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MIGRATION AND POPULATION STRUCTURE OF NORTHEASTERN PACIFIC WHALES OFF COASTAL BRITISH COLUMBIA: AN ANALYSIS OF COMMERCIAL WHALING RECORDS FROM 1908–1967

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ABSTRACT

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 distribution of sperm (*Physeter macrocephalus*), fin (*Balaenoptera physalus*), sei (*Balaenoptera borealis*), humpback (*Megaptera novaeangliae*), and blue (*Balaenoptera musculus*) whales. 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. During the later years of whaling (1948–1967), the mean lengths of captured whales declined significantly 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 historic whaling records reveal much about the migratory behavior and distribution of the large whales species as they once were, and may continue to be, in the northeastern Pacific. Verifying the persistence of these trends in the remnant populations is a necessary and logical next step.

Key words: whaling, sperm whale, blue whale, fin whale, sei whale, humpback whale, migration, population structure, British Columbia, North Pacific.

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 uncover 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 of these species in the North Pacific.

Pike and MacAskie (1969) provided an excellent biological overview of the whales found in British Columbian waters, but left important questions about the migration and population structure of these species unresolved. These questions can be addressed through a quantitative analysis of the extensive data recorded for 24,862 whales killed from British Columbian whaling stations during a 60-yr period (1908–1967). The size and completeness of the British Columbia catch data present a unique opportunity to identify seasonal

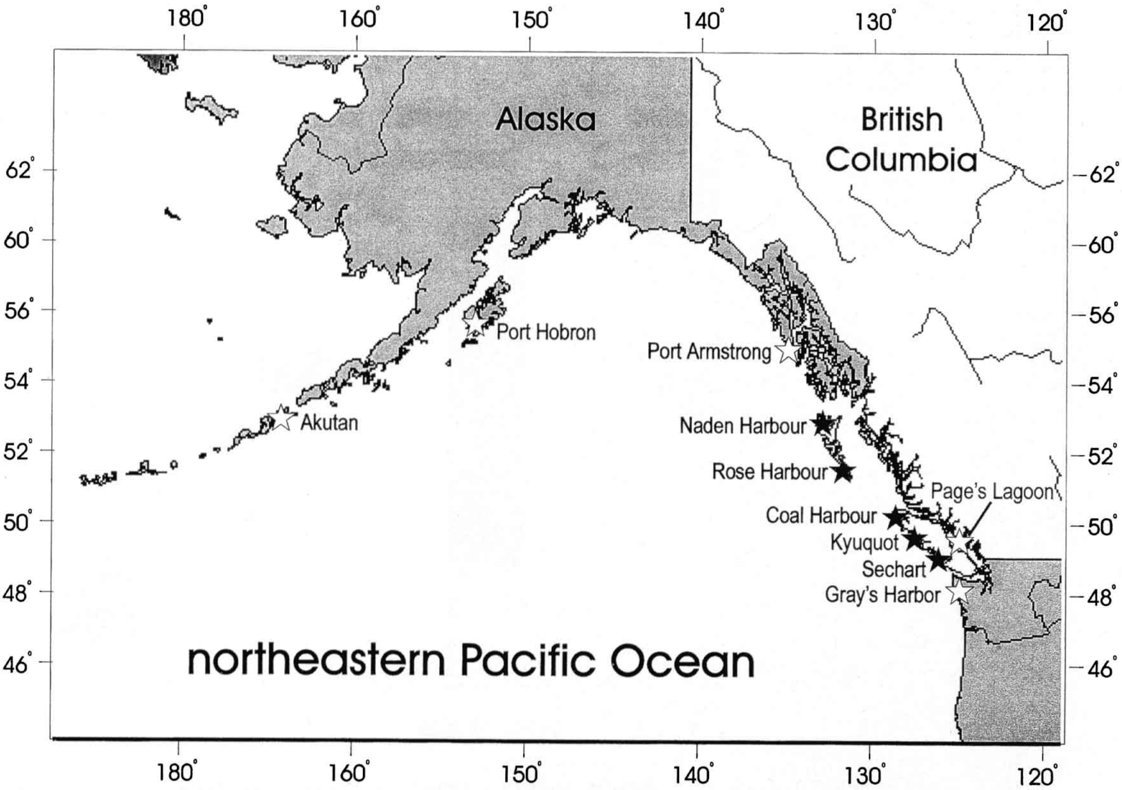

Figure 1. Locations of coastal whaling stations (1905–1967) in northeastern Pacific Ocean. Stations included in this study shown in black. Stations not analyzed shown in white.

abundance trends that were not apparent in previous studies of historic whaling records.

Our objective was to characterize the structure and timing of the seasonal migrations of sperm, fin, sei, blue, and humpback whales and to relate the catches to what is currently known about the population structure of these great whale species that were once commonly found in British Columbia waters. We begin with an overview of whaling in British Columbia and then describe the methods used to identify statistically significant annual and monthly trends. The results section outlines the findings, and the subsequent discussion provides an interpretation of the uncovered trends, taking into account the biases that are due to opportunistic rather than systematic data collection. Particular attention is paid to disentangling the biological significance from the regulatory, socioeconomic, and technological factors that may have biased the data. The monthly trends are related to existing literature, providing insights into the migration patterns and population structure of the great whales in the northeastern Pacific Ocean.

Whaling in British Columbia

Figure 1 shows the locations of the coastal whaling stations that operated in Washington, British Columbia, and Alaska during the 1900s. The stations

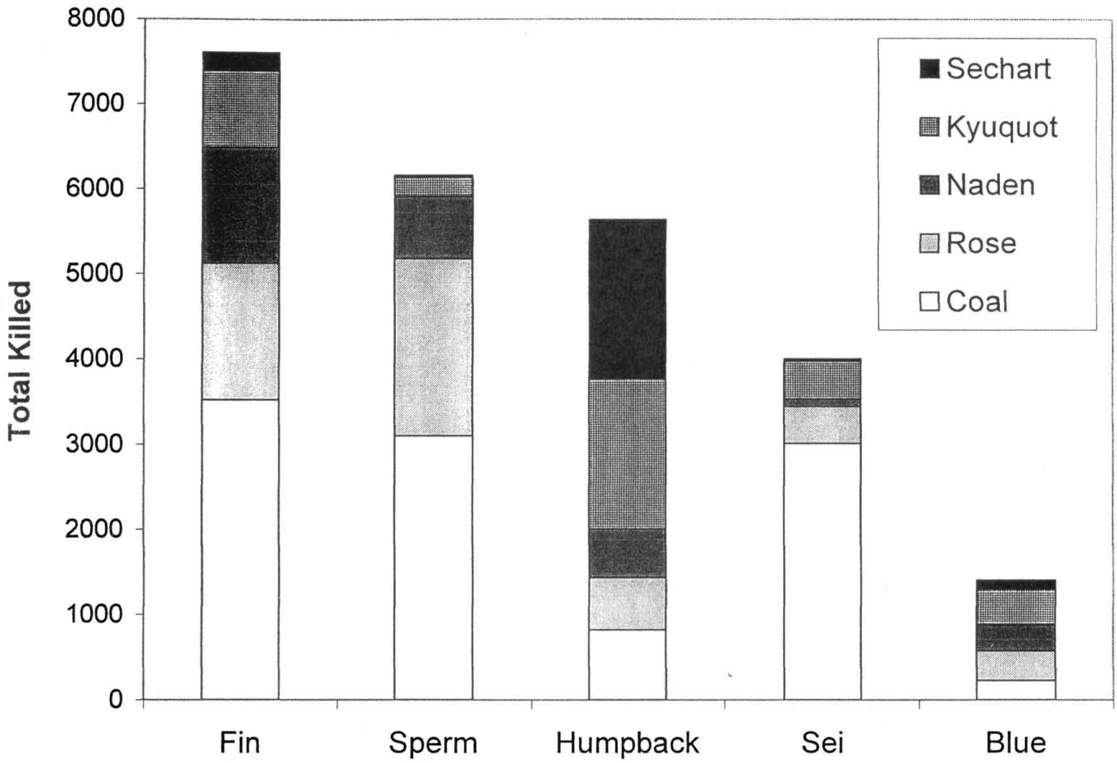

Figure 2. Distribution of five major target species among five British Columbia whaling stations. Stations ordered from top to bottom in order that they operated.

responsible for the majority of the kills from coastal stations operated in British Columbia between 1905 and 1967. Data collected from the British Columbian stations can be divided into two eras, based on years of operation. The first era, from 1905 to 1943, includes data from the Vancouver Island stations of Sechart (1905–1917) and Kyuquot (1908–1925), and the Queen Charlotte Islands stations of Rose Harbour (1910–1943) and Naden Harbour (1911–1941). The Coal Harbour station (1948 to 1967) was the only British Columbian station to operate after the Second World War. Data collected at this station comprise the second era.

Between 1908 and 1967, the British Columbian 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 (Fig. 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 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 from Coal Harbour in 1953 under a research permit. Gray and right whales were caught in small numbers due to reduced population sizes caused by earlier exploitation (*i.e.*, mid-1800s to early 1900's), while Baird's and minke whales were not favored because of their small size and low commercial value.

The degree to which killed whales were examined varied considerably, especially after 1948 when information on animal condition and stomach contents began to be recorded. The detailed morphometric measurements and stomach content analyses reported from 1962 to 1967 imply that the quality and consistency of these data collected in prior years is questionable. These data were therefore not included in this analysis.

Modern, shore-based, commercial whaling in the northeastern Pacific started in 1905 with the latest available technology. This included exploding harpoons and steam powered "catcher" vessels which allowed the exploitation of fin and blue whales, which were previously too fast and too strong to hunt. Further technological improvements included wireless telegraphy (1920s) and the use of spotting planes (1919) to track whale migrations (Rose Harbour and Naden Harbour, Tonnessen and 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.

The Canadian government imposed regulations affecting British Columbian whaling in 1905 in response to concern about the sustainability of harvests (Table 1). Data from 1908 to 1943 were available from company records only, and are of variable quality. The data quality improved with the ratification of the Geneva Convention for the Regulation of Whaling in 1933 which standardized data collection. Further improvements in the quality of the data occurred after 1950, when radar improved positional accuracy and additional data requirements were imposed by the International Whaling Commission (IWC 1950). Data for this period were obtained largely from the IWC and from the archives of the Canadian Department of Fisheries and Oceans (DFO).

During the second era of coastal whaling (1948–1967), operations at Coal Harbour were affected by a number of social factors including a changing workforce and marketing strategy. Unlike the previous era (1905–1943), 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 depletion of animals and competition from vegetable oils ended commercial whaling in British Columbia in 1967.

Methods for Data Analysis

We analyzed records from five of the six British Columbian whaling stations: Sechart, Naden Harbour, Rose Harbour, Kyuquot, and Coal Harbour.

Table 1. Summary of whaling regulations and international agreements affecting British Columbian land stations.

Year	Agency	Regulation
1905[a]	Government of Canada	24-h processing of catch required.
		Each station limited to 1 chaser boat (rescinded in 1910).
1929[b]	Government of Norway	Committee for Whaling Statistics established in Oslo, Norway, and systematic data collection begins.
1931[b]	League of Nations	Accepts Geneva Convention for the Regulation of Whaling
		Right whales, calves, immature, and lactating whales all protected. Requirements for logbooks and data reporting imposed.
		Ratified by most nations by 1935.
1937[b]	International Whaling Conference	Minimum length limits imposed for blue (70 feet), fin (55 feet), humpback (35 feet), and sperm (35 feet) whales.
		Gray whale protected[a].
1946[b]	Whaling Nations	International Convention for the Regulation of whaling signed. Previous restrictions restated and sei whale restriction added (40 feet).
1949[c]	First report of the IWC	Formation of the International Whaling Commission (IWC)
1966[d]	IWC	Blue whales protected in North Pacific.
1982[b]	IWC	Agreed to a moratorium on whaling beginning in 1985.

[a] Webb 1988; [b] Mizroch 1984; [c] IWC 1950; [d] Mizroch *et al.* 1984*a*.

Records from the station at Page's Lagoon and for the years prior to 1908 were not found and are presumed lost. The surviving records include company processing logs, catcher logbooks, and data sheets which were summarized in reports to the Bureau of International Whaling Statistics (now maintained by the IWC) (Table 2).

We analyzed the data for species where over 100 animals were killed (sperm, fin, sei, humpback, and blue whales) because the sample sizes for the remaining species (right, gray, minke, and Baird's beaked whales) were very low. Annual catch composition was determined using the entire catch of these five species (n = 24,801). Annual sex ratios were calculated as the proportion of males in the total catch. Sex specific data (n = 12,428) were not collected prior to 1924 and were collected consistently only at Coal Harbour.

We examined the data for seasonal and long-term trends in animals killed, body lengths (n = 12,158), and sex ratios. We compared lengths to estimates of age at sexual maturity and evaluated the change in proportion of mature animals on an annual and monthly basis. We pooled data from all stations to examine seasonal trends because the lower quality of the data from the first era (1905–1943) compromised any analyses of the geographic differences between the stations. Pooling the data increased the sample size for species that were most heavily exploited during the first era (blue and humpback whales) and emphasized seasonal trends that were common across space and time. 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 (1948–1967) and the earlier stations (1905–1943). Exploration of reproductive data included an examination of monthly and annual trends in pregnancy proportions (pregnant females over total mature females) 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 6,636 kills within 200 nmi (370 km) of Coal Harbour. Positional data from the first era, and for the years 1949–1951 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 test) on logistic regression models. Trends in means were tested for significance using a single factor ANOVA (analysis of variance, F test) on polynomial regressions. Polynomial regressions were calculated using 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.

Table 2. Sources of data for Coal Harbour (1948–1967), Sechart (1905–1917), Kyuquot (1908–1925), Rose Harbour (1910–1943), and Naden Harbour (1911–1941).

Source[a]	Years	Stations[b]	Data description
BIWS database[c]	1948–1959	C	Date, species, sex, length, fetuses and location of capture.
Plant tally books	1952–1955, 1963–1967	C	Date, species, sex, length, fetus sex, and fetus length of whales processed (1963–1967 have location of capture).
Catch slips	1958–1962	C	Date, time, species, location of capture.
Data sheets and 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 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 whale kill locations.
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 whale kill locations.

[a] Data for Sechart, Kyuquot, 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.

[b] C = Coal Harbour, K = Kyuquot, 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.

[c] The Bureau of International Whaling Statistics (BIWS) was the repository for whaling data from IWC member countries until it's incorporation into the IWC *circa* 1984 (D. Rice, pers. comm.).

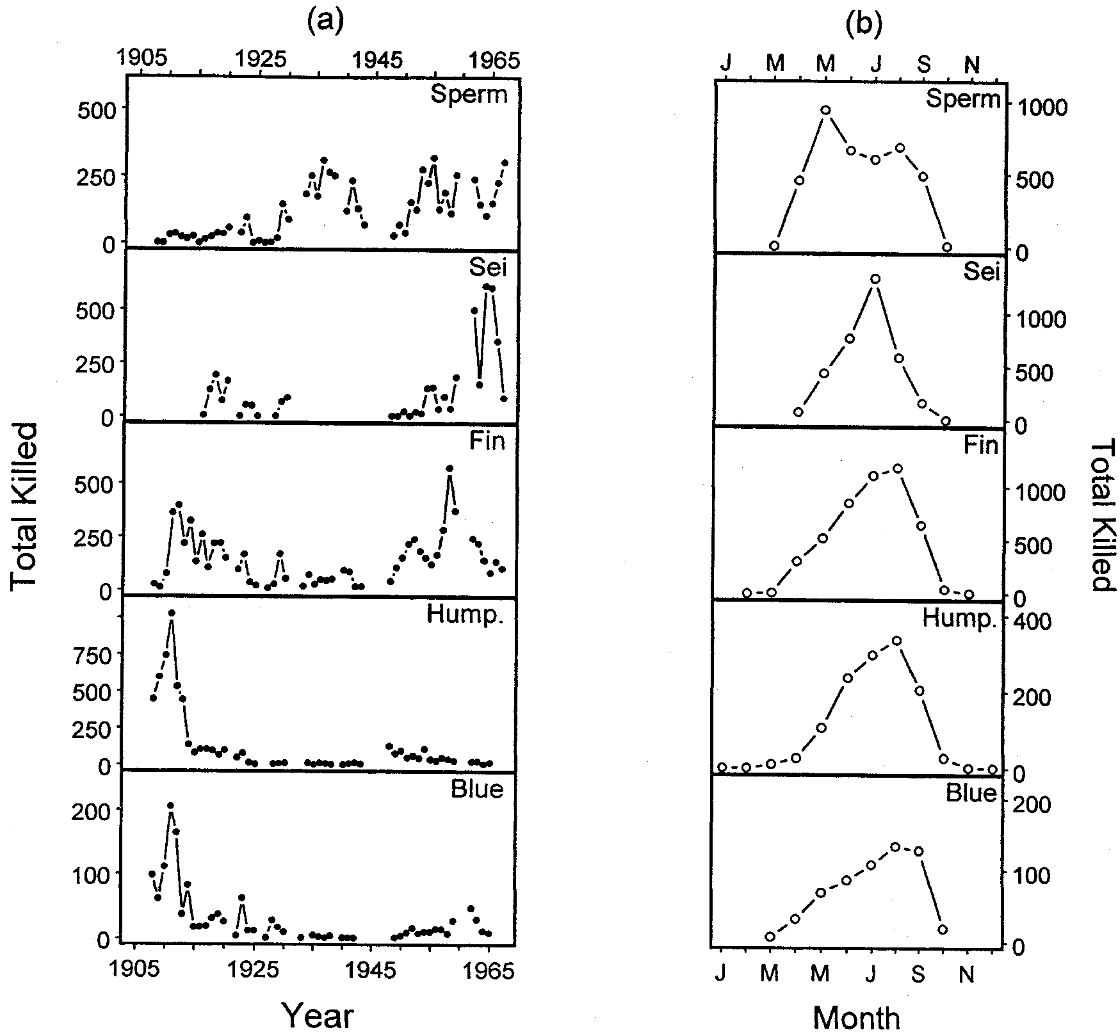

Figure 3. Total number of animals killed shown annually (a) and monthly (b), by species, for data pooled from all British Columbia whaling stations.

Results

Annual Catch Composition

The first era of modern, shore-based whaling in British Columbia (1905–1943) focused on humpback, blue, and fin whales (Fig. 2, 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 1905 and 1913 (Fig. 2). The majority of blue whales were caught before 1915, with Kyuquot, Naden Harbour, and Rose Harbour responsible for the majority of blue whale kills (Fig. 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 less than 20 in 1942 (Fig. 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 Islands stations of Naden Harbour and Rose Harbour caught most of the sperm whales during the first era (Fig. 2). The sei whale, the last species to be heavily exploited, was 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 (1948–1967) focused primarily on fin, sperm, and sei whales (Fig. 2) and was conducted entirely from Coal Harbour, on Vancouver Island. This period showed a dramatic rise and fall in the number of fin whales caught, peaking in 1958 with 573 animals. This was followed by a similar pattern in the sei whale catch (Fig. 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.

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. 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. 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 ($\chi^2_{(13)} = 494.79$, $P < 0.001$). This change in sex ratio reflects an increase in the catch of females rather than a decrease in the catch of males (Fig. 5). In contrast, the ratio of males to females caught was constant over time for fin and humpback whales, but highly variable for sei whales.

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. 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. 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–May) to an average of 72% (June–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–May, n = 148 for June–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

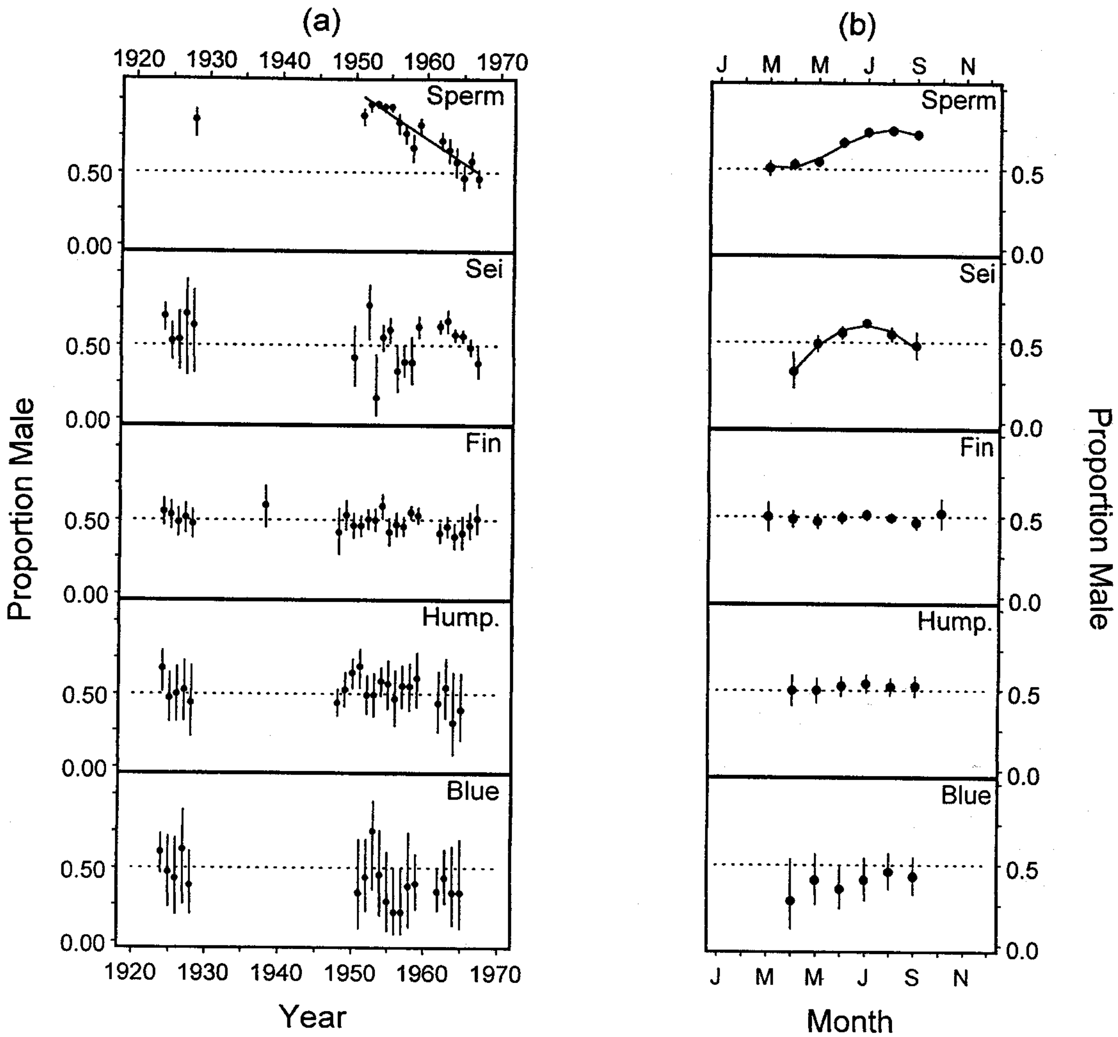

Figure 4. Proportion of males in total catch shown annually (a) and monthly (b), for data pooled from all British Columbia whaling stations. Dashed horizontal lines denote proportion of 0.50. Results shown with 95% confidence intervals calculated for proportional data, using expected value of 0.50. Statistically significant trends, based on regression analysis ($P < 0.05$), shown as trend lines.

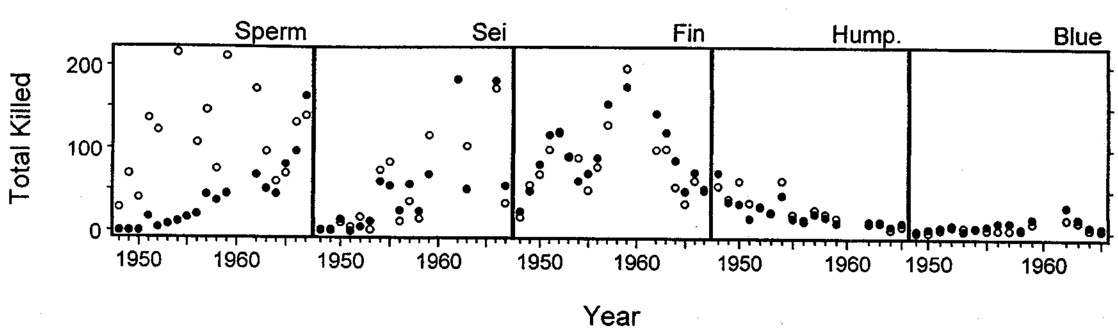

Figure 5. Total numbers of males (○) and females (●) caught from Coal Harbour 1948–1965 (humpback and blue whales) and 1947–1967 (sperm, sei, and fin whales).

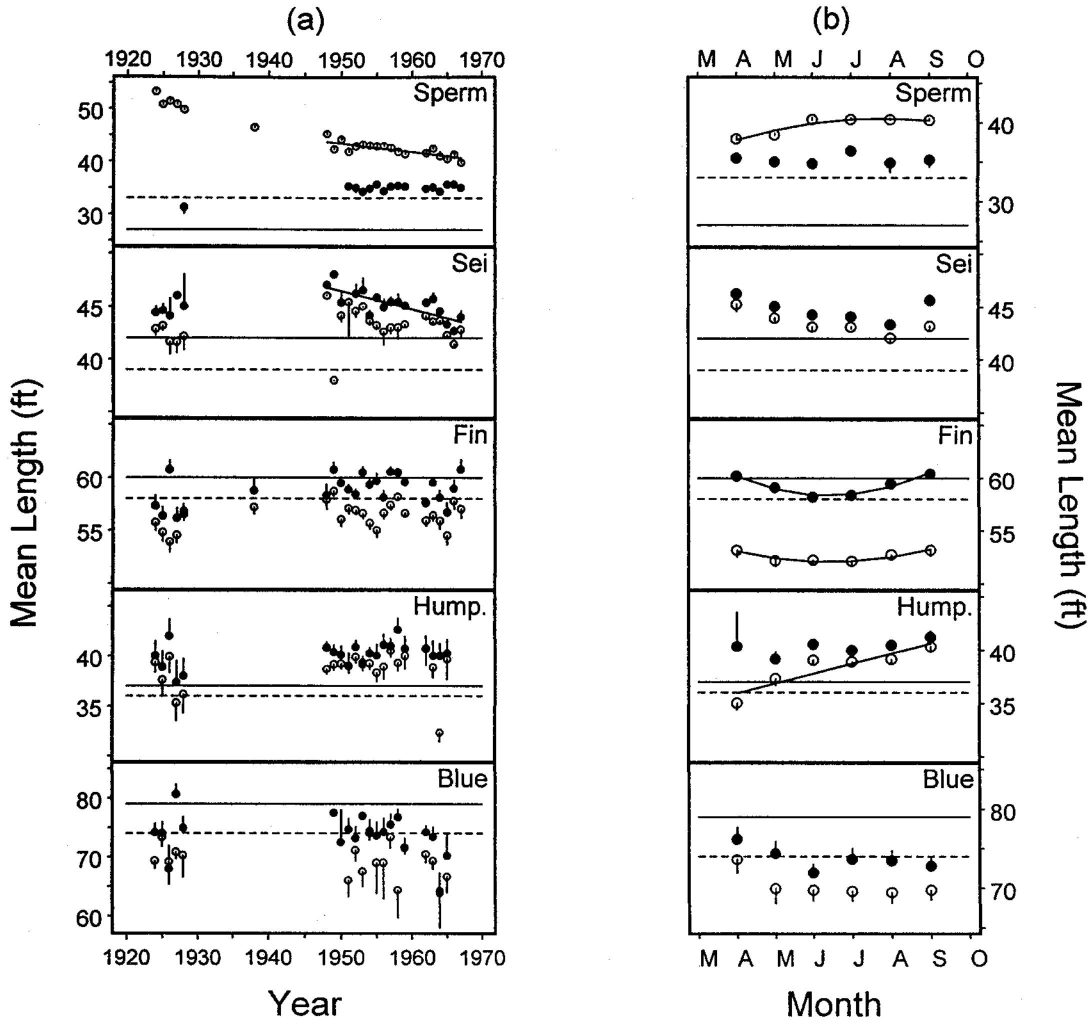

Figure 6. Mean lengths for males (○) and females (●), shown annually (a) and monthly (b), for data pooled from all British Columbia whaling stations. Horizontal lines represent estimated lengths at sexual maturity for males (- - -) and females (——). Results shown with standard error bars, in one direction only, for clarity. Statistically significant trends, based on regression analysis ($P < 0.05$), shown as trend lines.

were significant (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 occurred 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 ($F_{1,16} = 11.99$, $P = 0.003$, $r^2 = 0.44$). There were no significant trends in the mean annual lengths of fin, blue, or humpback whales (Fig. 6a).

Seasonal changes in mean lengths were examined by combining length data for all years, and all stations. Changes in mean monthly lengths are apparent for each of the species killed in British Columbia, though not always statistically significant, and not always for both sexes (Fig. 6b).

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 = 0.88). 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.

The mean lengths of fin whales caught showed a concave distribution with the shortest animals taken in June and August. This change was significant for both sexes (male: $F_{2,3}$ = 11.92, P = 0.037, r^2 = 0.89; female: $F_{2,3}$ = 29.15, P = 0.011, r^2 = 0.95). 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 = 0.67), 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 and Distance from Shore

The annual proportion of females killed that were pregnant decreased significantly for sperm, sei, and fin whales between 1948 and 1967 (Fig. 7a) (sperm: $\chi^2_{(16)}$ = 16.54, $P < 0.001$; sei: $\chi^2_{(16)}$ = 176.30, $P < 0.001$; fin: $\chi^2_{(16)}$ = 72.00, $P < 0.001$). Pregnant sei and blue whales 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. 7b).

Fetus lengths (Fig. 8) 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).

The distance between the locations where the whales were captured and the nearest coastline increased significantly over time (1948–1967) for both sexes of all species except for blue whales (Fig. 9a, Table 3). 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. 9b, Table 3).

Effort

Reliable effort data were available only from the Coal Harbour station (Fig. 10). Effort was examined by comparing the mean number of days that boats spent looking for whales by month (average for all years) and by year (average

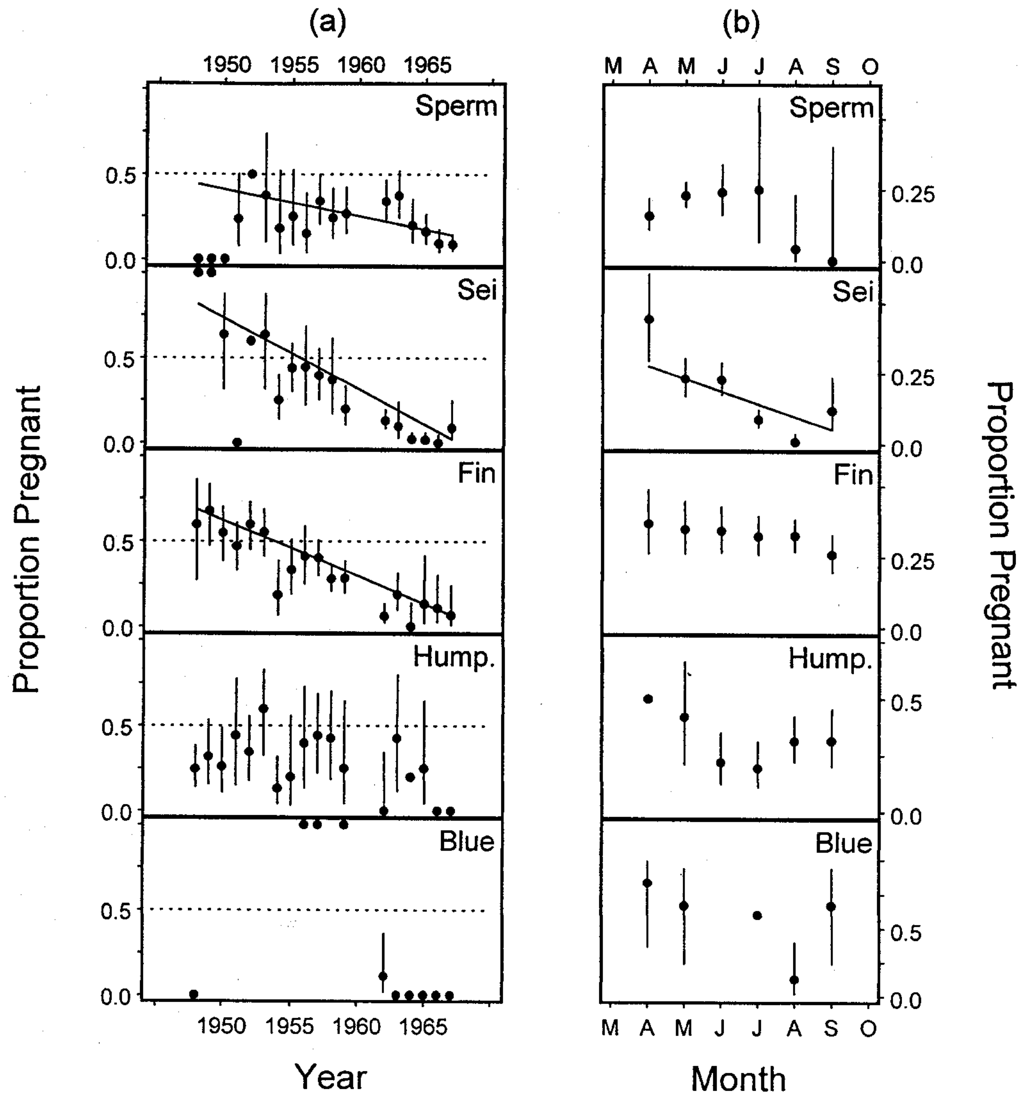

Figure 7. Proportion of pregnant females in catch, calculated as number of fetuses divided by catch of mature females, shown annually (a) and monthly (b). Horizontal lines on (a) denote proportion of 0.50. Results shown with 95% confidence intervals calculated for proportions using expected value of 0.50. Statistically significant trends, based on regression analysis ($P < 0.05$), shown as trend lines.

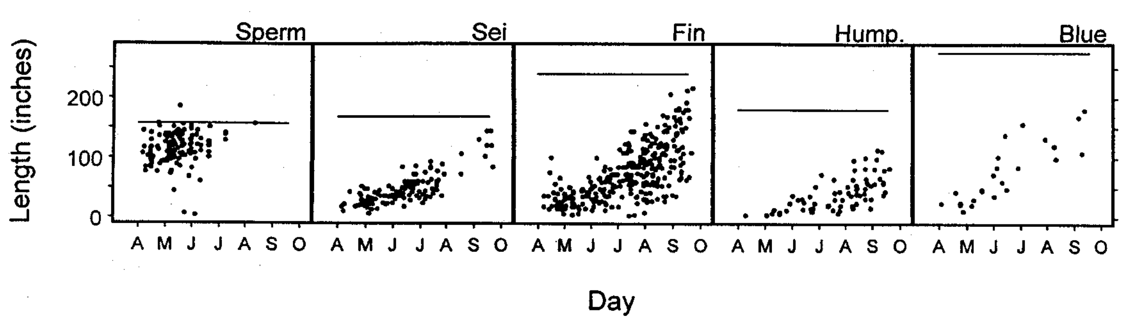

Figure 8. Lengths of measured fetuses *vs.* day of capture, by species. Horizontal lines represent estimated lengths at birth.

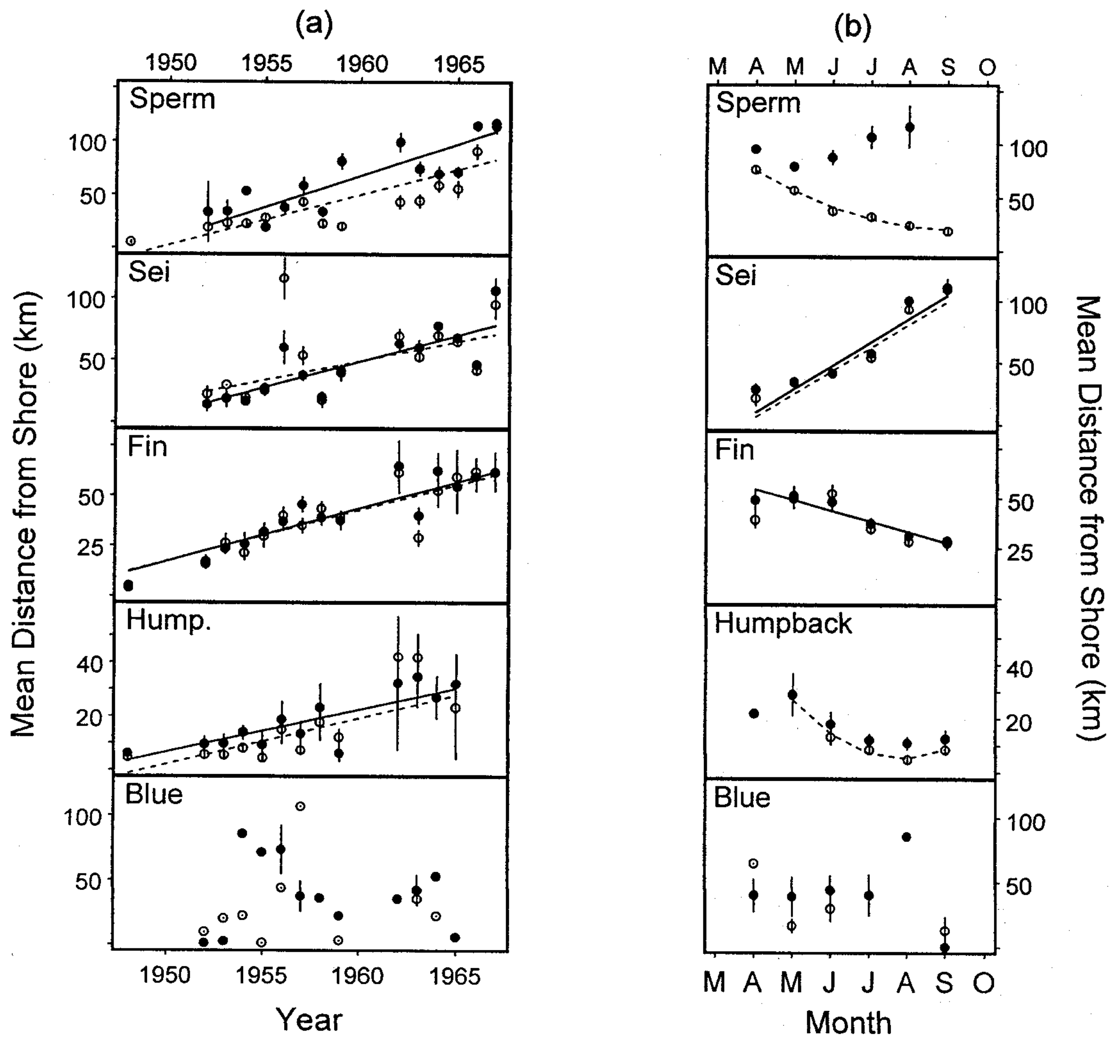

Figure 9. Mean distance from shore for males (○) and females (●) shown annually (a) and monthly (b) for Coal Harbour catch data only (1947–1967). Data shown with standard error bars. Statistically significant trends, based on regression anlaysis ($P <$ 0.05), shown as trend lines.

for all months). Regression analysis showed a significant increase in annual effort ($F_{1,15}$ = 13.36, P = 0.002, r^2 = 0.47) from 1948 to 1967. However, there was no statistically significant change in monthly effort (March–September), even when a quadratic function was used to represent peak effort in the height of summer ($F_{2,3}$ = 3.24, P = 0.18, r^2 = 0.68).

Discussion

Annual trends in the numbers of whales killed by British Columbian coastal stations are consistent with patterns of overexploitation of these whale species in other regions of the world. For example, Mizroch (1984) describes how exploitation moved progressively 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

Table 3. Summary of significant ($P < 0.05$) regression analysis results for annual and monthly mean distance from shore calculations by species and by sex.

		Annual distance from shore				Monthly distance from shore			
Species	Sex	D.F.	F	r^2	P	D.F.	F	r^2	P
Sperm	M	(1,13)	32.93	0.717	<0.001	(2,3)	152.40	0.99	0.001
	F	(1,12)	26.62	0.689	<0.001				
Sei	M	(1,12)	8.85	0.424	0.012	(1,4)	21.59	0.844	0.010
	F	(1,12)	18.10	0.601	0.001	(1,4)	23.16	0.853	0.009
Fin	M	(1,13)	25.39	0.661	<0.001				
	F	(1,13)	42.53	0.766	<0.001	(1,4)	34.00	0.872	0.002
Humpback	M	(1,10)	12.90	0.563	0.005	(2,2)	28.08	0.966	0.034
	F	(1,11)	32.88	0.749	<0.001				

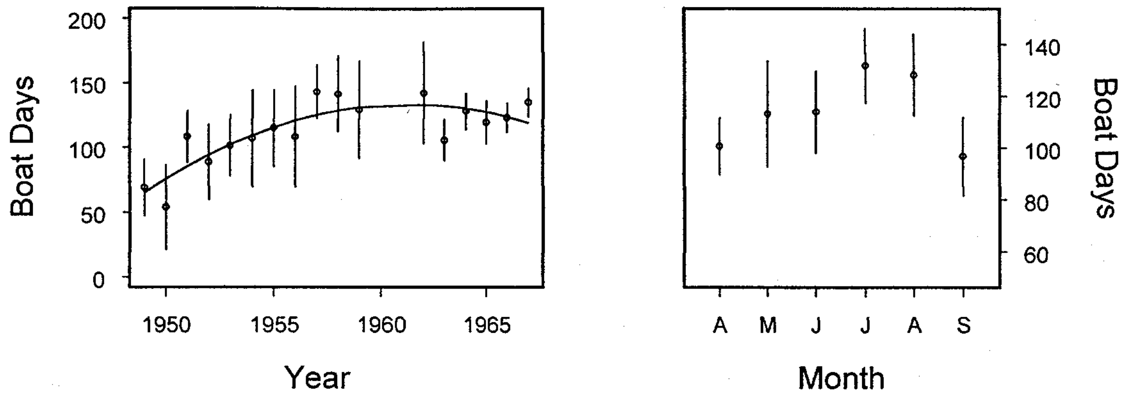

Figure 10. Mean annual and monthly whaling effort, measured as mean number of days that boats spent searching for whales from Coal Harbour (1948–1967). Results are shown with 95% confidence intervals. Annual effort increase significantly based on regression anlysis ($P < 0.05$).

coastal and pelagic whalers. Whaling records confirm the serial depletion of British Columbian whale populations between 1908 and 1967, with the catch moving from humpback and blue whales, to fin, sperm, and finally to sei whales. While the serial depletion was largely a function of the relative profitability and ease of capture of these species, significant technological and socioeconomic changes also affected the whalers species preference, search distance, and search efficiency.

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. Similarly, the monthly trends, while somewhat confounded by the pooling of data over many years and several sites, provide insights into the timing of migration, population structure, and social behavior of the great whales that were once commonly found in British Columbia's coastal waters. Pooling the large numbers of whales killed over a broad temporal and geographical range reduces interannual variability and emphasizes the commonalities that are reflective of the species' biology rather than the effects of technological change.

Annual Catch Composition

Humpback and blue whales, respectively the easiest and most lucrative to catch, dominated the early years of the first era (1905–1913). 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 Californian whaling 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 (1905–1943) rose as the fin whale catch declined (Fig. 3a). This 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-1920s as the price of whale oil (but not spermaceti 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 and Johnsen 1982). This oversupply of oil caused the British Columbian stations to close in those years. Whaling resumed in British Columbia 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 $9.50 or $10.50 per blue whale and $5.25 or $5.75 per fin or humpback whale, depending on length. Whalers received $10.00 each for sperm whales. The previous bonus schedule paid each whaler 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 total catch of sperm whales in British Columbia did not peak and decline as did the catches of the four baleen species (Fig. 3). Worldwide catches peaked in 1966–1967 (Gosho *et al.* 1984), and declined after the British Columbian stations closed. Sperm whale catches in British Columbia may have been on the verge of decline, given that the number of females in the catch was increasing (Fig. 5) as the size of the males in the catch was decreasing (Fig. 6).

Mean Annual Lengths

The significant decline in the mean annual lengths of male sperm whales and female sei whales during the second era of whaling can be attributed to their increased exploitation during this period (Fig. 6a). The reduced availability of large male sperm whales likely led to an increase in the number of females caught (Fig. 5). Male sperm whales were commercially more valuable than females because of their larger size (maximum lengths are 65 ft (19.8 m) for males and 40 ft (12.2 m) for females (Table 4). The 1935 restriction on taking nursing females (Table 1) likely contributed to this male bias. No decline in the mean length of female sperm whales was observed, likely due to the 35-ft (10.7-m) minimum length limit imposed in 1937 (Table 4). This

Table 4. 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[a]	est. max[a]	legal[a,b]
Sperm[c]	M	3001	43.7	64		33	65	
	F	717	35.1	49	13	27	40	35
Sei[d]	M	1822	43.0	56		39		
	F	1400	44.3	54	14	42	60	40
Fin[e]	M	2034	56.7	82		58		
	F	2106	59.1	82	20	60	88	55
Humpback[f]	M	516	39.1	51		36	49	
	F	444	40.4	56	15	37	52	35
Blue[g]	M	141	69.8	79		74		
	F	200	73.3	86	23	79	80	70

[a] Estimates for birth and length at maturity, maximum lengths, 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.* 1984*c*; [e] Mizroch *et al.* 1984*b*; [f] Leatherwood and Reeves 1983; [g] Mizroch *et al.* 1984*a*.

effectively limited the catch to all but the largest females. In contrast, the mean length of female sei whales in the Coal Harbour catch did decline, presumably because their maximum length was well above the minimum legal limit imposed in 1937 (Table 4).

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 1937 (Table 4). As with female sperm whales, a comparison of the mean catch lengths of blue and fin whales to the legal limits (Table 4) 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. 6a). In fact, mean lengths remained approximately three feet longer than the maturity estimate (Table 4). This suggests that mature animals were regularly within reach of the whalers. Since the mean lengths in the catch were consistently around 40 ft, it is unlikely the length restriction (35 ft) prevented a decline in mean lengths for this species.

The mean lengths of fin whales caught (both sexes) were mostly below the estimated length at sexual maturity (Table 4, Fig. 6a, 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 contained shorter animals, on average, than those in 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 4). This implies that blue whale migrations were spatially or temporally segregated based on length as has been suggested for sei and fin whale migrations (Horwood 1987, Mizroch *et al.* 1984*b*). However, given the prior exploitation of this species (1905–1943), and the lack of protection for blue whales until 1966 (Table 1), it is more likely that very few animals remained for the whalers to take.

Reproduction and Distance from Shore

The significant decreases in the annual pregnancy proportions in the catch of sperm, sei, and fin whales (Fig. 6a) is the strongest evidence of population-level effects by the whalers. By the early 1960s, few, if any, of the female sei and fin whales killed were pregnant. The catch of blue whales contained very few pregnancies throughout the entire second era (1948–1967). This change in the proportion of pregnant females (sperm, sei, and fin whales) cannot be interpreted as simply a change in reproductive rates because the samples analyzed were not taken randomly from the entire population. However, the change in pregnancy proportions does imply that the number of mature females was significantly reduced for these species. This, in turn, could have decreased the reproductive fitness, or reduced the range of a species, if matrilineal philopatry to feeding grounds (*e.g.*, sperm whales, Lyrholm 1998) was disrupted.

Annual mean distance from shore measurements (Fig. 9a) show that whales of all species (except blue whales) were caught farther from shore over time. While this could be interpreted as whales learning to avoid whaling vessels, 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 behavior 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 by sex. Females were generally found farther from shore than males, and the distance between the sexes increased through July and August as females moved progressively farther offshore and males moved progressively farther onshore (Fig. 9b). This movement made the males increasingly accessible to whalers from Coal Harbour. Male sperm whales were caught throughout the whaling season (April–September), while most females (over 90%) were caught between April and June. It is not clear whether males left the coastal area during winter months.

When considered in combination with existing knowledge about gestation and birth lengths, the sharp drop in the proportion of pregnant sperm whales in August (Fig. 7b) and the prevalence of near-term fetuses in May through June (Fig. 8) imply that calving took place off the coast of British Columbia sometime in July and August. The movement patterns of males and females and the evidence for calving in July and August further suggest the possibility of mating in British Columbian waters in late spring (April–May), before the females moved farther from the British Columbia coast to calve.

It is understood that sperm whales form 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 (*e.g.*, Whitehead *et al.* 1998, Christal *et al.* 1998). However few studies have examined sperm whale interactions at higher latitudes, and all recent references to sperm whale migration and mating assume that it is sufficiently described by Best (1979), who concluded that, in the southern hemisphere, breeding male sperm whales migrate to tropical latitudes to breed and return to higher latitudes at the end of the breeding season.

We suggest that sperm whale mating may take place in temperate latitudes, and that it occurred off the coast of British Columbia. Ohsumi (1965) concluded that, for North Pacific sperm whales, the modal breeding month was April, the gestation period was 16.4 mo, and that calving occurred between June and October with a mean birth length of 13.3 ft (4.0 m). These reproductive details are critical to the interpretation of the trends uncovered in our study.

The mean monthly distance from shore (Fig. 9b) combined with the monthly sex ratios (Fig. 7b) showed a spatial separation of the sexes beginning in June. Comparing fetus lengths to the mean length at birth (Fig. 8) suggests that calving occurred for these females in July and August off the coast of British Columbia. This was also noted by Pike and MacAskie (1969). This hypothesis is further supported by the monthly pregnancy proportions (Fig. 7b) 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.

The occurrence of mating in British Columbian waters is suggested by the relative proximity of males and females in April and May (Fig. 9b), 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 mating in April and May for calving to take place 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 in our analysis provide compelling evidence for mating followed by calving in British Columbian waters.

Sei Whales

Trends in monthly sex ratios, mean lengths, and proportion of females pregnant (Fig. 4b, 6b, 7b) 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 (Fig. 6b, 9b) 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. 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. 9b), combined with a lack of sei whales caught by contemporary stations in northern British Columbia and Alaska, suggests a northern limit for this sei whale population of 55°N. Length and pregnancy data (Fig. 6b, 7b) 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.* 1984*c*). 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 British Columbian catch is apparent from the decreasing mean monthly length of sei whales caught from May to August (Fig. 6b) and by the significant decrease in pregnant proportion over the course of the season (Fig. 7b), confirming that the pregnant females leading the migration were also the longest.

The large differences in the annual number of males and females caught (Fig. 5) also suggest some segregation by sex. However, trends in the mean lengths (Fig. 6b) and in the mean distance from shore (Fig. 9b) are very similar for both sexes. A plausible explanation for these trends is that both males and females staged their migration based on maturity, and that larger animals of both sexes migrated farther north. 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 sei whale abundance is markedly different from the other baleen species in the catch record (Fig. 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, with a significant offshore movement occurring during the summer (Fig. 9b). This is consistent with Masaki (1977) who reported high densities of sei whales off Vancouver Island in June and July, and farther offshore in August. Masaki (1977) also showed high densities of sei whales off the Queen Charlotte Islands and the northern Gulf of Alaska in May. Horwood (1987) presented total Japanese catch (1952–1972) and sighting (1965–1978) data which also showed concentrations in the northern Gulf of Alaska and off Vancouver Island. These data suggest that the single, putative eastern North Pacific stock (Masaki 1977) may have been composed of two groups which exploited food resources on opposite sides of the Alaskan gyre. The reappearance of mature sei whales in the catch in September (Fig. 6b), including mature females (Fig. 4b, 7b, 8), may reflect the start of the returning southward migration by one of these groups.

Fin Whales

The monthly length data (Fig. 6b) suggest an age-structured migration with larger fin whales arriving in British Columbian waters ahead of smaller ones. The monthly proportion of pregnant females (Fig. 7b) 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. 9b), providing no evidence of spatial segregation by sex. The stable pregnancy rate from April to September (Fig. 7b), the sigmoid rise in the number of whales killed (Fig. 3b), and the monthly decrease in distance from shore (Fig. 9b), all suggest that these animals returned to British Columbian waters to feed. Annual and monthly mean lengths (Figs. 6a, 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. 6a), it appears that the animals in the British Columbian subpopulation were generally shorter than the estimated length at maturity. Fetal growth is well represented in all months, until females approached term in late September (Fig. 8). The sudden drop in fin whale catches in September (Fig. 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 British Columbian 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 British Columbia stations, which is comparable to their proportion in the catch from Alaskan stations during the same period.

According to Pike and MacAskie (1969), the British Columbia catch contained both migrating animals and some shorter animals thought to feed in British Columbian waters. Fujino (1964) suggested that an isolated stock existed off British Columbia, in addition to eastern and western North Pacific stocks. The trends in our study, which show an increasing availability over the course of the season (Fig. 3b) and the presence of mature females throughout the season (Fig. 7b), support this suggestion.

Humpback Whales

The large catches of humpback whales by the British Columbian stations between 1908 and 1917 (Fig. 3a) appear to have depleted a subpopulation that was distinct from the ones subsequently exploited in California (1919–1926) and western Alaska (1912–1939). These data suggest there may have been at least three historic subpopulations in the northeast Pacific. The parallel decline in humpback whale catches at all of the operating British Columbian stations (Sechart, Kyuquot, Rose Harbour, and Naden Harbour; Table 3) implies that the British Columbian subpopulation reached at least 54°N. A seasonal increase in the proportion of mature animals and pregnant females (Fig. 6b, 7b) further suggests an age-structured migration, where immature animals appeared on the feeding grounds before the mature animals. Based on the early accounts of whaling in British Columbia, humpback whales appear to have frequented feeding grounds in both Barkley Sound and the Strait of Georgia during winter months (Merilees 1985). The animals using these grounds were extirpated in the early years of coastal whaling and have not yet returned.

The suggestion that at least three 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 British Columbia 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 (between 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 Akutan and Port Hobcon in the western Gulf of Alaska (Fig. 1) 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, we believe it is more likely that the exploitation affected subpopulations that were segregated spatially during at least part of the year.

Other studies also support the separation of the northeastern Pacific humpback whales into subpopulations. Baker *et al.* (1986) proposed that the northeastern 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 British Columbia and no exchange with southeastern Alaska.

Calambokidis *et al.* (1997) extended this work by assessing the exchange between the three North Pacific wintering grounds (Japan, Hawaii, and Mexico) and feeding grounds in southeastern Alaska, British Columbia, and the California-Washington region (Ca-Wa). They found a high degree of interchange between Hawaii and southeastern Alaska, and between Mexico and Ca-Wa. British Columbia showed a low rate of interchange with all three wintering grounds. A significant degree of exchange is currently observed between British Columbia and southeastern Alaska (Straley and Ellis, unpublished data). These results suggest that feeding areas in British Columbia may be slowly filling through dispersal from the other feeding areas. Whether, historically, the British Columbian feeding grounds supported a subpopulation discrete from those in southeastern Alaska, or whether a single subpopulation ranged from southern British Columbia to southeastern Alaska, is not clear, and may never be known.

The proportion of mature humpbacks in British Columbia of both sexes increased as the season progressed (Fig. 7b). The largest animals were 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 British Columbia catch record which shows monthly and annual sex ratios close to 50% (Figs. 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 southeastern 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 or migration speeds (Gabriele *et al.* 1996). Pregnant and immature animals would appear to benefit very little from time spent on the breeding (wintering) 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 British Columbian 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 British Columbia and Alaska stations suggests that there were two discrete feeding areas for blue whales—the Aleutian Islands and the northern coast of British Columbia. The seasonal timing of the catches from these two stations suggests that blue whales arrived at the feeding grounds at different times. What is not clear is whether a single population moved between the two feeding areas, or whether there were two subpopulations, each frequenting one of the areas. However, Reeves *et al.* (1998) suggest that at least five subpopulations exist in the North Pacific, two of which are thought to frequent 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 in British Columbia 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 annual predominance of immature animals in the British Columbian catch (Fig. 6a) 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 (Fig. 6b, 7b) support the hypothesis of an age-structured migration, led by mature animals, to feeding grounds beyond the reach of the British Columbia coastal stations.

Blue whale catches by the British Columbian stations increased over the course of the season peaking in August (Fig. 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 (1969) suggested that blue whales were usually found well offshore. The decrease in mean female lengths over the course of the summer (Fig. 6b), and a steadily decreasing pregnant proportion (Fig. 7b) implies an age-based segregation in the migration similar to that suggested for fin and sei whales (Horwood 1987, Mizroch *et al.* 1984*c*). The general lack of mature animals in the blue whale catch (Figs. 6a, 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 British Columbian waters before the whaling season.

The female bias in the monthly sex ratio (Fig. 4b) and in the last part of the second era (Fig. 4a) is likely due to a lack of males above the legal length (70 ft), which appear to have been available only in April (Fig. 6a). This could be interpreted as additional support for the sex-based spatial segregation of this species but is perhaps more likely a function of overexploitation.

Conclusions

Analysis of the British Columbian historic whaling records reveals the effects of overexploitation on sperm, fin, sei, humpback, and blue whale populations. A British Columbian subpopulation of humpback whales, and possibly a subpopulation of fin whales, appear to have been extirpated. The proportion of pregnant sperm, fin, and sei whales was dramatically reduced, and large numbers of mature animals were removed over a 20-yr period. This likely affected the social and population structures of these species in ways which will never be fully understood, and which may persist to this day. The data support the contention that resident humpback and fin whales existed in the coastal waters of British Columbia and show that sei and blue whales migrated past Vancouver Island. The data also suggest that sperm whales once mated and calved in British Columbian waters.

While we recognize that ours are not the only possible interpretations of these data, we feel our conclusions reflect a reasonable integration of the observed trends, the biases associated with the data collected, and the current understanding of these species. Although strictly applicable only to the historic distributions of these animals, the hypothesized trends and behaviors may persist today in the remnant populations.

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