MARINE MAMMAL SCIENCE, 18(3):663–679 (July 2002)

DIETS OF FIN, SEI, AND SPERM WHALES IN BRITISH COLUMBIA: AN ANALYSIS OF COMMERCIAL WHALING RECORDS, 1963–1967

ROWENNA D. FLINN
ANDREW W. TRITES
EDWARD J. GREGR
Marine Mammal Research Unit,
Fisheries Centre,
Department of Zoology,
University of British Columbia,
Hut B3, Room 18, 6248 Biosciences Road,
Vancouver, British Columbia V6T 1Z4, Canada
E-mail: consortium@zoology.ubc.ca

R. IAN PERRY
Fisheries and Oceans Canada,
Pacific Biological Station,
Nanaimo, British Columbia V9R 5K6, Canada

ABSTRACT

Diets of fin (*Balaenoptera physalus*), sei (*Balaenoptera borealis*), and sperm whales (*Physeter macrocephalus*) were estimated from the stomach contents of individuals killed along the British Columbia coast from 1963 to 1967. The dominant prey types of fin whales were euphausiids, with minor contributions from copepods and fish. Sei whale stomachs contained primarily copepods in three years, whereas euphausiids or a variety of fish dominated the diet in the other two years. Sperm whales consumed primarily North Pacific giant squid (*Moroteuthis robusta*), but secondary prey differed between males and females. Female sperm whales frequently consumed ragfish (*Icosteus* spp.) and other fish, whereas the male diet also contained rockfish (*Sebastes* spp.). The high abundance of euphausiids along the British Columbia coast likely contributed to the presence of a summer resident population of fin whales. The high abundance of large copepods farther north probably influenced the migration of sei whales through the offshore waters of British Columbia. Sperm whale stomach contents differed by sex reflecting location and possibly breeding behaviors.

Key words: fin whale, *Balaenoptera physalus,* sei whale, *Balaenoptera borealis,* sperm whale, *Physeter macrocephalus,* diet, stomach contents, British Columbia, North Pacific.

The only information available about the diets of fin (*Balaenoptera physalus*), sei (*Balaenoptera borealis*), and sperm (*Physeter macrocephalus*) whales in British Columbia comes from Pike (1950). These reports, based on data from 1936 to 1937 and 1948 to 1949, found that baleen whales fed primarily on small euphausiids, with the occasional stomach containing copepods. Sperm whales primarily fed on two species of squid, a small species (*Gonatus fabricii*) and the North Pacific giant squid (*Moroteuthis robusta*). The second most frequent prey was ragfish (*Icosteus aenigmaticus*), followed by rockfish (*Sebastes* spp.), skate (*Raja* spp.), lamprey (*Entosphenus* spp.), octopi, small codfish, and squid eggs.

Given that it is unlikely that large-scale diet studies using the stomach contents of fin, sei, and sperm whales will ever again be conducted in British Columbia, a detailed analysis of the historic data is warranted. Knowing what whales eat along the British Columbia coast may help to understand why these species frequent this area and why some species (*i.e.,* sei whales) are migratory while others appear to be resident (*i.e.,* fin and sperm whales) (Gregr *et al.* 2000). Understanding the diets of these species could also be useful in determining multispecies interactions, and how commercial fisheries may affect these interactions. Although our analysis is based on historical data, the interpretations are likely to provide guidance to understanding the present and future feeding interactions among these whales in this area. Diets of whales have been examined in other whaling areas, including California (Clapham *et al.* 1997), Newfoundland (Piatt *et al.* 1989), and Norway (Christensen *et al.* 1992); but in the North Pacific, the majority of the studies include regions farther offshore or north of British Columbia (Kawakami 1980; Kawamura 1980, 1982; Nemoto and Kasuya 1965).

We analyzed the stomach contents of 2,728 fin, sei, and sperm whales killed in British Columbia from 1963 to 1967. We begin with a historic overview of whaling along the British Columbia coast, and provide a brief description of the historic whaling database and how the data were used to determine the feeding success and prey of fin, sei, and sperm whales. We contrast the diets of fin whales with those of sei whales, and the diets of male sperm whales with those of female sperm whales. Finally, we discuss the factors that might influence the types of prey consumed and the movement patterns of fin, sei, and sperm whales in British Columbia.

Methods

The data used for our analysis were taken from whales killed by the Coal Harbour whaling station (Fig. 1), which was established in 1943 and operated until 1967. Whaling at this station typically lasted from April to September (Nichol and Heise 1992). The International Whaling Commission (established in 1946) required that a biologist be assigned to the whaling station to collect biological data. Gordon Pike was hired by the Canadian Department of Fisheries and Oceans to record data from fin, sei, humpback, blue (*Balaenoptera musculus*), and sperm whales. He conducted research on age estimation and

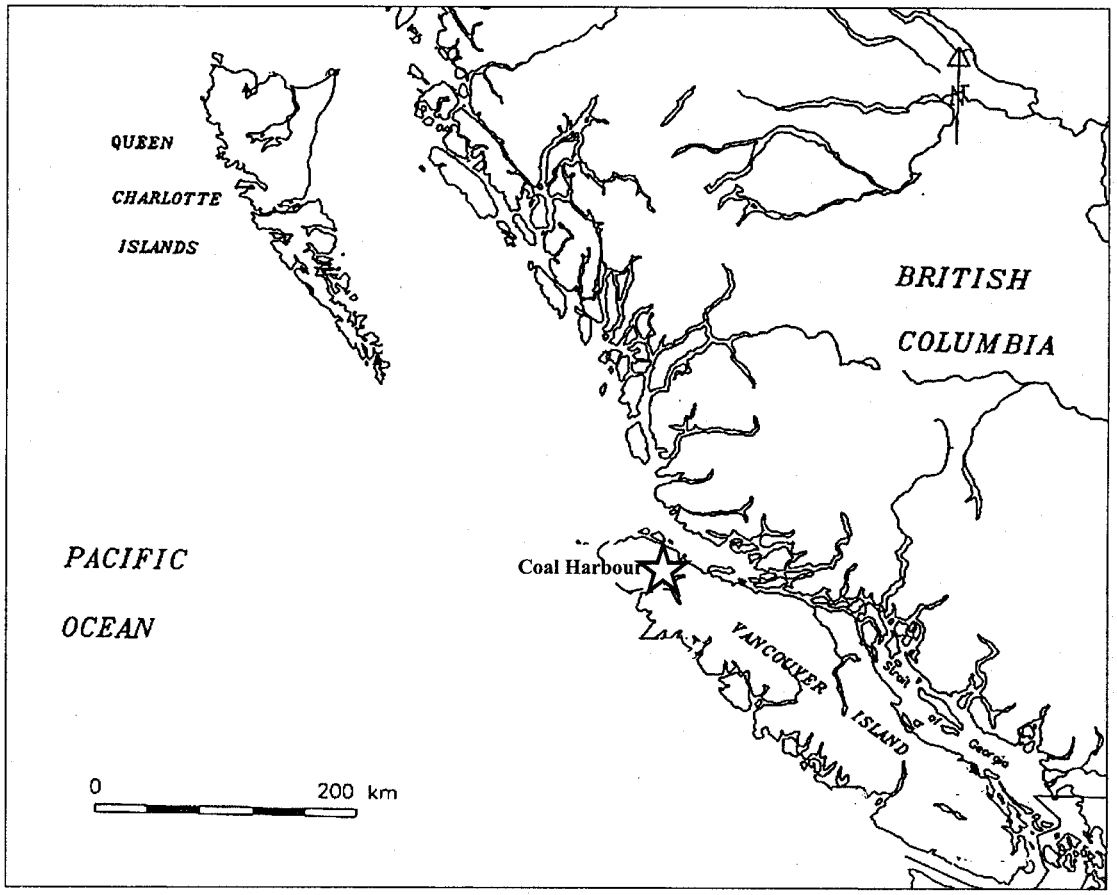

Figure 1. Location of Coal Harbour whaling station in British Columbia. Adapted from Nichol and Heise (1992).

size at sexual maturity, and recorded seasonal changes in blubber thickness, diet, schooling, and migration behavior, most of which remains unpublished (Nichol and Heise 1992). The whaling data recorded from 1905 to 1967 was compiled into the Historic Whaling Database (Nichol *et al.*, in press), and contains information on reproduction, diet composition, and morphometrics.

We analyzed stomach content data recorded from 1963 to 1967 because of the higher quality and quantity of data recorded during these years (Table 1). Data from 1947 to 1959 were not specific, with some contents classified only

Table 1. Total number of fin, sei, and sperm whales caught by year.

	Fin		Sei		Sperm	
Year	Male	Female	Male	Female	Male	Female
1963	99	119	102	52	96	51
1964	54	86	322	237	59	46
1965	29	45	341	262	65	80
1966	59	67	102	111	72	41
1967	45	47	26	39	116	153
Total	286	364	893	701	408	371

as red or orange feed, whereas diet information collected between 1960 and 1962 was not available for both sexes or for all three species of whales.

For each whale killed, prey in the stomach was recorded as "present," "trace," "empty," and "not examined." "Present" meant the stomach was either half-full or had five gallons of prey or more (Nichol *et al.,* in press). "Trace" quantities were recorded for anything smaller than "present" quantities. Stomachs "not examined" were not included in our analysis. There is no record of the methods used to determine stomach quantities (Nichol *et al.*, in press). Nor is it known which stomach (given that whales have more than one stomach) was sampled.

For analysis, the species of prey were grouped into copepods (including identified *Calanus cristata*), euphausiids (including identified *Thysanoessa spinifera* and *Euphausia pacifica*), and miscellaneous fishes. The only exception was if a species of prey occurred at high frequencies, and warranted separate treatment (such as North Pacific giant squid in sperm whale diets). The taxonomy of copepods has changed since these data were collected in the 1960s, with *Calanus cristata* being renamed *Neocalanus cristatus.* We assumed that the *C. cristata* noted in the original data were the large-bodied, deep-water copepods of the genus now called *Neocalanus* spp. There is no record as to how the contents were identified. Fin whale diets were grouped into euphausiids, copepods, and miscellaneous prey, including ragfish (*Icosteus* spp.), fish, squid, and octopus. The stomach contents of the sei whales were grouped into euphausiids, copepods and fish, including saury (*Cololabis saira*), whiting (also known as walleye pollock, *Theragra chalcogramma*), lantern fish (family Myctophidae), herring (*Clupea harengus pallasi*), and other unidentified miscellaneous fish. The sperm whale diets were grouped into squid, North Pacific giant squid (*Moroteuthis robusta*), ragfish, rockfish (*Sebastes* spp.), and other fish (dogfish, Squalus acanthias; lamprey, *Lampetra* sp.; skate, and hake, *Merluccius productus*).

Frequency of occurrences of stomach contents were compared between sexes, years and months using contingency analyses with average expected frequencies of greater than 6.0 stomachs (Zar 1999). Differences were considered to be statistically significant at the 0.05 level.

Results

Fin Whales

Stomach contents were examined for 578 of 650 fin whales taken between 1963 and 1967. Most of the fin whale stomachs examined were empty, and some had present and trace amounts of food (Fig. 2). There was no apparent difference between the types of prey found in stomachs with trace amounts and those that were full. Nor was there any difference noted between the diets of male and female fin whales ($\chi^2_2 = 2.08$, $P = 0.24$, $n = 265$).

The non-empty fin whale stomachs contained mainly euphausiids in all five years (Fig. 2). However, the diet differed significantly between years ($\chi^2_8 =$

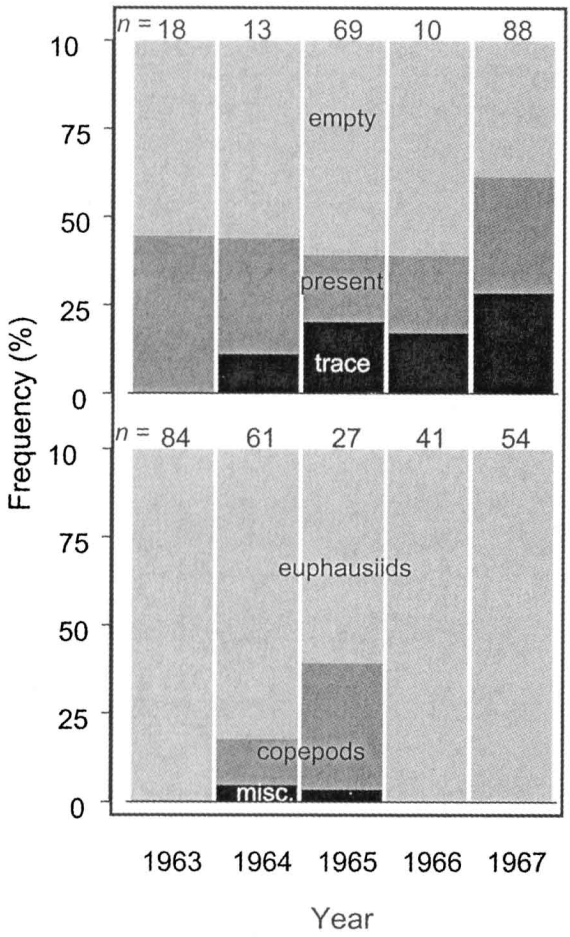

Figure 2. Percent of stomachs from fin whales that contained prey, trace amounts, or were empty (top panel). Stomachs with prey (bottom panel) contained euphausiids, copepods, and miscellaneous species (squid, ragfish, octopus, and miscellaneous fish). Number of stomachs (n) shown above each panel.

50.81, $P < 0.001$, $n = 265$). In particular, stomachs contained higher percentages of copepods, fish, and cephalopods in 1964 and 1965 than in other years (Table 2). Within years, however, there were no significant monthly differences in the composition of the fin whale diet ($\chi^2_{10} = 11.79$, $P = 0.30$, $n = 265$; Fig. 3).

Sei Whales

Sei whales were caught in much larger numbers than the fin and sperm whales. Stomach contents were examined in 1,453 out of the 1,594 whales that were killed from 1963 to 1967. The stomach quantities were similar to those of the fin whales in that empty stomachs made up the majority of occurrences (Fig. 4). The frequency of occurrence of prey found in stomachs with trace amounts did not differ significantly from those with full stomachs ($\chi^2_2 = 3.51$, $P = 0.17$, $n = 463$).

Small differences between the frequency of plankton found in the stomachs of male and female sei whales were statistically significant ($\chi^2_1 = 5.14$, $P =$

Table 2. Numbers (*n*) of fin, sei, and sperm whale stomachs with prey and frequency of occurrence (%) of reported prey. Note that combined diet of sperm whales is not included because diets of males and females were significantly different.

Prey by species	Male					Female					Combined				
	1963	1964	1965	1966	1967	1963	1964	1965	1966	1967	1963	1964	1965	1966	1967
Fin (*n*)	30	25	10	21	21	54	36	17	20	33	84	61	27	41	54
euphausiids	96.7	80.8	70.0	100.0	100.0	94.6	83.3	55.6	95.2	100.0	95.8	82.3	60.7	100.0	100.0
copepods	3.3	7.7	30.0	0.0	0.0	5.4	16.7	38.9	4.8	0.0	4.2	12.9	35.7	0.0	0.0
squid	0.0	3.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0
ragfish	0.0	3.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0
octopus	0.0	3.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0
misc. fish	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.6	0.0	0.0	0.0	0.0	3.6	0.0	0.0
Sei (*n*)	35	97	94	22	8	18	68	86	33	13	53	159	178	54	21
euphausiids	2.6	4.1	1.1	77.3	12.5	4.5	10.8	5.8	57.6	7.1	3.3	7.0	3.4	65.4	9.1
copepods	89.8	89.7	90.5	4.5	0.0	81.0	83.8	90.7	3.0	7.1	85.2	87.1	90.5	3.6	4.6
saury	5.1	6.2	6.4	9.1	12.5	14.3	5.4	3.5	33.3	0.0	8.2	5.8	5.0	23.6	4.6
whiting	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	28.6	0.0	0.0	0.0	0.0	18.2
lamprey	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0
laternfish	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0
herring	0.0	0.0	0.0	0.0	0.0	4.8	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0
misc. fish	0.0	0.0	1.1	9.1	75.0	0.0	0.0	0.0	6.1	57.2	0.0	0.0	0.6	7.3	63.6
Sperm (*n*)	73	34	47	30	79	35	25	49	15	71					
small squid	1.2	0.0	0.0	0.0	0.0	13.8	0.0	4.1	0.0	0.0					
giant squid	40.2	45.6	50.6	61.2	73.8	40.0	65.7	57.5	73.7	76.1					
ragfish	13.6	26.5	25.9	12.2	15.9	26.2	31.4	30.1	21.1	14.1					
dogfish	13.6	5.9	0.0	0.0	0.0	6.2	2.8	0.0	0.0	0.0					
rockfish	26.0	16.2	18.8	18.4	10.3	1.5	0.0	4.1	0.0	5.4					
lamprey	2.4	2.9	0.0	4.1	0.0	10.8	0.0	4.1	5.3	3.3					
skate	3.0	2.9	2.4	4.1	0.0	1.5	0.0	0.0	0.0	1.1					
hake	0.0	0.0	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0					

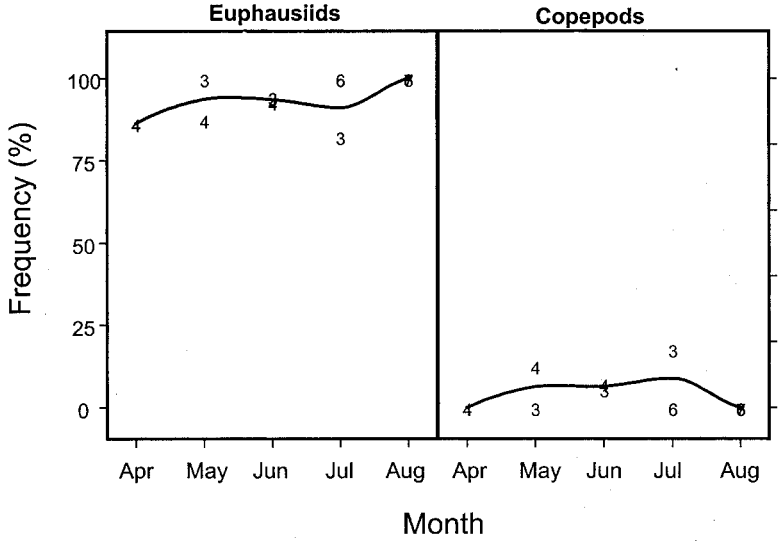

Figure 3. Seasonal changes in frequencies of occurrence of dominant prey found in fin whale stomachs. Only months with $n > 10$ included. Numbers in each panel indicate year (*i.e.*, 3 = 1963, 4 = 1964, 5 = 1965, 6 = 1966, and 7 = 1967). Data were fit with locally weighted regression (loess, $f = 0.667$).

0.02, $n = 463$). However, the difference may not be biologically meaningful as the general trend for both sexes was similar. Pooling the data showed that the frequency of prey (copepods, euphausiids, and a variety of fish) differed significantly by year ($\chi^2_8 = 165.40$, $P < 0.001$, $n = 463$; Fig. 4). A sharp drop in copepods and an increase in fish occurred in 1966 and 1967. Most of the fish were saury, whiting, and other miscellaneous fish (Table 2).

Monthly trends in the types of prey consumed were more apparent for sei whales than for fin whales. Sei whale stomach contents differed significantly by month ($\chi^2_{10} = 139.04$, $P < 0.001$, $n = 389$; Fig. 5). Monthly decreases occurred in both the euphausiids (May–September) and copepods (July–September), while saury increased (July–September). Data from 1966 and 1967 were excluded from the seasonal analysis because too few sei whales were killed in some months during these two years.

Sperm Whales

Stomach contents were examined for 697 of the 779 sperm whales killed. There were significant differences between the number of males and females with full, trace, and empty stomachs ($\chi^2_3 = 14.39$, $P = 0.002$, $n = 779$), with males tending to have fewer empty stomachs (Fig. 6). Types of prey found in stomachs with trace and full amounts also differed by sex. Females had significantly more North Pacific giant squid in full stomachs than in stomachs with trace amounts ($\chi^2_1 = 5.47$, $P = 0.02$, $n = 194$), while ragfish were present more frequently in full stomachs (males: $\chi^2_1 = 20.68$, $P < 0.001$, $n = 263$; females: $\chi^2_1 = 19.44$, $P < 0.001$, $n = 194$). In males, rockfish and dogfish were present in significantly larger frequencies in full stomachs than

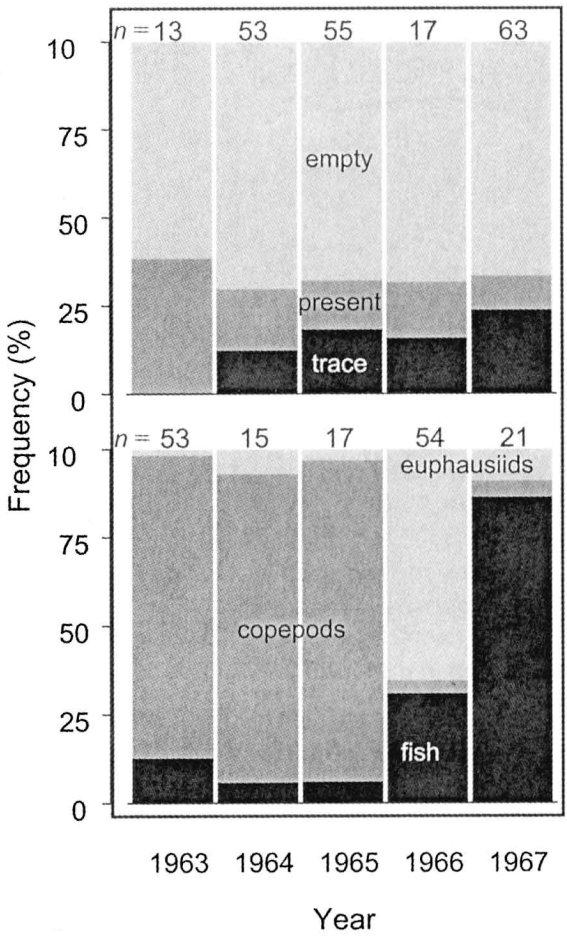

Figure 4. Percent of stomachs from sei whales (males and females combined) that contained prey, trace amounts, or were empty (top panel). Stomachs with prey (bottom panel) contained euphausiids, copepods, and fish (saury, whiting, lantern fish, herring, and miscellaneous fish). Numbers of stomachs (n) shown above each panel.

in those with trace amounts (rockfish: $\chi^2_1 = 19.56$, $P < 0.001$, $n = 263$; dogfish: $\chi^2_1 = 7.24$, $P = 0.01$, $n = 263$).

Diets of male and female sperm whales were significantly different ($\chi^2_4 = 20.56$, $P < 0.001$, $n = 457$) and were also significantly different between years (males: $\chi^2_{16} = 58.67$, $P < 0.001$, $n = 263$; females: $\chi^2_{12} = 38.50$, $P < 0.001$, $n = 194$). North Pacific giant squid were the dominant prey of both sexes, but species of fish varied between males and females (Fig. 6). Small squid were present only in low frequencies in a few years (Table 2). Ragfish occurred frequently as prey in both male and female sperm whales and were consistently present in all five years. Rockfish, which occurred infrequently in the females, tended to be present in the males in similar frequencies to the ragfish. The miscellaneous fish were present in both sexes, but were less frequent in females.

Seasonal changes in the diet of male and female sperm whales are apparent when each month is averaged across years (Fig. 7). These changes were statistically significant for the males ($\chi^2_{20} = 54.46$, $P < 0.001$, $n = 263$), but not for the females ($\chi^2_{12} = 17.75$, $P = 0.12$, $n = 194$). Seasonal changes in diet

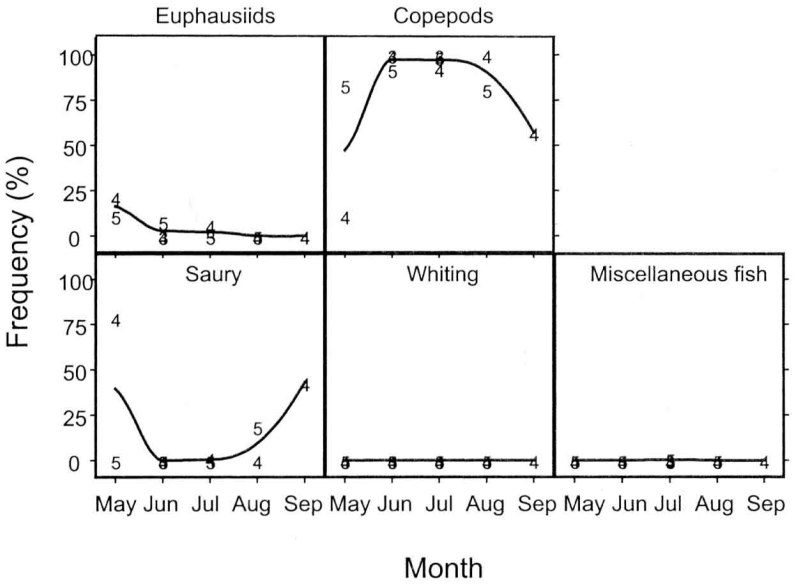

Figure 5. Seasonal changes in frequencies of occurrence of dominant prey found in sei whale stomachs. Only months with $n > 10$ included (no data were used from 1966 and 1967 due to low sample size). Numbers in each panel indicate year (*i.e.*, 3 = 1963, 4 = 1964 and 5 = 1965). Data were fit with locally weighted regression (loess, $f = 0.667$).

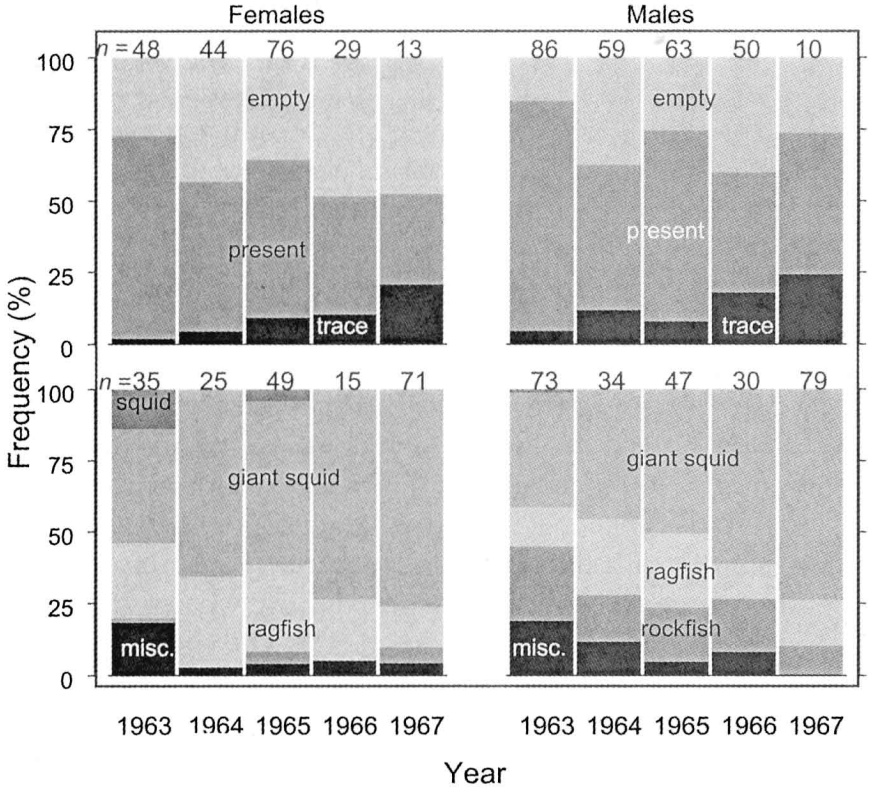

Figure 6. Percent of male and female stomachs from sperm whales that contained prey, trace amounts, or were empty (top panels). Stomachs with prey (bottom panels) contained squid, giant squid, ragfish, rockfish, and miscellaneous species (dogfish, lamprey, skate, and hake). Number of stomachs (n) shown above each panel.

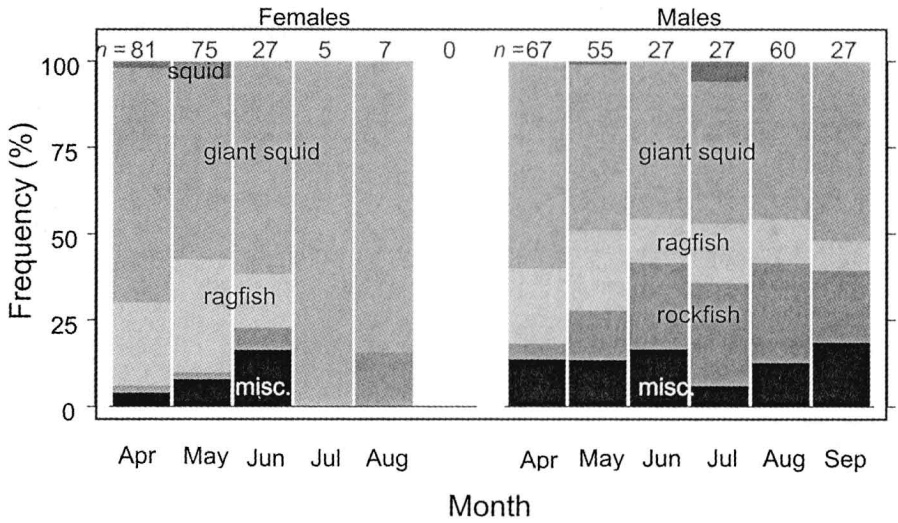

Figure 7. Seasonal average percent of male and female stomachs from sperm whales that contained squid, giant squid, ragfish, rockfish, and miscellaneous species (dogfish, lamprey, skate, and hake). Number of stomachs (*n*) shown above each panel.

showed the same general trend in both sexes for ragfish and rockfish, but differed for North Pacific giant squid. Ragfish consumption decreased over the season, while rockfish consumption increased. Frequencies of North Pacific giant squid in stomachs increased in the females, but decreased in the males.

Discussion

The stomach content data analyzed here are the only extensive data available for sperm, sei, and fin whales in the coastal waters of British Columbia, and augment the preliminary observations of Pike (1950). Although the data are from only five years (1963–1967), they indicate a relatively simple diet that is consistent with what is known about the diets of these species in other parts of the North Pacific (Kawakami 1980; Kawamura 1973, 1980, 1982). These results are similar to those reported for sei and sperm whales in the North Atlantic, but differ for fin whales (Christensen *et al.* 1992).

The data show a high frequency of empty stomachs and some annual and monthly variability in prey consumed. Fin whales feed primarily on euphausiids, while sei whales consume high frequencies of copepods, but will feed also on euphausiids and fish in large quantities. In the North Atlantic, fin whales consume copepods and fish, while the sei whales have an apparent preference for copepods (Christensen *et al.* 1992). The sperm whale diet in the North Pacific varies with sex, but consists mainly of North Pacific giant squid and certain types of fish (primarily ragfish and rockfish).

Baleen Whales, Zooplankton, and Fish

Fin and sei whales fed primarily on euphausiids and copepods. Copepods make up a large portion of the total biomass of the zooplankton community

in all areas of the British Columbia coast, especially in spring and early summer (Mackas and Tsuda 1999). Euphausiids also dominate the zooplankton community, but their abundance is more dependent on the season and coastal location (Mackas and Tsuda 1999). The relative dominance and the consistency of the zooplankton biomass likely influences where the whales feed in British Columbia.

The high abundance of euphausiids along the coasts of British Columbia is largely related to the continental shelf break and other bathymetric features. The most abundant euphausiid on the British Columbia continental shelf is *Thysanoessa spinifera,* while *Euphausia pacifica* is more abundant off of the shelf (Mackas and Galbraith 1992). A weak north-to-south gradient is also present in euphausiid abundance, with increasing concentrations northward along the British Columbia coast (Mackas and Galbraith 1992). Large-bodied copepods occur in higher abundance farther offshore and farther north in deeper ocean regions, but can also increase locally through the same current-bathymetry interactions that concentrate euphausiids. Parsons *et al.* (1969) reported higher copepod abundance about the periphery of the NE Pacific gyre, with highest surface concentrations in the subarctic and Alaskan Current systems. *Neocalanus* spp. tend to be more abundant as one moves north along the west coast of Vancouver Island (Mackas and Galbraith 1992). Their seasonal ontogenetic migration is reflected in the decrease in copepod frequency in the late summer of the sei whale diet (Fig. 5). This general split in the distribution of euphausiids and large-bodied copepods off the British Columbia coast may influence fin and sei whale life histories.

Fin whales are believed to return to feed in British Columbia waters each year, while the sei whales migrate through the area to feed either farther north or offshore (Gregr *et al.* 2000). The high, localized abundance of euphausiids around bathymetric margins allows the fin whales to migrate to the British Columbia coast and feed in these areas continuously through the summer. The higher concentrations of copepods farther north and offshore likely encourages the farther migration of the sei whales to more suitable feeding grounds.

Both fin and sei whales were killed along the shelf break and just beyond (Fig. 8) where a large and relatively constant biomass of euphausiids and copepods occurs (Mackas 1992). The peaks in plankton biomass are not as large as on the inner shelf, but are consistent through the summer (Mackas 1992). As both species of whales primarily feed at the shelf break and seaward, the reliability of the zooplankton at these locations provides predictable feeding areas throughout the summer, whether they remain in the area or pass through.

The tendency displayed by fin and sei whales for a particular type of zooplankton is related to specialized feeding behavior and the location of zooplankton in the water column. Both species depend upon aggregations of zooplankton (Nemoto and Kawamura 1977). Fin whales are "swallowers" with ventral grooves that allow the whale's mouth to expand to engulf large mouthfuls of water and food. They then use their tongue to force the water out through the baleen to sieve out the zooplankton (Kawamura 1980). This type

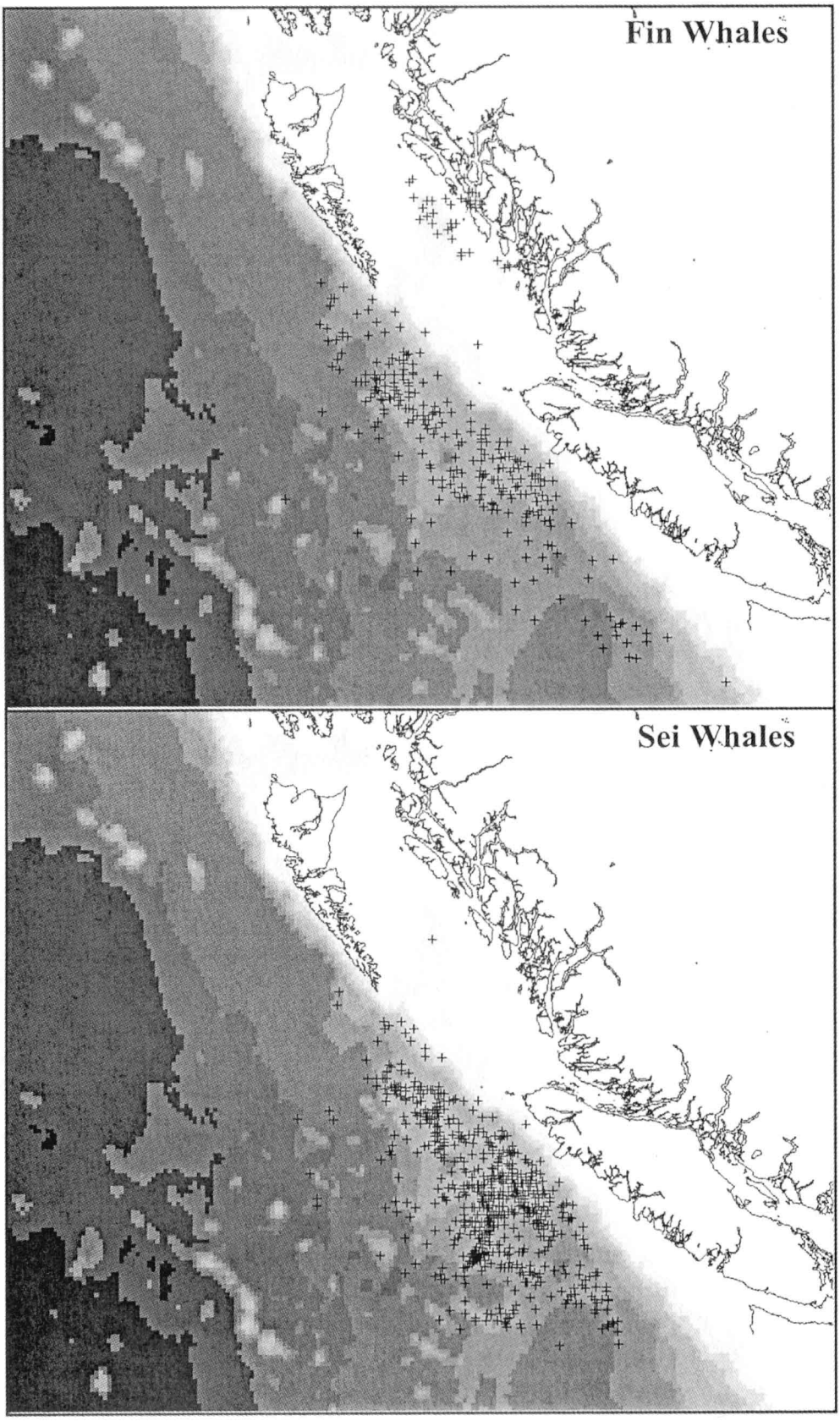

Figure 8. Locations of fin whales and sei whales killed off coast of British Columbia between 1963 and 1967. Shading (light to dark) shows bathymetry at 200-m intervals.

of feeding occurs during a dive, and is consistent with the deep distributions of euphausiids (Mackas and Fisher 1969) and with the high frequency of euphausiids in fin whale stomachs.

Sei whales are both "swallowers" and "skimmers" (Kawamura 1980). Skimming behavior occurs at the surface as the whale swims with its head partially above water with its mouth half open. The zooplankton are filtered by the baleen as the water rushes out of the whale's mouth (Kawamura 1980). Feeding of this type at the surface is consistent with the large presence of copepods in the sei whale stomachs, which spend most of their time in the upper 150 m and exhibit weak diel migration at this time of year (Mauchline and Fisher 1969). This tendency for fin and sei whales to consume either euphausiids or copepods is apparent in other areas such as Japan (Kawamura 1982) and the Gulf of Alaska (Nemoto and Kasuya 1965).

The low frequency of fish in the fin whale diet is surprising when compared to the larger role that they play in other areas, such as the North Atlantic where there is a strong seasonal dietary presence of fish during the spring and winter (Christensen *et al.* 1992). The summer diet of fin whales in the North Atlantic is dominated by crustaceans, and is similar to that of the North Pacific. Fish in the diet of the whales killed off the coast of British Columbia were primarily found in the stomachs of fin whales during the spring, suggesting a similar seasonality as in the North Atlantic. With regard to sei whales, the frequency of fish observed in their stomachs is comparable to other parts of the North Pacific, but not the North Atlantic. This difference is likely due to differences in prey assemblages and availability with geographic location (Bowen and Siniff 1999).

The percentage of whale stomachs from the British Columbia catch that contained prey was consistent for the five years examined for both species of whales (39%–61% of the stomachs had prey for fin whales and 30%–38% for sei whales). These ranges are slightly lower than Japanese whaling data that showed averages of 52%–60% of stomachs with prey for fin whales and 44%–60% for sei whales (Kawamura 1982). The large number of fin and sei whales with empty stomachs may reflect their frequency of feeding. Kawamura (1971) suggested that most fin and sei whales usually feed once a day in the morning. Those whales killed with empty stomachs may have already finished digesting their previous meal. It is unlikely that empty stomachs where the result of vomiting food items while being hunted and killed, given the behavior reported by Kawamura (1971).

Sperm Whales, Squid, and Fish

Sperm whales off British Columbia are spatially segregated by sex, with females showing a greater mean monthly distance from shore, and males occurring closer to shore (Fig. 9) (Gregr and Trites 2001). This separation, which increases over the season, may be due to calving that is hypothesized to occur in waters farther offshore between July and August (Gregr *et al.* 2000). The separation of males and females is also apparent in what they ate and by the

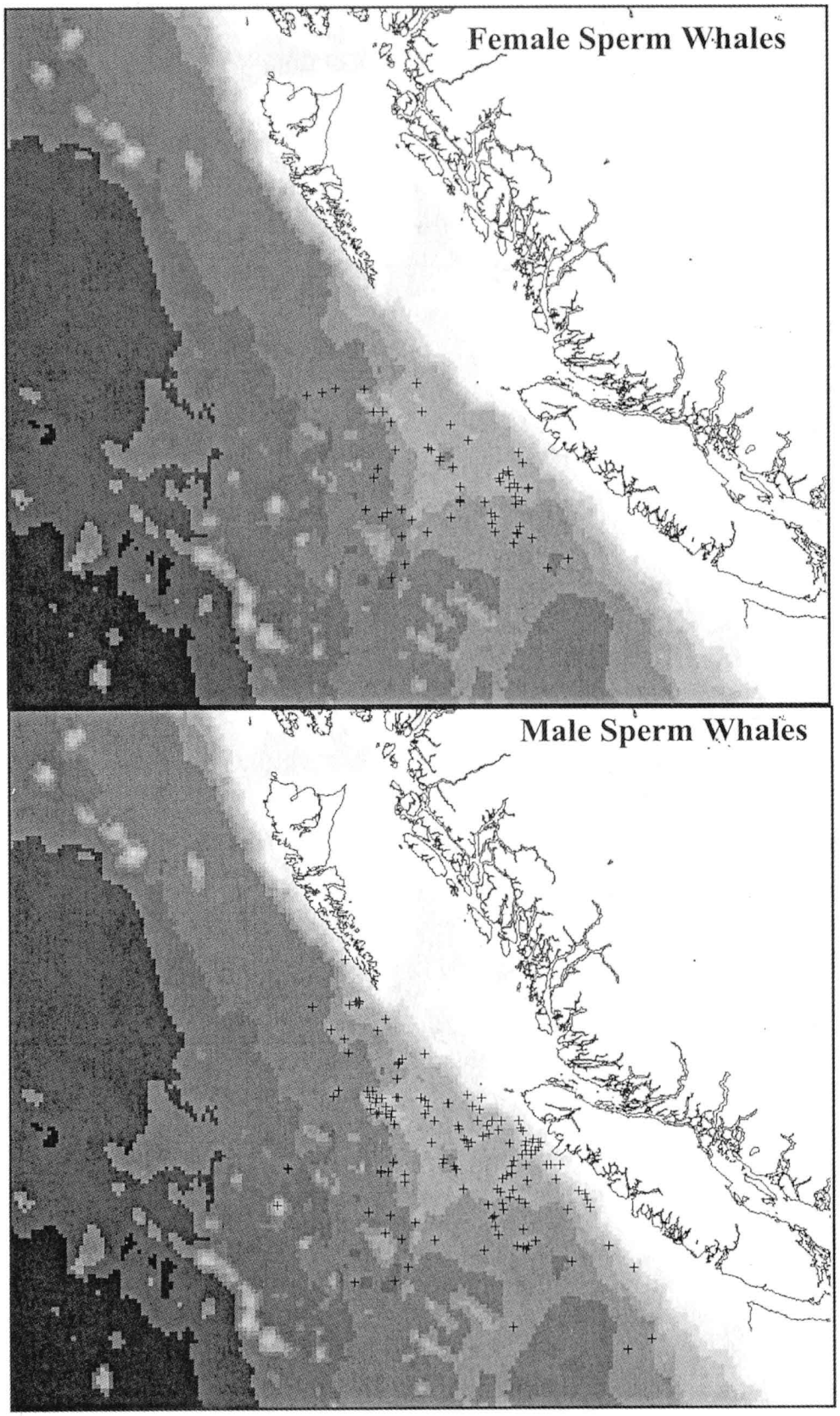

Figure 9. Location of female and male sperm whales killed off coast of British Columbia between 1963 and 1967. Shading (light to dark) shows bathymetry at 200-m intervals.

fullness of their stomachs, which may reflect a relationship between distance from shore and the abundance and diversity of available prey.

Female sperm whales tended to have lower frequencies of prey (Fig. 6). This may be due to females forgoing feeding to care for their calves, which are unable to dive as deep as their mothers (Kawakami 1980). Empty stomachs may also reflect feeding conditions. In the Galapagos, Whitehead (1996) found that upwelling events increased feeding success, in contrast to El Niño conditions. Variation in prey availability may cause whales to fast while waiting for conditions to improve. Fasting by sperm whales is supported by research in Scotland, which found interannual variations in fatness related to changes in feeding conditions (Whitehead 1996).

The segregation of males and females is reflected in their diet late in the season. In April and May, when sperm whale mating is believed to take place (Gregr *et al.* 2000), males and females both consume fish and North Pacific giant squid (Fig. 7). Later in the season, males have a higher frequency of rockfish in their stomachs and generally tend to eat more fish than females (Fig. 7). This may be due to the proximity of males to the continental shelf, which is a less favorable habitat for the pelagic North Pacific giant squid (Hochberg and Fields 1980). Rockfish and ragfish occupy a number of different habitats along the coast, with rockfish in particular occurring along the continental shelf and slope (Hart 1973).

Female sperm whales eat fewer fish than male sperm whales, due perhaps to their movement offshore away from the males. Fish form a high percentage of the female diet from April to June, but are replaced by pelagic squid as the females move offshore to calve in July and August. In August a deep water species of rockfish (Hart 1973) likely comprises the rockfish portion of the female sperm whale diet.

Conclusions

Our analysis of stomach contents broadens the picture of the diets of fin, sei, and sperm whales caught off British Columbia during the 1960s compared to earlier descriptions (Pike 1950). It adds to the few studies that have looked at this area in detail and provides a picture of how diet is influenced by foraging behavior and life history. The consistency and dominance of the zooplankton community may influence the life history of the fin and sei whales, with the abundance of euphausiids contributing to the presence of a resident summertime fin whale population. Similarly, the frequency of large copepods farther north and offshore likely encourages the migration of the sei whales through British Columbia offshore waters. As for female sperm whales, their high frequency of empty stomachs may reflect the cost of calving, with shifts in stomach contents reflecting changes in behavior rather than prey availability or preference. The diet of male sperm whales probably reflects their continuous presence closer to shore.

Acknowledgments

We are grateful to Arliss Winship for his assistance with AWK programming, and to Pamela Rosenbaum for her invaluable support. Funding was provided by Parks Canada and Fisheries and Oceans Canada. The manuscript was improved by comments from Arne Bjorge and an anonymous reviewer.

Literature Cited

Bowen, W. D., and D. B. Siniff. 1999. Distribution, population biology, and feeding ecology of marine mammals. Pages 423–484 *in* J. E. Reynolds III and S. A. Rommel, eds. Biology of marine mammals. Smithsonian Institution Press, Washington, DC.

Christensen, I., T. Haug and N. Øien. 1992. A review of feeding and reproduction in large baleen whales (*Mysticeti*) and sperm whales *Physeter macrocephalus* in Norwegian and adjacent waters. Fauna Norvegica, Series A 13:39–48.

Clapham, P. J., S. Leatherwood, I. Szczepaniak and R. L. Brownell, Jr. 1997. Catches of humpback and other whales from shore stations at Moss Landing and Trinidad, California, 1919–1926. Marine Mammal Science 13:368–394.

Gregr, E., L. Nichol, J. K. B. Ford, G. Ellis and A. W. Trites. 2000. Migration and population structure of northeastern Pacific whales off coastal British Columbia: An analysis of commercial whaling records from 1908–1967. Marine Mammal Science 16:699–727.

Gregr, E. J., and A. W. Trites. 2001. Predictions of critical habitat for five whale species in the waters of coastal British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 58:1265–1285.

Hart, J. L. 1973. Pacific fishes of Canada. Bulletin of the Fisheries Research Board of Canada 180. 740 pp.

Hochberg, F. G., and W. G. Fields. 1980. Cephalopoda: The squids and octopuses. Pages 429–444 *in* R. H. Morris, D. P. Abbott and E. C. Haderlie, eds. Intertidal invertebrates of California. Stanford University Press, Stanford, CA.

Kawakami, T. 1980. A review of sperm whale food. Scientific Reports of the Whales Research Institute, Tokyo 32:199–218.

Kawamura, A. 1971. Influence of chasing time to stomach contents of baleen and sperm whales. Scienctific Reports of the Whales Research Institute, Tokyo 23: 27–36.

Kawamura, A. 1973. Food and feeding of sei whale caught in the waters south of 40°N in the North Pacific. Scientific Reports of the Whales Research Institute, Tokyo 25:219–236.

Kawamura, A. 1980. A review of food of balaenopterid whales. Scientific Reports of the Whales Research Institute, Tokyo 32:155–197.

Kawamura, A. 1982. Food habits and prey distributions of three rorqual species in the North Pacific Ocean. Scientific Reports of the Whales Research Institute, Tokyo 34:59–91.

Mackas, D. L. 1992. Seasonal cycle of zooplankton off southwestern British Columbia: 1979–89. Canadian Journal of Fisheries and Aquatic Sciences 49:903–921.

Mackas, D. L., and M. Galbraith. 1992. Zooplankton on the west coast of Vancouver Island: Distribution and availability to marine birds. Pages 15–29 *in* K. Vermeer, R. W. Butler and K. H. Morgan, eds. The ecology, status and conservation of marine and shoreline birds on the west coast of Vancouver Island. Occasional Paper Number 75, Canadian Wildlife Service. Ottawa.

Mackas, D. L., and A. Tsuda. 1999. Mesozooplankton in the eastern and western subarctic Pacific: Community structure, seasonal life histories, and interannual variability. Progress in Oceanography 43:335–363.

MAUCHLINE, J., AND L. R. FISHER. 1969. The biology of euphausiids. Advances in Marine Biology 7:1–454.

NEMOTO, T., AND T. KASUYA. 1965. Foods of baleen whales in the Gulf of Alaska of the North Pacific. Scientific Reports of the Whales Research Institute, Tokyo 19: 45–51.

NEMOTO, T., AND A. KAWAMURA. 1977. Characteristics of food habits and distribution of baleen whales with special reference to the abundance of North Pacific sei and Bryde's whales. Report of the International Whaling Commission (Special Issue 1):80–87.

NICHOL, L. M., E. J. GREGR, R. D. FLINN, J. K. B. FORD, A. PEACOCK, R. GURNEY AND L. MICHALUK. In press. BC commercial whaling catch data 1908 to 1967: A detailed description of the BC Historical Whaling Database. Canadian Technical Report of Fisheries and Aquatic Sciences. 80 pp.

NICHOL, L., AND K. HEISE. 1992. The historical occurrence of large whales off the Queen Charlotte Islands. Prepared For South Moresby/Gwaii Haanas National Parks Reserve, Canadian Parks Service, Queen Charlotte City, BC. 68 pp.

PARSONS, T. R., L. F. GIOVANDO AND R. J. LEBRASSEUR. 1969. The advent of the spring bloom in the eastern subarctic Pacific Ocean. Journal of the Fisheries Research Board of Canada 23:539–546.

PIATT, J. F., D. A. METHVEN, A. E. BURGER, R. L. MCLAGAN, V. MERCER AND E. CREELMAN. 1989. Baleen whales and their prey in a coastal environment. Canadian Journal of Zoology 67:1523–1530.

PIKE, G. 1950. Stomach contents of whales caught off the coast of British Columbia. Fisheries Research Board Canadian Pacific Progress Report 83:27–28.

WHITEHEAD, H. 1996. Variation in the feeding success of sperm whales: Temporal scale, spatial scale and relationship to migrations. Journal of Animal Ecology 65: 429–438.

ZAR, J. H. 1999. Biostatistical analysis. 4th edition. Prentice Hall, Upper Saddle River, NJ.

Received: 12 October 2000
Accepted: 18 October 2001