing samples. These results highlight the need for quantitative methods to evaluate the distribution of spatial data, and for testing this and other models of habitat.

The sensitivity of the model predictions to the oceanographic model showed that while the different predictor data sets (i.e. all, hot, and other) generated predictions that were statistically very different, the resulting probability plots were almost identical.

This can be interpreted in a number of ways. It is possible that the relationships captured by my habitat models are relatively insensitive to variations in temperature and salinity, suggesting that these two predictors are of less significance than the others. Alternatively, and perhaps more likely, it may be that the oceanographic model does not provide the necessary spatial resolution 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 serve to address this and other similar questions about the relative importance of the predictor variables. More sophisticated statistical methods are also needed to ensure that spurious statistical significance is not interpreted as biological significance.

Model Biases

Data independence

Although I 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 my 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 autocorrelation at monthly time scales and spatial scales likely on the order of hundreds or a few thousand kilometers. Similarly, since whales are known take advantage of food source concentrations and congregate in areas of high food abundance, this implies strong spatial and temporal autocorrelation at a scale of metres and minutes.

Autocorrelation at these finer scales is further implied for all species in this 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 this case. Rather, the questions that need to be answered are: At what temporal and spatial scales are whales correlated, and what are the processes responsible? While I do not attempt to answer the first question, the question of processes is central to my study.

I make the assumption that these processes are in some way related to the independent predictor variables I used in the models. However the lack of independence, both within and among these predictors, complicates the interpretation of the habitat models. Since my sampling unit is a grid cell, it is clear that spatial autocorrelation will exist for all the independent variables I considered (i.e. the value at a particular grid cell will not be independent of the values of its neighbors).

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 in identifying 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 Component Analysis) does not provide any additional insight into what defines whale habitat and may, in fact, complicate the analysis by introducing abstract component terms.

Thus, while accepting that there is a significant lack of independence in both the dependent and predictor data sets, I have not attempted to correct for these effects, and consequently the degrees of freedom reported for the results are artificially high. Nevertheless, I this lack of independence is offset to some degree 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.

The effort assumption

The assumption of equal effort throughout the study area defined by a 150 nm search radius from the Coal Harbour whaling station is central to this study, and therefore warrants detailed consideration. Based on information available on the British Columbia coastal whaling industry, whalers traveled up to 200 nm from shore and often remained at sea for several days (Webb 1988, Pike and MacAskie 1968). Captured whales were often marked and floated for later recovery, while the vessels pursued additional animals. It is therefore likely that animals encountered in nearshore areas were killed prior to the whalers proceeding further offshore. Evidence for the annual movement of whaling effort further offshore is provided in Chapter One, where I showed that the annual mean distance from shore for animals killed for all four species changed significantly between 1948 and 1967. It can safely be assumed that the whalers 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 1,508 grid cells within

the 150 nm area. If the monthly time scale is included, the likelihood of equal effort over all 9,030 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 would require considerable additional research and analysis making it beyond the scope of this study.

The behaviour of the whalers may serve to mitigate the effect of unequal effort to some degree. It can be assumed that the whalers were operating with fairly detailed knowledge of where whales were commonly found. The whaling captains during the Coal Harbour had considerable experience to draw upon since the fishery began in the early 1900s and many were veterans of the previous era (Webb 1988). Thus, it is possible that regions where few data appear, did in fact contain very few whales even though they may not have been heavily searched.

The greatest effect of non random sampling on the results would be to bias the predictions towards certain values of the predictor variables, or to 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, making it unlikely that the whales were sampled randomly in time. The consequence of a sampling bias towards months more favourable for offshore fishing (June, July, August) would cause the contribution of the month variable to have an exaggerated effect on the predictions. This would make it difficult to disentangle the real process of whale migration and the bias imposed by increased effort in the summer months.

The effects of nonrandom spatial sampling are more difficult to evaluate. One worst case scenario would be the existence a region of good habitat within the study area that was not

frequented by the whalers. This region would be treated as empty of whales, reducing the accuracy with which my models predicted whale presence. The effect would be to bias my habitat predictions towards the oceanographic conditions found in the more commonly searched areas. Since cells closer to Coal Harbour were likely searched with greater effort than those at a distance, by treating all cells equally the predictions are biased towards oceanographic conditions at the more distant cells.

Nevertheless, I believe that areas of predicted high probability represent an aspect of whale habitat. The problems discussed here only raise the question of the relative importance of the habitats described, and do not invalidate the study. While we may debate whether the habitats described here are “critical” or “important” or simply “suitable”, we must acknowledge they have some level of importance to these species.

Concurrency of biological and oceanographic data

In this study, I analysed whaling data from 1948 to 1967 with independent oceanographic data pooled over the years 1980 to 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. I therefore chose data density over data currency.

I have shown that this lack of temporal currency between the dependent and independent variables has significant effects on the habitat predictions using a 10 km grid size. However at larger spatial scales, I would expect the two predictions to converge as the localized differences in temperature were averaged out by pooling with their neighbours. A more sophisticated oceanographic model is needed to explore how the response to changes in ocean temperature and salinity is mediated by scale effects.

Future Work

This study can be considered as both a preliminary set of habitat predictions for five whale species that frequent BC waters, and as a new method for constructing habitat models using regression techniques. Follow up work could therefore focus on a number of different aspects including: a more detailed analysis of the habitat of a particular species; extending the existing model to a larger geographic area; improving the methods; or exploring the effects of scale.

A detailed analysis of the habitat predictions could include field tests of the predictions. Long term experiments can be envisioned which track the recovery of these relatively depleted populations since, if the predictions are accurate, any increase in populations size ought to be reflected first in the areas of highest predicted probability.

The integration of oceanographic point data from California, Washington, Oregon and Alaska could be used to extend the models to a larger geographic area, extending the relationships proposed here to the entire Northeast Pacific Ocean. Alternatively, new models could be constructed using positional data from other whale fisheries in the North Pacific (i.e. the pelagic fishery). This would allow the comparison of models from other areas of the North Pacific, possibly at a much larger spatial scale, to be compared to the models from my study.

Improvements to the model, particularly those that address the problems of autocorrelation and fishing effort described above, are another avenue of future work. The model could be adapted to weight cells in the study grid based on some assumption about the distribution of effort. A detailed study of the correlations within and between the variables could also be conducted and would likely provide a considerable improvement to the model fit. A method of weighting the independent variables, with weights assigned according to some categorical analysis (i.e. Principal Components) may also improve the model predictions.

Finally, the generic nature and flexibility of Cause&Effect make it ideal to address the theoretical aspects of space and scale issues in a practical, visual manner. The ability to quickly generate and view predictions at various spatial and temporal scales could help emphasize the difficulties associated with scale, and help investigate the linkages between pattern and process. For example, comparing the relationships identified in this study with those from a similar study of the North Pacific would help identify the scales over which the hypothesized processes operate.

Conclusions

This chapter explored the relationships between whale distributions and physical oceanography at two time scales (annual and monthly). Preliminary analysis, using scatter plots of whale presence-absence and fitted lowess curves showed that all species exhibited linear or quadratic responses to a number of the independent predictor variables. These relationships, when combined into a probability model of whale distributions, generated predictions that could be interpreted as measures of habitat suitability.

The model identified the oceanic shelf break off British Columbia, and a large area about 100 nm offshore of northern Vancouver Island as critical habitat for sei, fin and male sperm whales. Humpback, blue and female sperm whales appeared relatively insensitive to the predictor variables, however the sample size for these three groups was significantly smaller (by an order of magnitude). The habitat predictions lend support to the hypotheses about sperm whale breeding in British Columbia offshore waters, and predict suitable humpback whale habitat in sheltered bays and straits throughout coastal British Columbia.

A possible explanation for why the offshore area forms a habitat patch for sperm whales is that the highly variable topography is ideal cephalopod habitat. This variable topography, combined

with a number of converging currents, may create a region of mesoscale fronts and eddies which entrain nutrients and primary production making it an attractive foraging area for baleen species as well.

The methods and software developed as part of this study provide a new approach for generating habitat predictions based on measurements of the physical environment. The methodology first considers the individual relationships between a species and the physical environment, which then define the variable scope of the regression models. The habitat modeling software allows easy integration of diverse data sets, and provides a powerful environment for presenting the predictions of critical habitat.

This work extends previous studies which have been limited to correlation analysis between whale species and various oceanographic features. I 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. My 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.

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Appendix A: Presence-Absence Scatter Plots

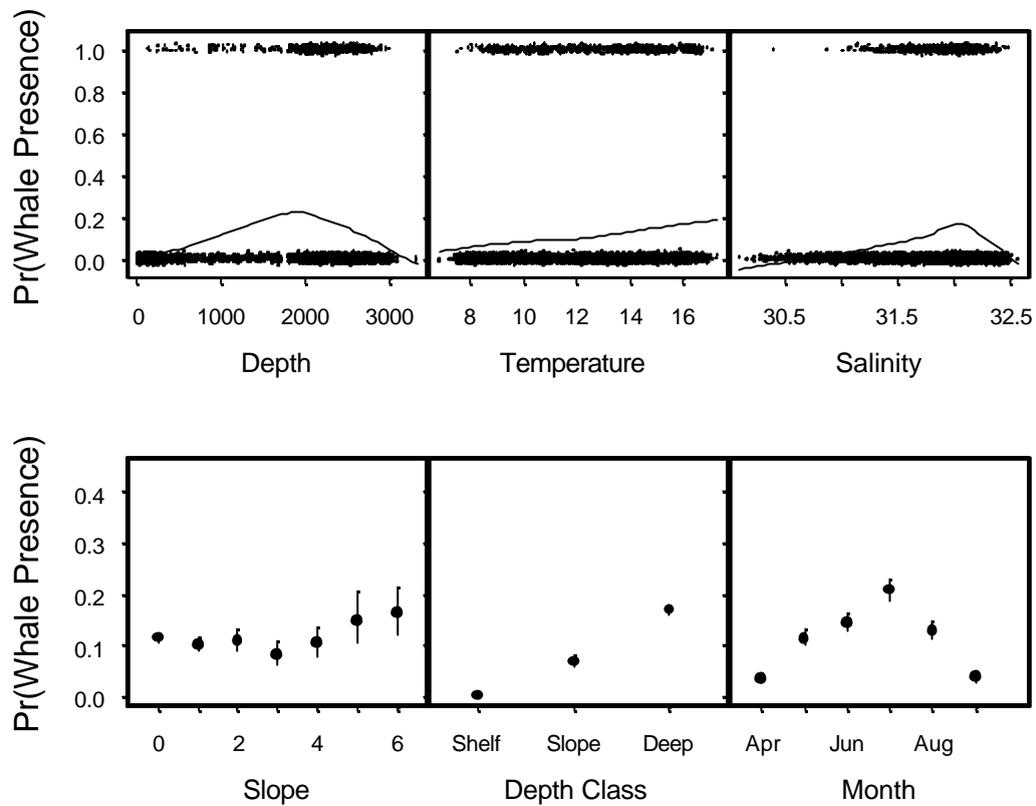


Figure A.1: Sei Whale: Scatter plots (top row) of the three continuous independent variables vs. presence-absence and frequency plots of presence (bottom row) for the three categorical independent variables. The scatter plots are fitted with lowess plots using a span of $2/3$ which gives a probability of whale occurrence, and the observed presence-absence data are jittered to emphasize data density. The frequency plots are shown with 95% confidence intervals.

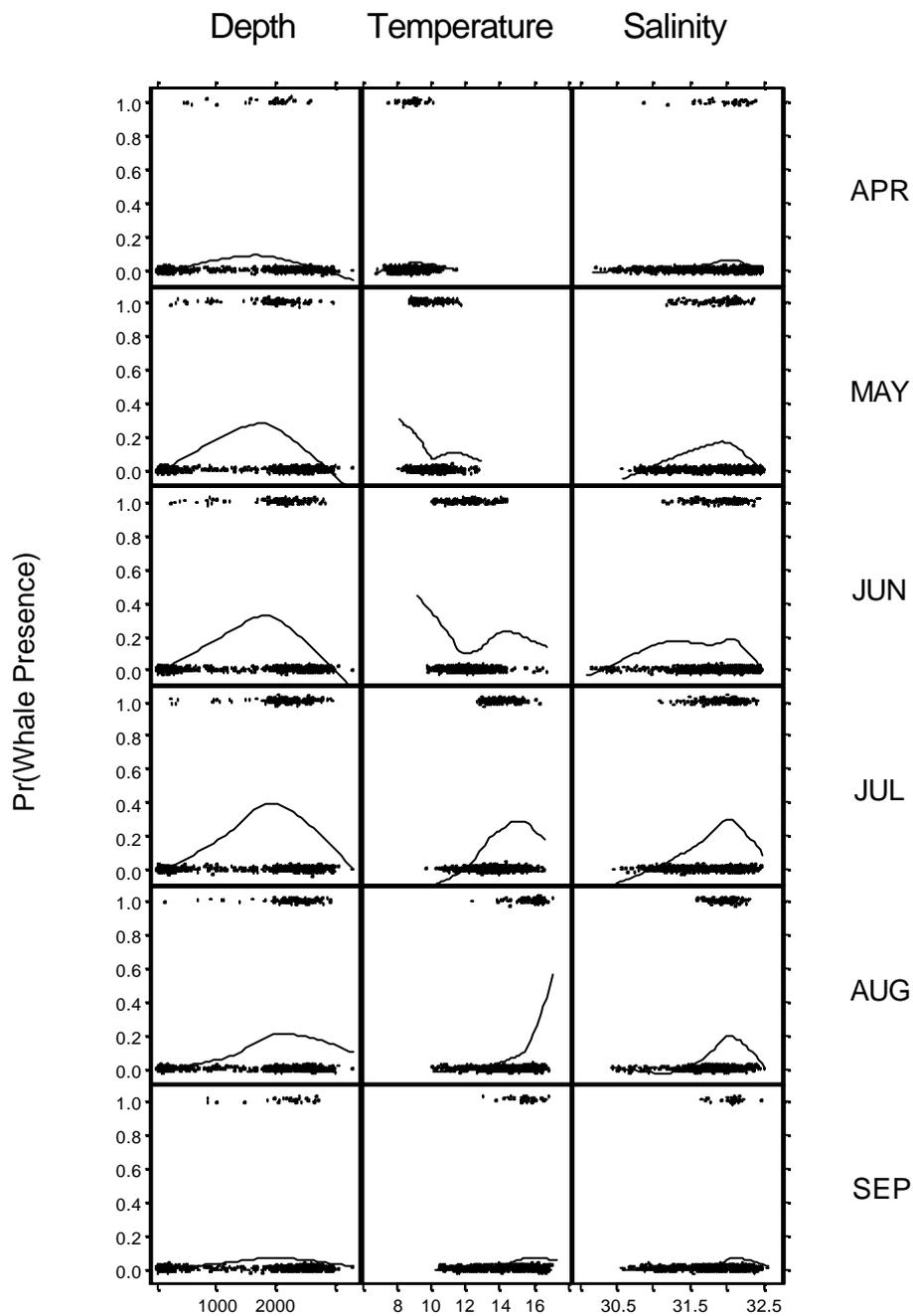


Figure A.2: Sei Whale: Monthly scatter plots of the three continuous independent variables vs. presence-absence showing the interactions with the month categorical variable. Lowess curves are fitted to each plot with a span of 2/3 giving probability of whale occurrence. Actual observed presence-absence are plotted with a jitter factor to emphasize data density.

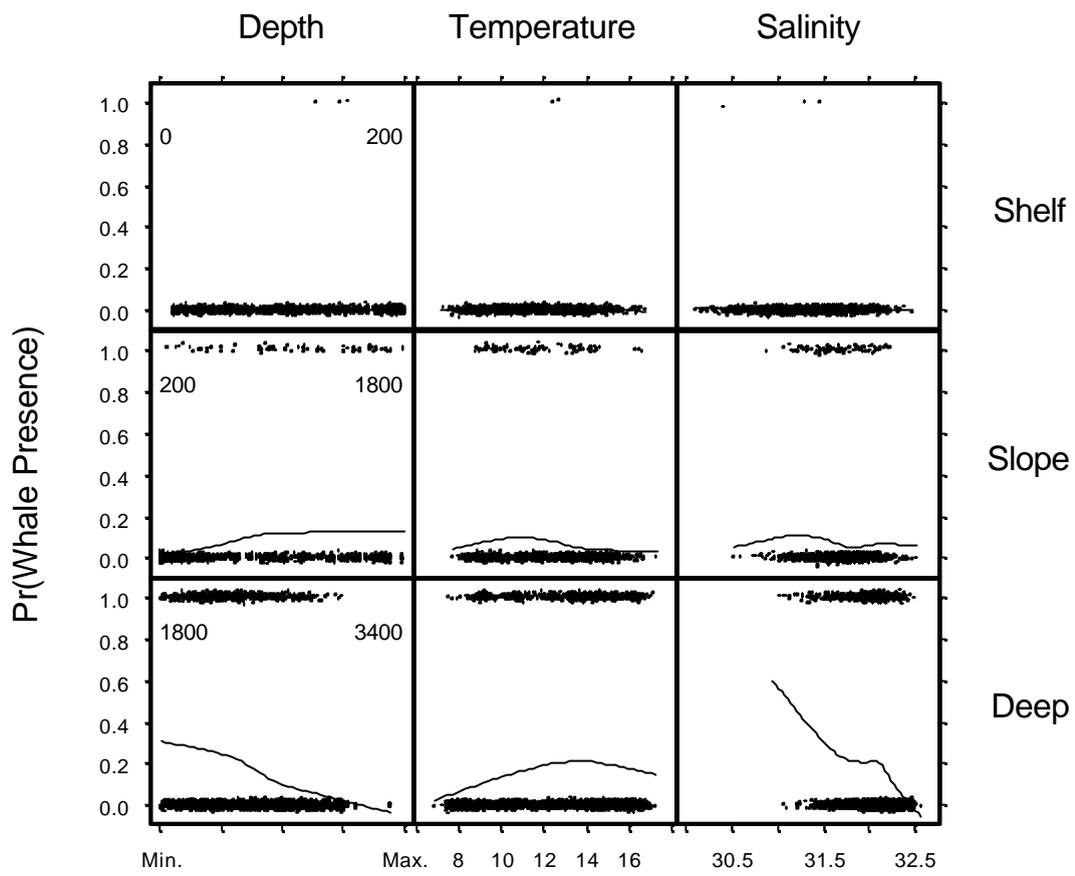


Figure A.3: Sei Whale: Scatter plots of the three continuous independent variables vs. presence-absence for each depth class showing the interaction with the depth class categorical variable. Lowess curves are fitted to each plot with a span of 2/3 giving probability of whale occurrence. Actual observed presence-absence are plotted with a jitter factor to emphasize data density.

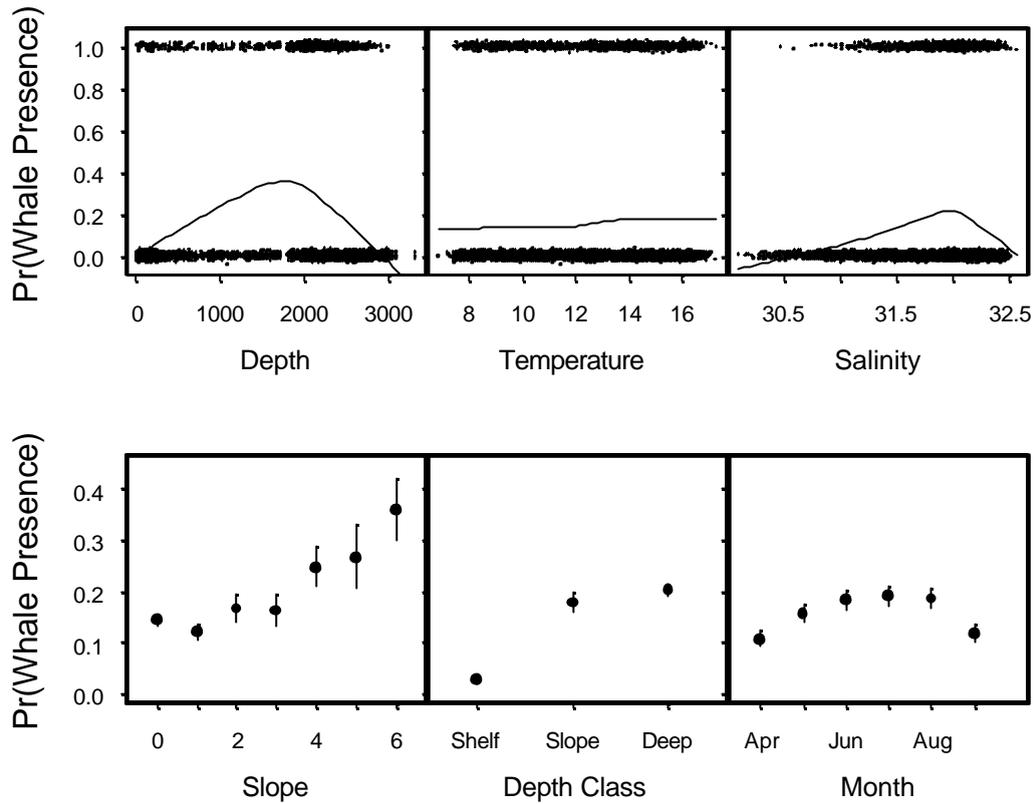


Figure A.4: Fin Whale: Scatter plots (top row) of the three continuous independent variables vs. presence-absence and frequency plots of presence (bottom row) for the three categorical independent variables. The scatter plots are fitted with lowess plots using a span of 2/3 which gives a probability of whale occurrence, and the observed presence-absence data are jittered to emphasize data density. The frequency plots are shown with 95% confidence intervals.

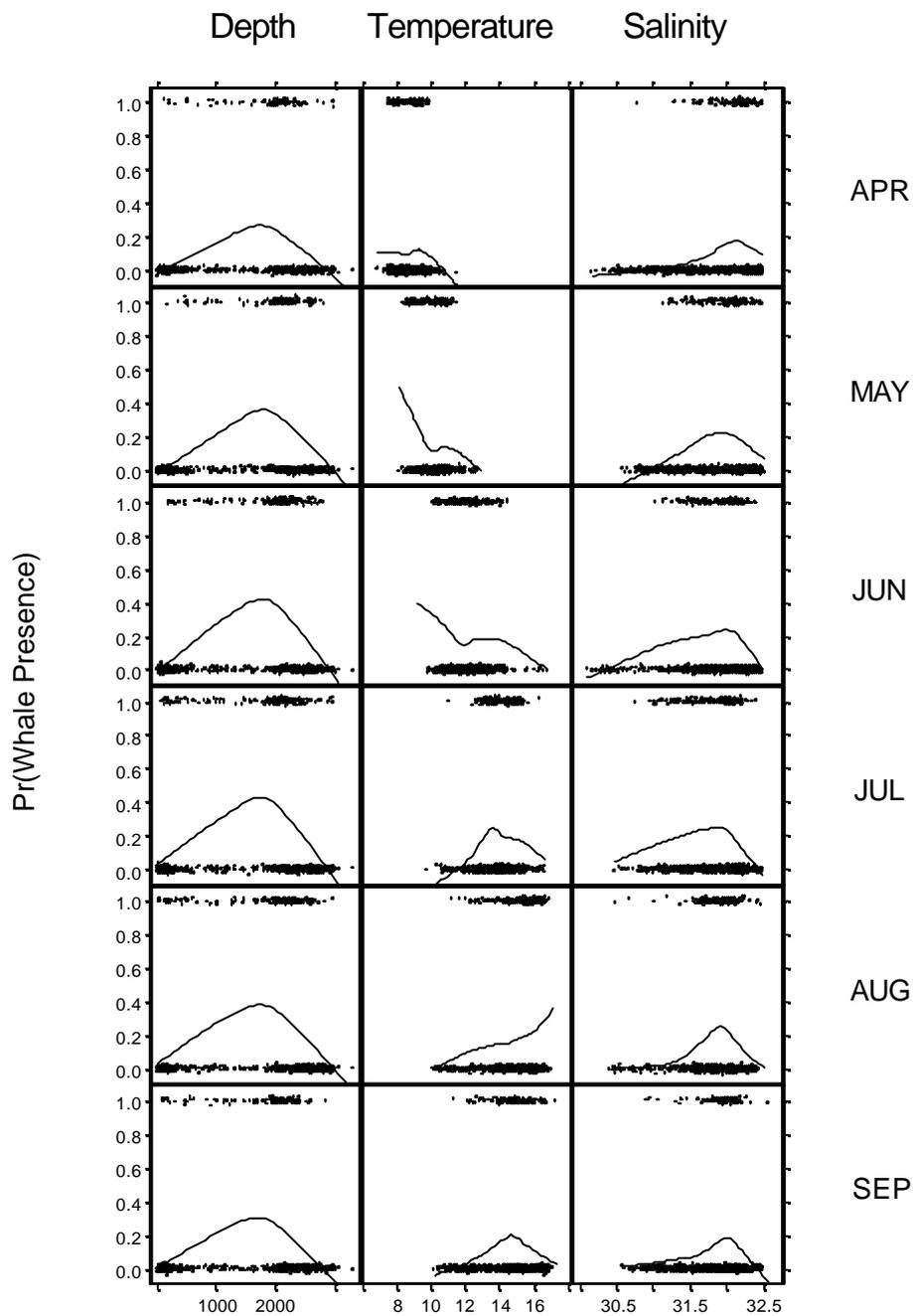


Figure A.5: Fin Whale: Monthly scatter plots of the three continuous independent variables vs. presence-absence showing the interactions with the month categorical variable. Lowess curves are fitted to each plot with a span of 2/3 giving probability of whale occurrence. Actual observed presence-absence are plotted with a jitter factor to emphasize data density.

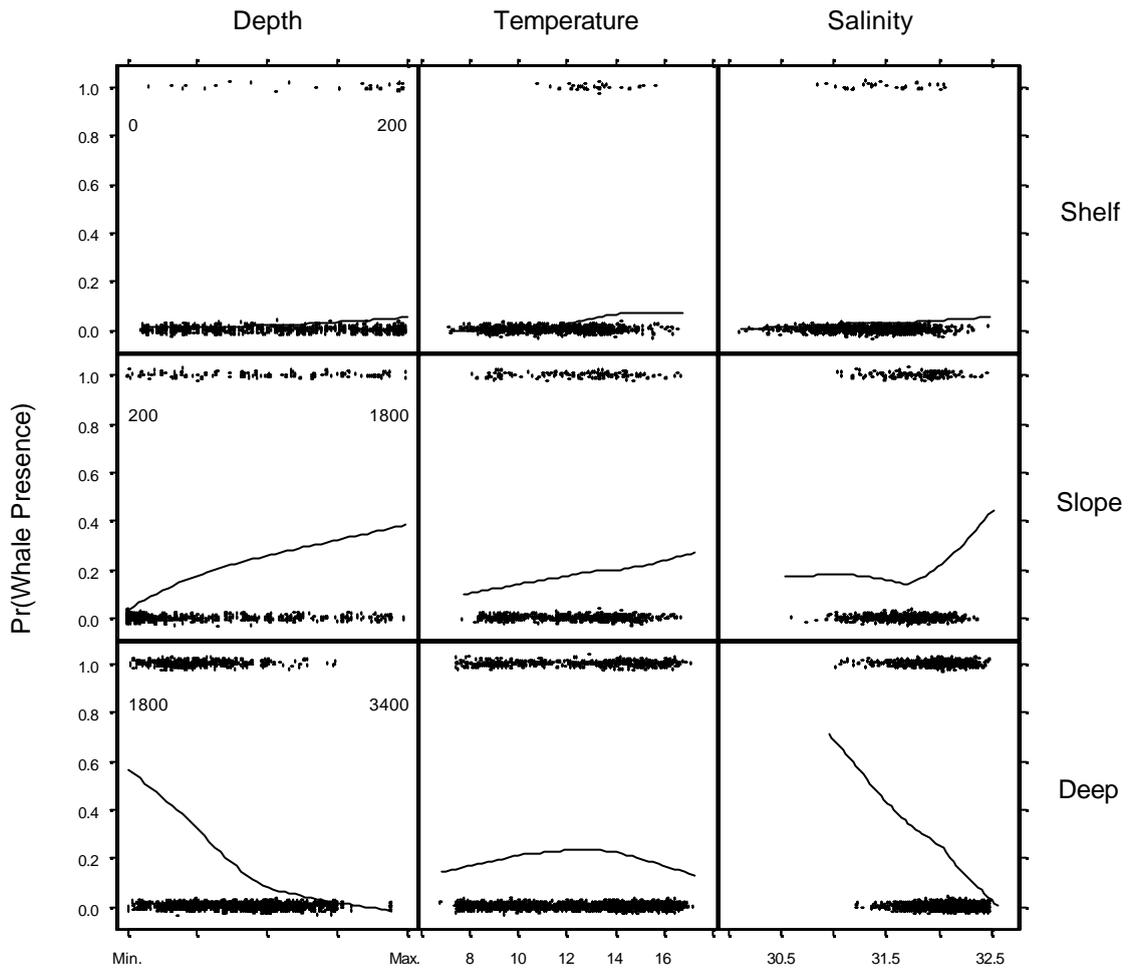


Figure A.6: Fin Whale: Scatter plots of the three continuous independent variables vs. presence-absence for each depth class showing the interaction with the depth class categorical variable. Lowess curves are fitted to each plot with a span of $2/3$ giving probability of whale occurrence. Actual observed presence-absence are plotted with a jitter factor to emphasize data density.

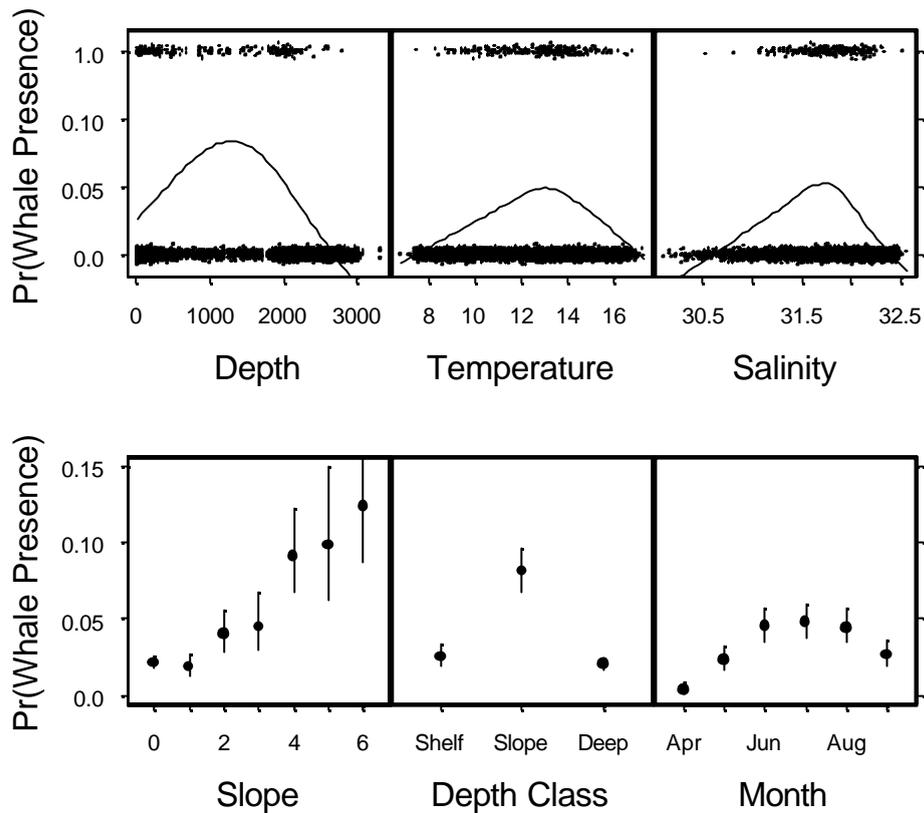


Figure A.7: Humpback Whale: Scatter plots (top row) of the three continuous independent variables vs. presence-absence and frequency plots of presence (bottom row) for the three categorical independent variables. The scatter plots are fitted with lowess plots using a span of $2/3$ which gives a probability of whale occurrence. Due to the large number of absence cells, the y-axis has been adjusted to emphasize the effect, and to allow the observed presence data to be shown. Presence absence data are jittered to emphasize data density. The frequency plots are shown with 95% confidence intervals.

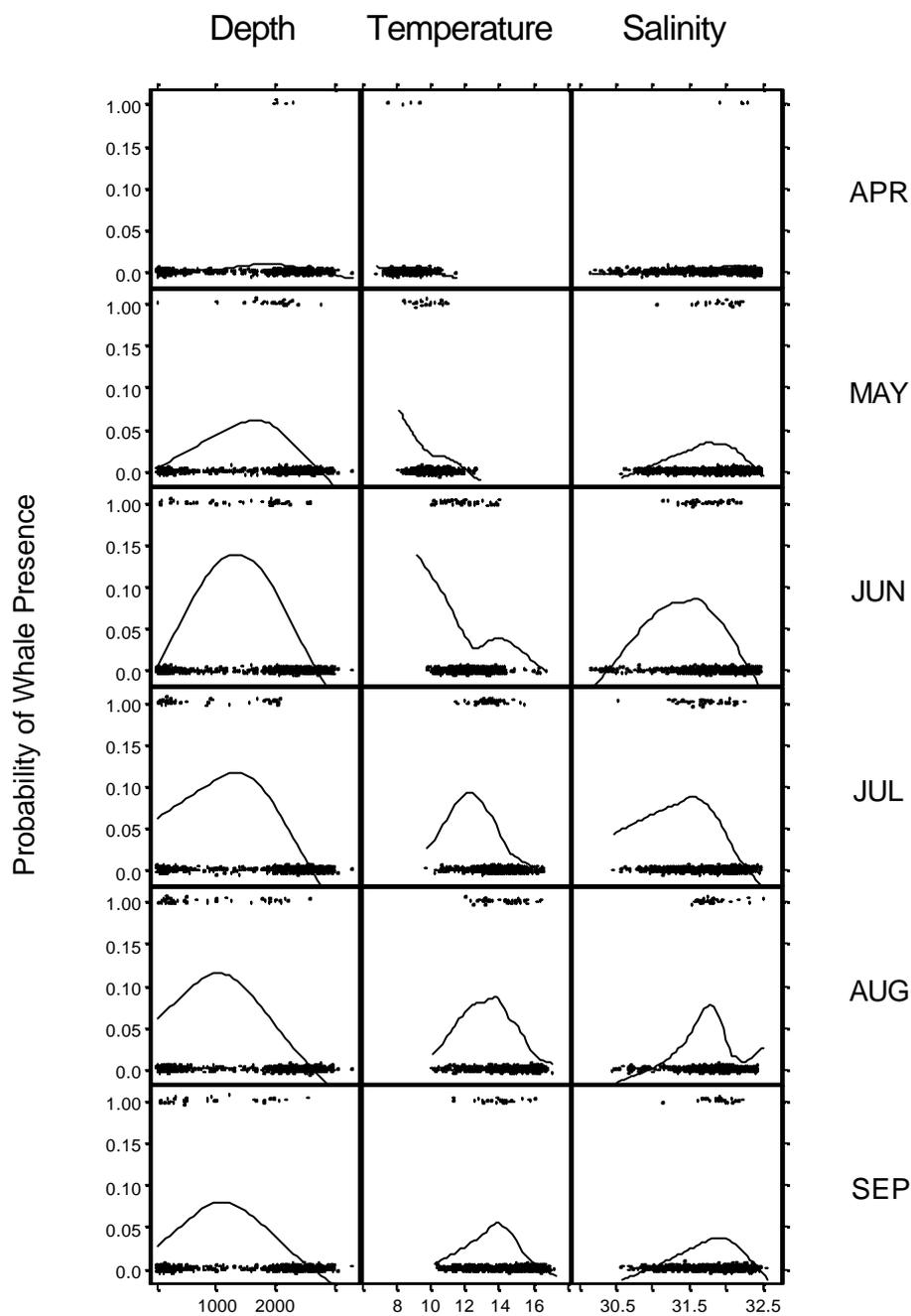


Figure A.8: Humpback Whale: Monthly scatter plots of the three continuous independent variables vs. presence-absence showing the interactions with the month categorical variable. Lowess curves are fitted to each plot with a span of 2/3 giving probability of whale occurrence. Due to the large number of absence cells, the y-axis has been adjusted to emphasize the effect, and to allow the observed presence data to be shown. Presence absence data are jittered to emphasize data density.

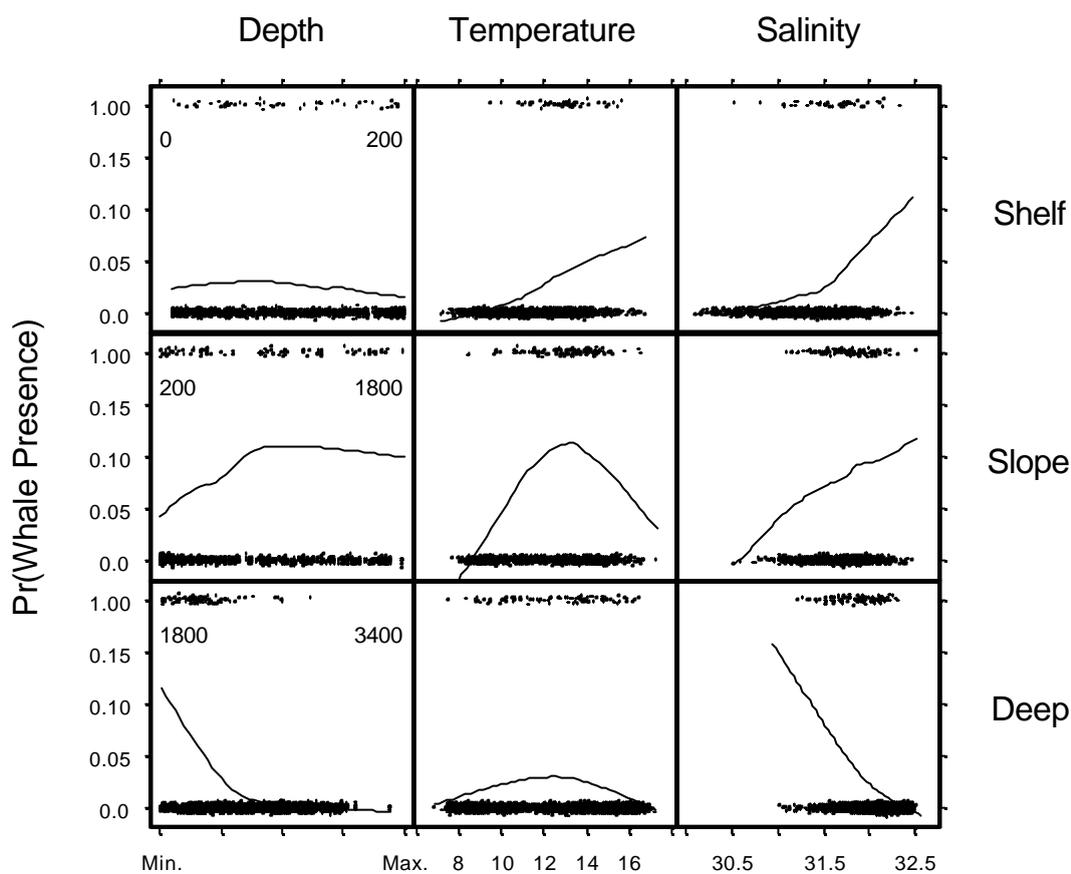


Figure A.9: Humpback Whale: Scatter plots of the three continuous independent variables vs. presence-absence for each depth class showing the interaction with the depth class categorical variable. Lowess curves are fitted to each plot with a span of $2/3$ giving probability of whale occurrence. Due to the large number of absence cells, the y-axis has been adjusted to emphasize the effect, and to allow the observed presence data to be shown. Presence absence data are jittered to emphasize data density.

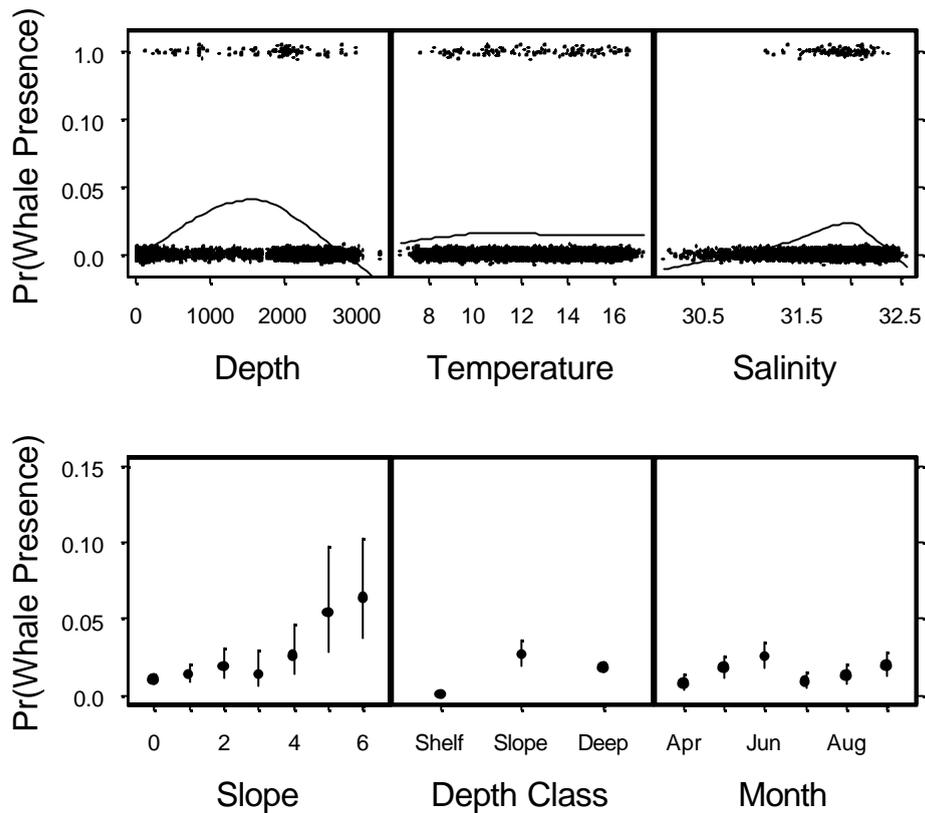


Figure A.10: Blue Whale: Scatter plots (top row) of the three continuous independent variables vs. presence-absence and frequency plots of presence (bottom row) for the three categorical independent variables. The scatter plots are fitted with lowess plots using a span of 2/3 which gives a probability of whale occurrence. Due to the large number of absence cells, the y-axis has been adjusted to emphasize the effect, and to allow the observed presence data to be shown. Presence absence data are jittered to emphasize data density. The frequency plots are shown with 95% confidence intervals.

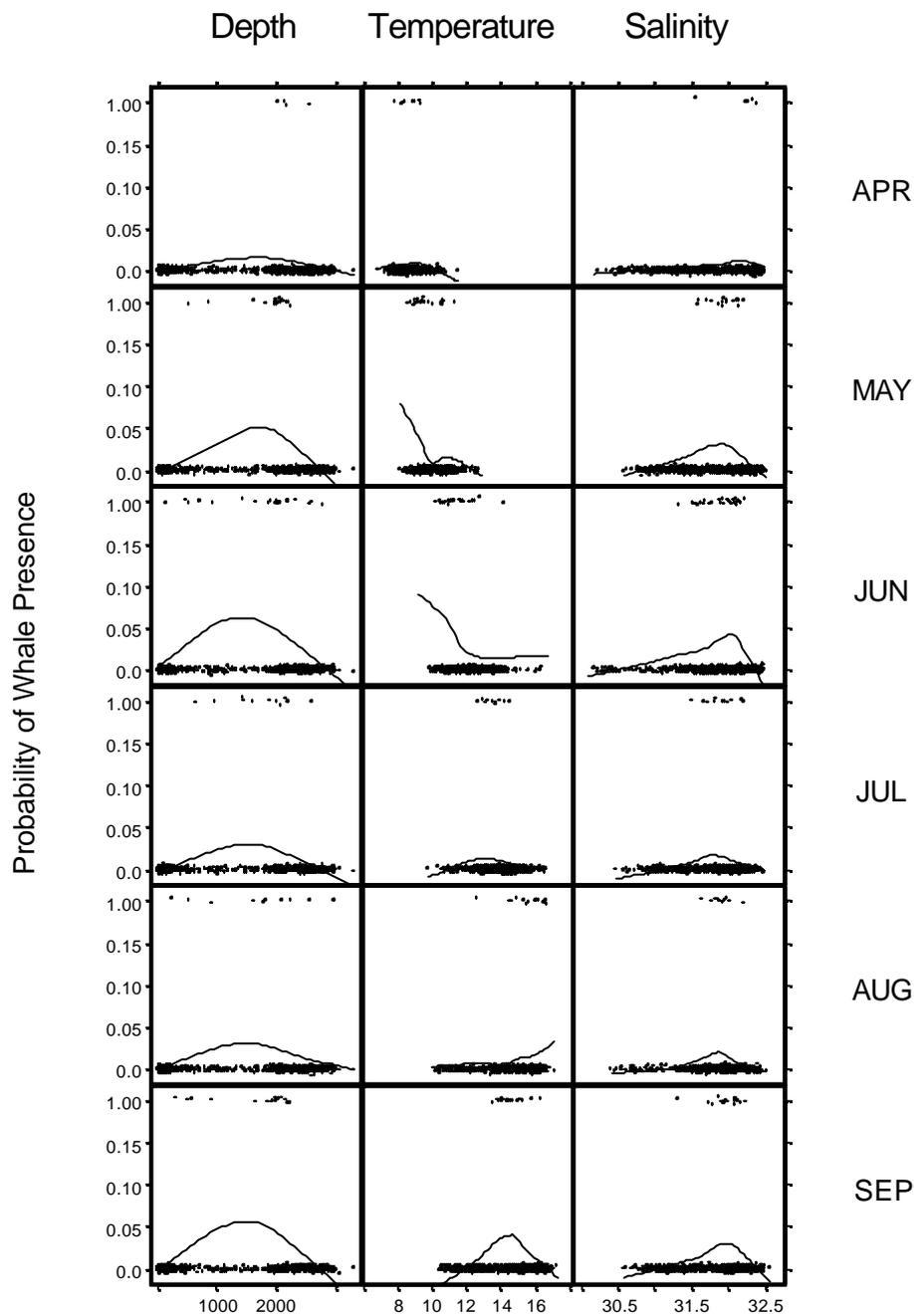


Figure A.11: Blue Whale: Monthly scatter plots of the three continuous independent variables vs. presence-absence showing the interactions with the month categorical variable. Lowess curves are fitted to each plot with a span of 2/3 giving probability of whale occurrence. Due to the large number of absence cells, the y-axis has been adjusted to emphasize the effect, and to allow the observed presence data to be shown. Presence absence data are jittered to emphasize data density.

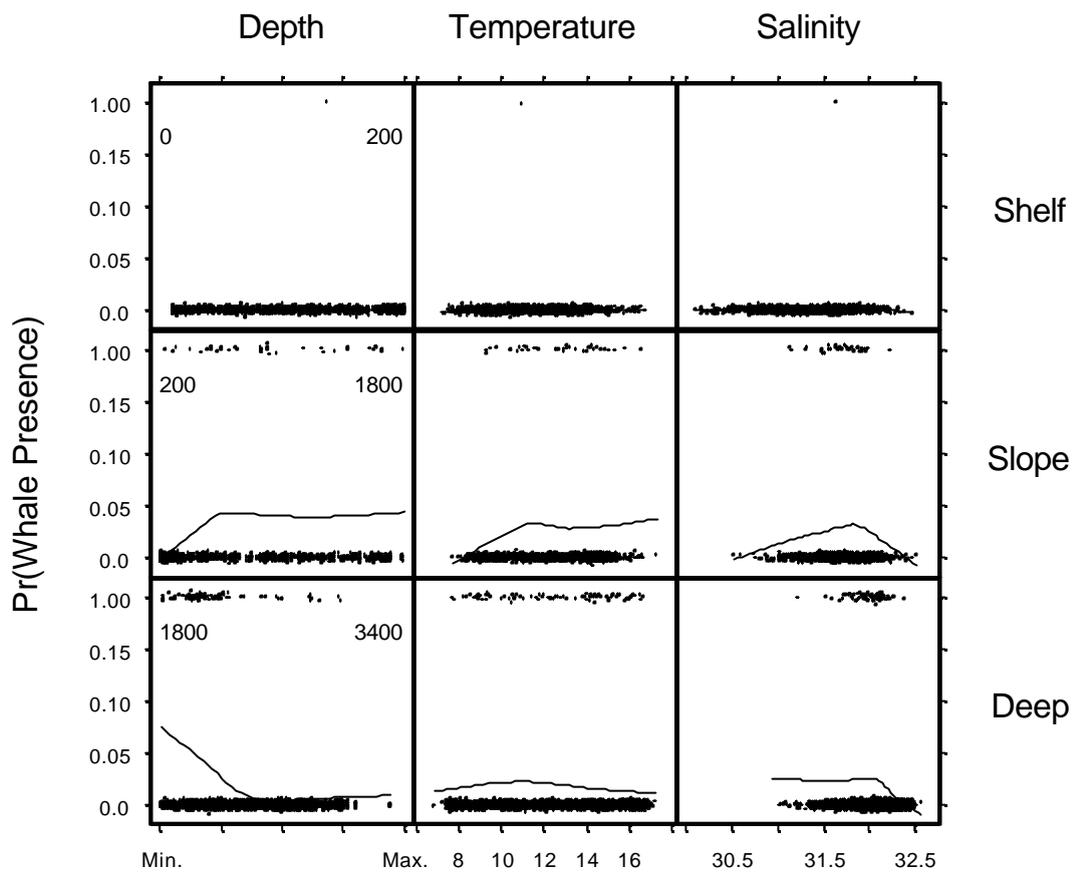


Figure A.12: Blue Whale: Scatter plots of the three continuous independent variables vs. presence-absence for each depth class showing the interaction with the depth class categorical variable. Lowess curves are fitted to each plot with a span of $2/3$ giving probability of whale occurrence. Due to the large number of absence cells, the y-axis has been adjusted to emphasize the effect, and to allow the observed presence data to be shown. Presence absence data are jittered to emphasize data density.

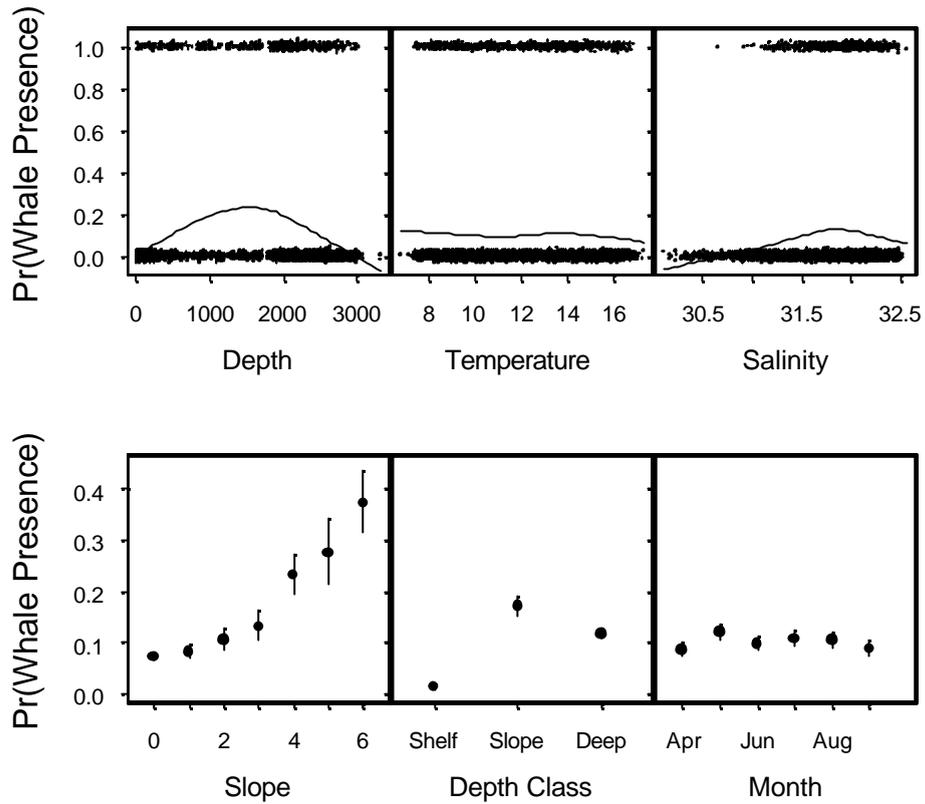


Figure A.13: Sperm Whale (male): Scatter plots (top row) of the three continuous independent variables vs. presence-absence and frequency plots of presence (bottom row) for the three categorical independent variables. The scatter plots are fitted with lowess plots using a span of $2/3$ which gives a probability of whale occurrence, and the observed presence-absence data are jittered to emphasize data density. The frequency plots are shown with 95% confidence intervals.

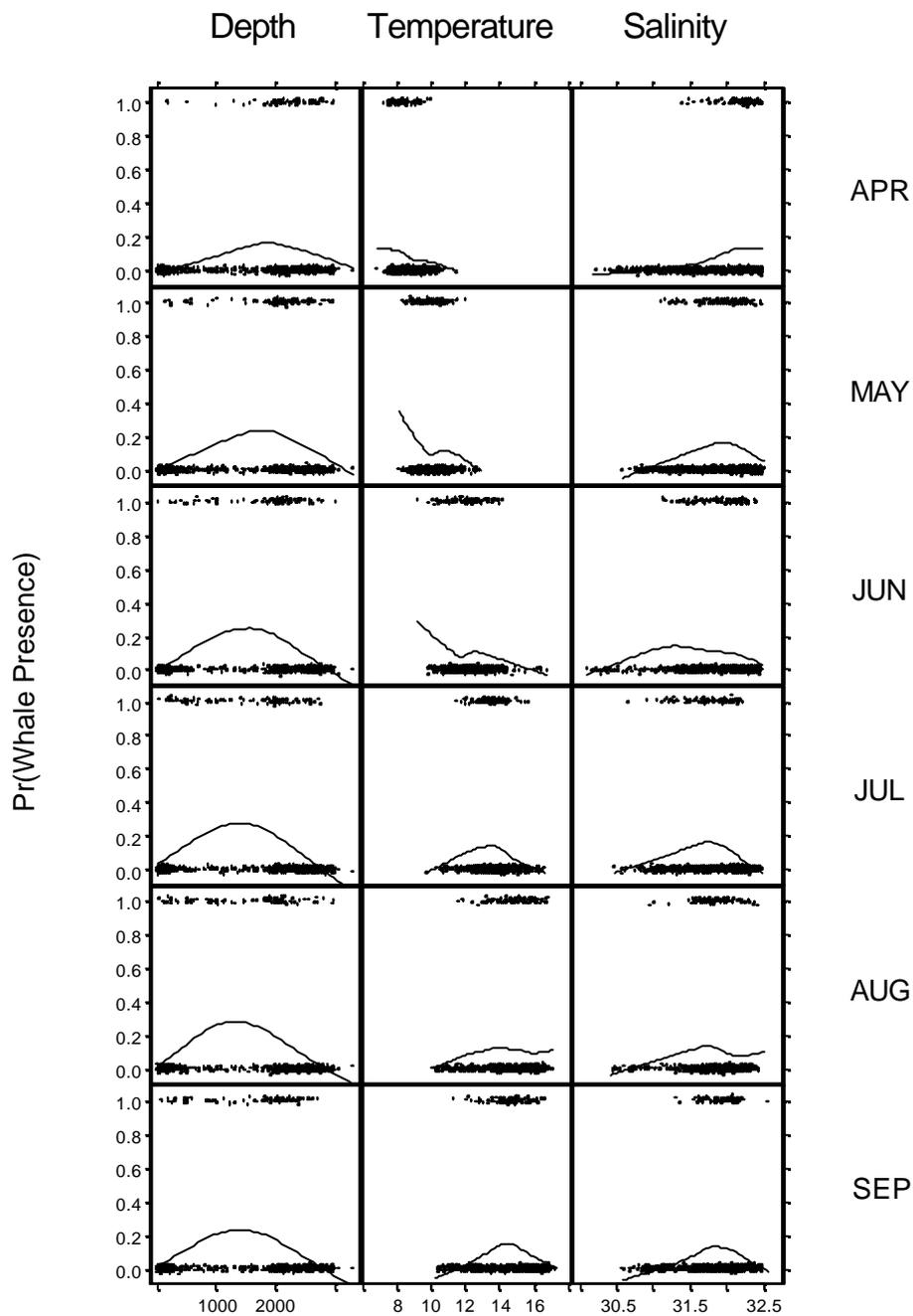


Figure A.14: Sperm Whale (male): Monthly scatter plots of the three continuous independent variables vs. presence-absence showing the interactions with the month categorical variable. Lowess curves are fitted to each plot with a span of 2/3 giving probability of whale occurrence. Actual observed presence-absence are plotted with a jitter factor to emphasize data density.

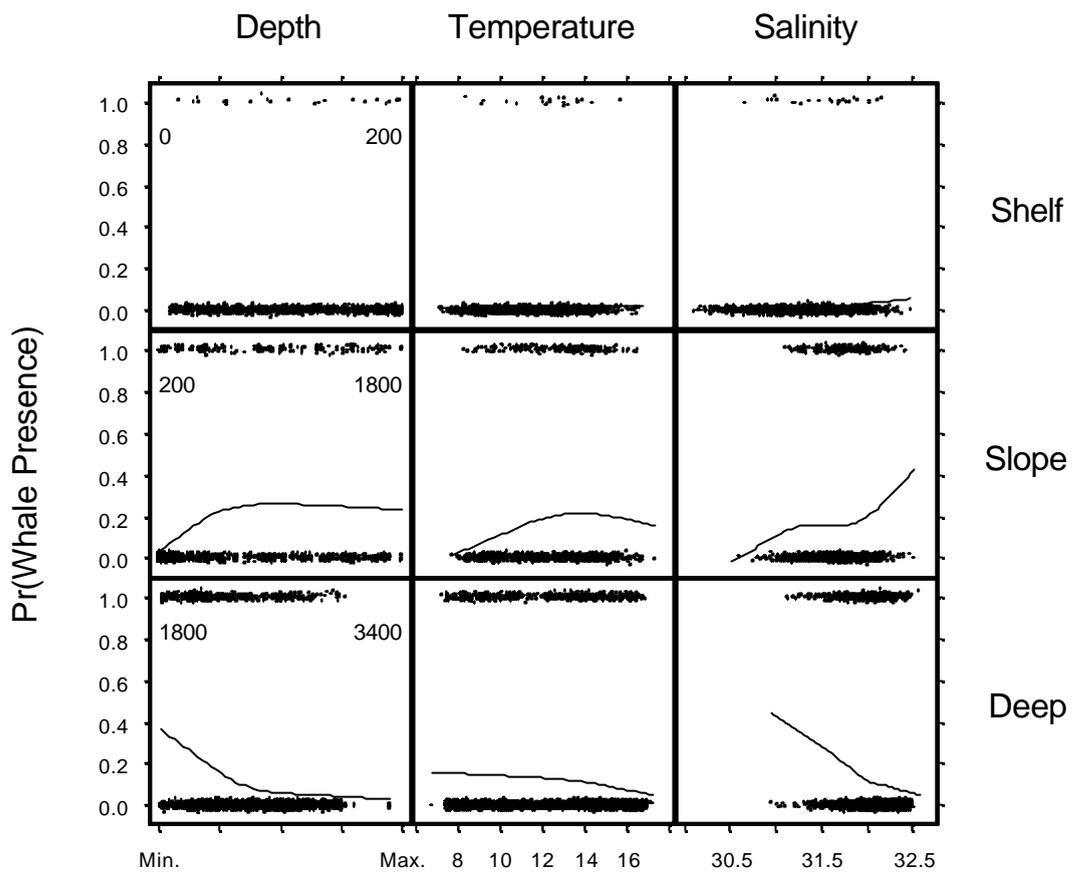


Figure A.15: Sperm Whale (male): Scatter plots of the three continuous independent variables vs. presence-absence for each depth class showing the interaction with the depth class categorical variable. Lowess curves are fitted to each plot with a span of 2/3 giving probability of whale occurrence. Actual observed presence-absence are plotted with a jitter factor to emphasize data density.

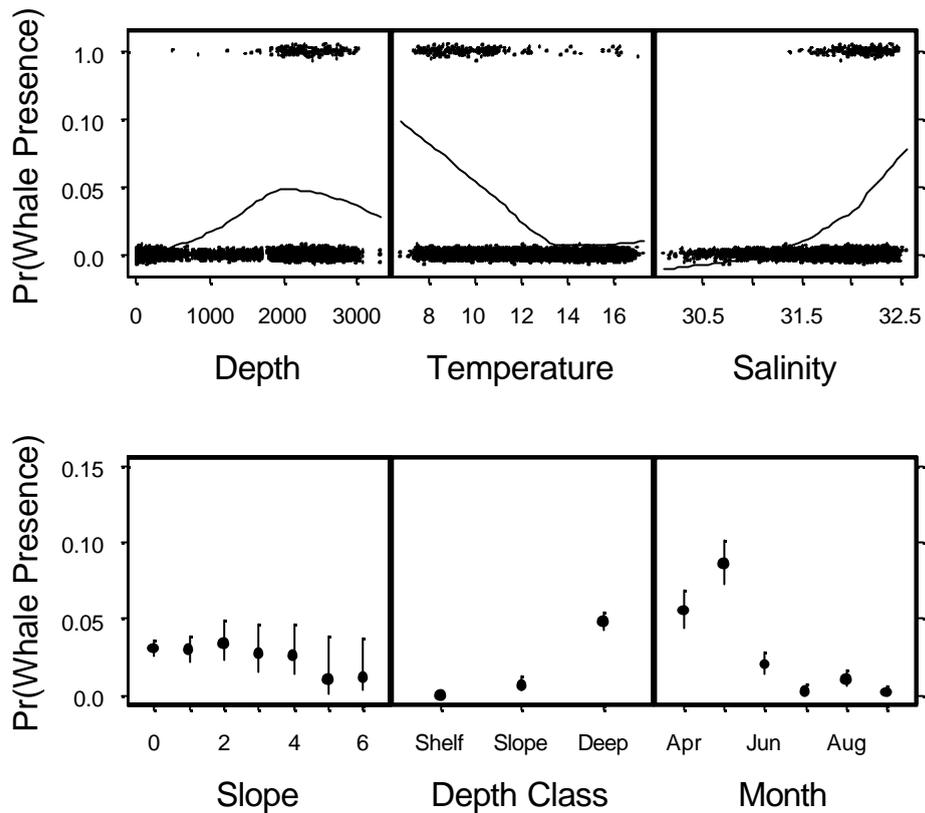


Figure A.16: Sperm Whale (female): Scatter plots (top row) of the three continuous independent variables vs. presence-absence and frequency plots of presence (bottom row) for the three categorical independent variables. The scatter plots are fitted with lowess plots using a span of $2/3$ which gives a probability of whale occurrence. Due to the large number of absence cells, the y-axis has been adjusted to emphasize the effect, and to allow the observed presence data to be shown. Presence absence data are jittered to emphasize data density. The frequency plots are shown with 95% confidence intervals.

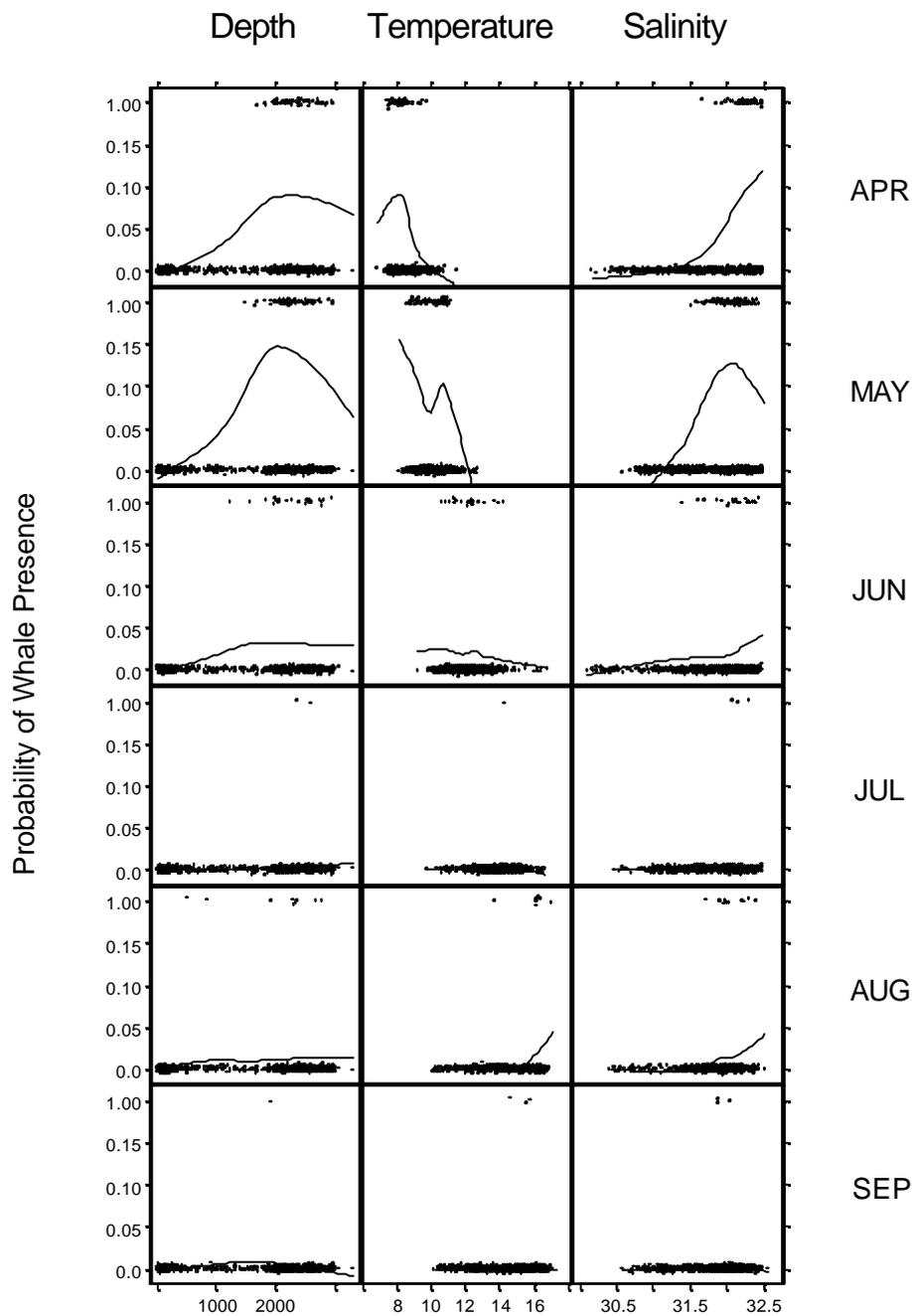


Figure A.17: Sperm Whale (female): Monthly scatter plots of the three continuous independent variables vs. presence-absence showing the interactions with the month categorical variable. Lowess curves are fitted to each plot with a span of 2/3 giving probability of whale occurrence. Due to the large number of absence cells, the y-axis has been adjusted to emphasize the effect, and to allow the observed presence data to be shown. Presence absence data are jittered to emphasize data density.

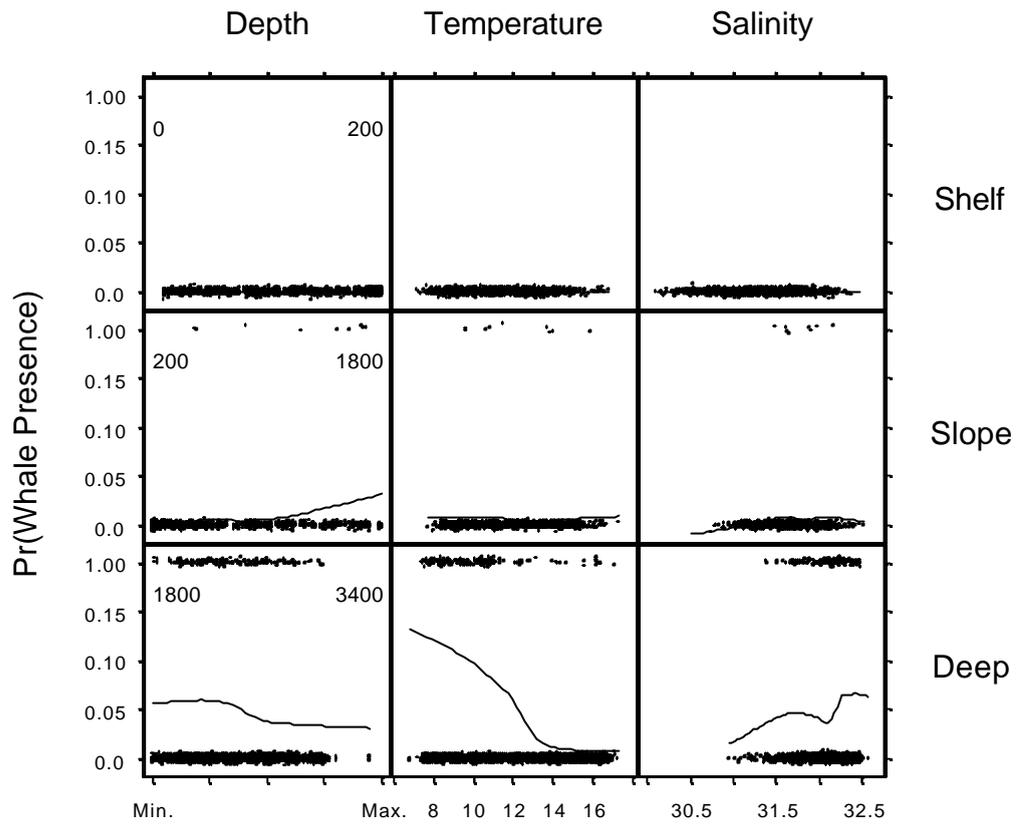


Figure A.18: Sperm Whale (female): Scatter plots of the three continuous independent variables vs. presence-absence for each depth class showing the interaction with the depth class categorical variable. Lowess curves are fitted to each plot with a span of 2/3 giving probability of whale occurrence. Actual observed presence-absence are plotted with a jitter factor to emphasize data density.

Appendix B: Regression Methods

My objective for this study was to define regions of critical habitat, and to represent these regions in terms of degrees of criticality. This required my analysis to generate probabilities of whale occurrence, which could then be interpreted as habitat preferences.

The accepted method for predicting probabilities is logistic regression. Logistic regression is typically used to model binomial data and therefore has no assumptions about the distribution or variances of the independent variables (Tabachnick and Fidell 1996). However because using logistic regression requires a binary response variable such as presence-absence, this would fail to capture the fact that I had count data for the cells, rather than only presence-absence.

Poisson regression, like logistic regression, is a Generalized Linear Model (GLM), but it is appropriate for regressing a count variable on several predictors. The count predictions from the Poisson model can then be transformed into logistic type probabilities using the following transform:

$$\Pr(\textit{Presence}) = 1 - e^{-\mathbf{u}} \quad \textit{where } \mathbf{u} \textit{ is the Poisson prediction.} \quad \text{Equation B.1}$$

Model building and analysis using GLMs proceeds in a similar way to linear regression. The main difference is that GLMs use different parametric models have different assumptions regarding the distribution of errors (Hosmer and Lemeshow 1989). These differences are modeled using a different link function for different types of GLMs (Chambers and Hastie 1993).

In logistic regression, the values of the dependent variable must be bound on the range [0,1].

This is accomplished through a series of transformations that first create an odds ratio by dividing the probability of the event (i.e. whale presence) occurring by the probability of the event not occurring: $P(y=1)/1-P(y=1)$. Taking the natural logarithm of this odds ratio gives the probability for the event.

The logistic regression model, shown as the natural log of the odds ratio, is given by:

$$P(y = 1) = \frac{e^f}{1 + e^f} \quad \text{where} \quad f = a + b_1x_1 + b_2x_2 + \dots + b_kx_k \quad \text{Equation B.2}$$

The linear component of the logistic regression is contained in the logit (f in Equation B.2), and represents the contribution of the predictor variables to the probability occurrence. Due to the binary nature of the logistic regression, the error distribution in the dependent variable is assumed to be binomial, rather than normal as is commonly used in linear regression (Hosmer and Lemeshow 1989).

In testing logistic regressions, G_M and R^2_L are considered analogs to the F ratio test and the R^2 coefficient of determination used in linear regression (Menard 1995). G_M is defined as $G_M = D_0 - D_M$. For the null model, D_0 is equivalent to the total sum of squares (SST) and D_M is analogous to the error sum of squares (SSE). Thus, the G_M statistic represents the reduction in deviance due to the independent variables in the model under consideration. The most natural choice for testing the proportion of variance explained by the model (R^2) is the equivalent of SSR/SST , or G_M/D_0 . This is denoted as R^2_L , and is a measure of how much the inclusion of the independent variables reduces the variance when compared to the null model., Hosmer and Lemeshow (1989) and Menard (1995) provide additional details on logistic regression, while Dobson (1990) provides an overview of Generalized Linear Models.