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Interannual Trends in Pacific Cod *(Gadus Macrocephalus)* Predation on Three Commercially Important Crab Species in the Eastern Bering Sea

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Interannual Trends in Pacific Cod (*Gadus macrocephalus*) Predation on Three Commercially Important Crab Species in the Eastern Bering Sea

by

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ABSTRACT

Pacific cod (Gadus macrocephalus) food habits data from 1981, 1984, and 1985 in the eastern Bering Sea were analyzed to determine interannual trends in consumption of three commercially important species of crabs: the red king crab (Paralithodes camtschatica) and two species of snow crab (Chionoecetes bairdi and C. opilio). Soft-shell female red king crab were consumed during spring in Bristol Bay. Estimates of the number of red king crab consumed by the Pacific cod population were 3.8%, 2.8%, and 1.4% of the female red king crab standing stock in the respective sampling years of 1981, 1984, and 1985. This implied that Pacific cod were not the major force behind the observed decline in numbers of female red king crab in the population from 1981 to 1985. Pacific cod consumed male and female snow crab ranging in size from about 5 to 90 mm carapace width throughout the sampling period of May through September. Geographic distribution of C. opilio predation by cod extended southward from 1981 to 1985 and may have been related to the southern extension of cooler bottom waters less than 3°C in 1984 and 1985. Predation mortality of C. bairdi by cod was estimated to be about 84.4%, 95%, and 94% of the population of age 1 crab during 1981, 1984, and 1985, respectively. Annual predation removals of age 1 C. opilio was 28%, 57%, and 27%, respectively, of the reconstructed population numbers of age 1 crab in the 3 years sampled. Chionoecetes bairdi are more vulnerable to cod predation because of their high spatial overlap with cod populations, whereas unknown portions of the C. opilio juvenile population are north of the main survey area. Results from this study suggest that predation by cod may be an important factor influencing survival of ages 1-2 snow crab in the eastern Bering Sea.

INTRODUCTION

Pacific cod (*Gadus macrocephalus*) abundance in the eastern Bering Sea has increased over the last decade primarily due to the entrance of two strong year classes in 1978 and 1979. Stock biomass levels have been about 1 million metric tons (t) since 1982 and a growing domestic fishery for this species is responsible for most of the catch which totalled 134,000 t in 1986 (Thompson and Shimada 1987). Because Pacific cod are documented predators of soft-shell red king crab (*Paralithodes camtschatica*) and juvenile snow crab (*Chionoecetes opilio* and *C. bairdi*) (Mito 1974; Feder 1977; Jewett 1978; Livingston et al. 1986; and Shimada et al. 1988) there has been an increase in speculation linking the decline of crab stocks with the increase in Pacific cod population size. The eastern Bering Sea red king crab population has been decreasing from a maximum achieved in 1977; suggested reasons for the decline include weak year class production and large increases in natural mortality which might be attributed to predation by Pacific cod, disease, or incidental catch in trawl fisheries (Otto 1986). Speculations have also implicated Pacific cod in the decline of red king crab abundance in the Kodiak region of the Gulf of Alaska (Blau 1986) and the disappearance of certain year classes of *C. opilio* snow crab in the eastern Bering Sea (Incze and Schumacher 1986). Unfortunately, there has not been enough evidence to determine thus far whether Pacific cod have indeed been responsible for these declines in crab populations.

The regulation of prey population size by a predator population requires that prey mortality rate increase with prey population size (direct density-dependent mortality) (Holling 1959). Thus we need to examine changes in Pacific cod diet with changes in crab population abundance to determine whether cod change their rate of predation on crab when crab abundance changes. Total removals of crab by cod need to be estimated and compared with crab population size to determine whether the percent removals of crab by cod changed with changes in crab density, thus showing whether cod predation is a density-dependent factor regulating crab population size.

The purpose of this study is to examine the interannual trends in Pacific cod predation on three commercially important crab species in the eastern Bering Sea: red king crab and C. opilio and C. bairdi snow crabs. Three years of Pacific cod food habits data from 1981, 1984, and 1985 will be analyzed to determine:

1) the areas where crab predation occurs, and whether this changes in different years and can be related to environmental variables,
2) changes in the percent by weight and size distribution of crab in the diet by year, and
3) total amounts of crab consumed by the Pacific cod population for each year calculated from food habits data, daily ration, and Pacific cod population abundance estimates.

Estimated removals of crab by Pacific cod for each year will be compared with the size distribution and population levels of crab estimated from annual research surveys.

METHODS

Sample Collection and Laboratory Analysis

Stomachs were collected from 4,023 Pacific cod (30-107 cm fork length (FL)) during 3 yr (1981, 1984, and 1985) in the eastern Bering Sea (Fig. 1, Table 1). Samples were taken from May through September using bottom trawl gear on research and commercial fishing vessels. Sampling

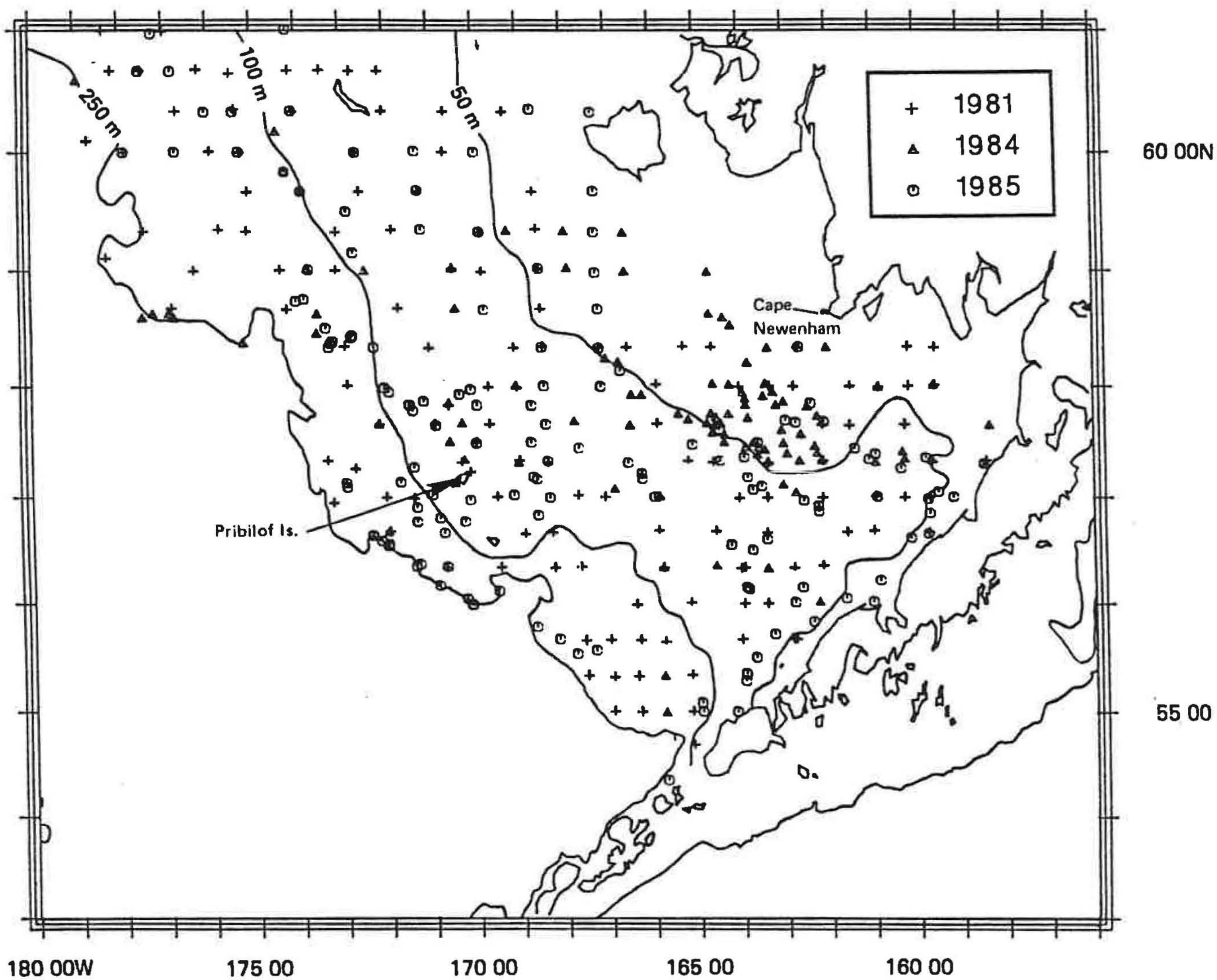

Figure 1.--Haul locations where Pacific cod, Gadus macrocephalus, stomach samples were taken during 1981, 1984, and 1985 in the eastern Bering Sea.

Table 1.--Stomach sample collection information of Pacific cod taken in 1981, 1984, and 1985 in the eastern Bering Sea.

Year	Sampling dates	Number of hauls	Sampling times (ADT)	Number of stomachs			Sampling platform
				30-59cm	>60cm	Total	
1981	5/23 - 8/3	145	0600 - 2000	1130	527	1657	research vessels
1984	5/9 - 9/29	157	0000 - 2359	560	410	970	research vessels foreign commercial vessels
1985	5/5 - 9/30	148	0000 - 2359	870	706	1576	research vessels foreign commercial vessels

occurred throughout the 24-h day in 1984 and 1985 and from 0600h to 2000h Alaska daylight time in 1981. Stomachs were removed at sea and placed in cloth bags labelled with information regarding the location of capture and the length, sex, and sexual maturity of the fish. Individual fish weights were calculated using a length-weight relationship developed for Pacific cod in the eastern Bering Sea (Bakkala et al. 1986). Fish showing evidence of regurgitation (i.e., food in the mouth or throat, or a flaccid stomach) were not included in the sample. Stomachs were preserved in 10% formalin and sent to the laboratory in Seattle for analysis. In the laboratory the samples were transferred to 70% ethyl alcohol. Contents were identified to the lowest taxonomic level possible and enumerated. Wet weights were recorded after the contents were blotted with paper towels. Whole snow crabs in the stomachs were measured to the nearest millimeter carapace width (CW) and king crabs were measured to the nearest millimeter carapace length (CL).

Data Analysis

Pacific cod were divided into two size groups for data analysis: 30-59 cm FL and $\geq$60 cm FL. Previous studies (Livingston et al. 1986; Shimada et al. 1988) show that cod become increasingly piscivorous beyond 60 cm FL and mean stomach content weight as a percentage of body weight is also much larger for cod greater than 60 cm in length. Thus, the food habits and daily ration need to be examined separately for the two size groups of cod.

The areas of crab consumption by cod were derived by plotting the areal distribution of the percent by weight of each species of crab in the diet for each year. A polygon encompassing the area where each species of crab was consumed was obtained for each year. The percentage by weight of a crab species in the diet of each size group of cod was calculated solely from stomachs taken inside the crab consumption area. To eliminate spatial sampling bias (i.e., samples unevenly distributed within a crab consumption area), the percent by weight of crab in the diet was calculated by taking the average of the percentages for each 20 nmi wide square where stomachs were sampled within a crab consumption area.

Estimates of the total amount of each crab species consumed by the Pacific cod population during the sampling period for each year was calculated according to Mehl and Westgard (1983):

$$C(i) = DR(i) \times D \times B(i) \times P(i) \qquad (1)$$

where C(i) is the consumption (by weight) of crab by cod belonging to size group i, DR(i) is the daily ration (as a percentage of body weight daily, %BWD) of cod size group i, D is the number of days in the sampling period of May through September where crab were vulnerable to predation (D = 153 for snow crab, D = 30 for red king crab), B(i) is the biomass of cod size group i, and P(i) is the proportion (by weight) of the crab species in the diet of cod size group i.

Since recent studies indicate that prey size or weight is an important factor influencing gastric evacuation rates in fish (Jobling 1987; Ursin et al. 1985), Pacific cod daily ration (R) was calculated using mean stomach content weight (S) in grams for each year and cod size group in the following equations from Ursin et al. (1985). These equations describe daily ration for Atlantic cod, _Gadus morhua_ (whose diet and morphology are very similar to Pacific cod), as a function of prey weight (w) in grams, and bottom temperature (T) in °C:

$$R = aS \text{ where } a = a_0 w^{a_1} \text{ and } a_0 = a_{00} e^{.096T} \qquad (2)$$

and $a_0 = 0.61\ d^{-1}$, $a_{00} = 0.33$, and $a_1 = -0.36$ for North Sea temperatures were adjusted for the Bering Sea using the average bottom temperature for cod stations sampled in each year from expendable bathythermographs obtained at most stations.

Pacific cod biomass was estimated using data collected during resource assessment surveys conducted each year by the Resource Assessment and Conservation Engineering (RACE) Division of the Northwest and Alaska Fisheries Center (NWAFC). The catch per unit of effort (CPUE) of cod in kg/nmi^2 was calculated using the area swept method for each 20 nmi wide square where resource assessment trawls were performed in each crab consumption area. The cod CPUE was then separated into the CPUE for each cod size group using the resource assessment survey length frequency information. Total biomass for each cod size group could then be calculated as the sum of the CPUEs multiplied by the area of a 20 nmi wide square (400 nmi^2).

Population estimates and size distributions of crab from assessment surveys were provided by Robert Otto, Director of the Kodiak Laboratory of the RACE Division in the NWAFC. Population assessment methods for crab are described in Otto (1986).

Although size-at-age determinations are uncertain for snow crab, crab were separated into age classes using the following carapace width-at-age tables for _C. opilio_ and _C. bairdi_ commonly used by crab biologists at the NWAFC. (J. Reeves, NWAFC, pers. commun. May 1988):

	Carapace width (mm)	
Age	C. opilio	C. bairdi
0	<5	<9
1	5-24	9-34
2	25-39	35-49

3	40-59	50-69
4	60-74	70-84
5	75-94	85-104
6+	$\geq$ 95	$\geq$105

Ice edge locations were estimated from ice edge atlases published by the Joint Ice Center (1981, 1984, and 1985) at the Naval Polar Oceanography Center in Suitland, MD which rely principally on satellite imagery for the observations. In each year, the chosen ice edge location was determined to be the last observed southernmost ice edge extent during spring before the permanent ice retreat.

RESULTS

Geographic Distribution of Crab Consumption by Year

In all 3 yr, red king crab were consumed by cod in the area bounded by 165°00'W in the west and 58°30'N in the north. The areas where Pacific cod consumed red king crab are shown in Figures 2-4. Bottom depths ranged from 31 to 100 m at stations where red king crab were consumed. Dates when red king crab were found in stomachs were from May through July. There was no noticeable trend over years with regard to areas where legs were consumed versus areas where whole red king crab were eaten.

The percentage by weight of legs in the diet of cod at each station was generally less than 25% for all 3 yr. The percentage of whole king crab eaten at each station seemed to decrease from 1981 to 1985.

The geographic distribution of _C. opilio_ and _C. bairdi_ snow crabs in Pacific cod stomachs during 1981, 1984, and 1985 are shown in Figures 5-7. The figures also show the approximate ice edge location before the final ice retreat for each year. In 1981, small percentages (<25% by weight) of

C. bairdi were found in Pacific cod stomachs around the Pribilof Islands and also at bottom depths of 50-100 m in the area southeast of the Pribilofs (Fig. 5). In contrast, this species was consumed over a much broader area of the southeastern Bering Sea shelf during 1984 and 1985 (Figs. 6 and 7). C. bairdi also appeared in stomach contents of cod caught near the shelf edge at 200 m, even in areas northwest of the Pribilof Islands. This species was encountered in stomach contents throughout the sampling period of May through September.

In general, consumption of C. opilio did not overlap much geographically with the areas where C. bairdi were consumed except near the Pribilof Islands. Most C. opilio were eaten north of the Pribilof Islands in a broad band encompassing depths from 35 to 200 m, although the highest percentages by weight in Pacific cod stomachs seemed to be in the middle shelf area with bottom depths of 50 to 100 m. In 1981, high percentages by weight of C. opilio appeared in the diet north of 59°00'N, corresponding with the location of the ice edge before its retreat in that year. While the southward extension of predation appeared to go down to 57°30'N in 1984, the percentages by weight in the diet were not as high as in 1981. In 1985, cod diets were composed of fairly high percentages by weight of C. opilio as far south as 56°30'N; the ice edge in that year was at approximately the same latitude.

Differences in Diet Composition within Areas by Year and Cod Size

Logistic regression of the frequencies of occurrence for each crab species in the two Pacific cod size groups for 1981, 1984, and 1985 was performed using the BMDPLR routine in the BMDP statistical software package (Dixon 1983); results from the analysis are presented in Table 2. Figures 8-10 show the percent frequencies of occurrence (%FO) and percentages by weight (%W) of each crab species by year and cod size group. The most significant

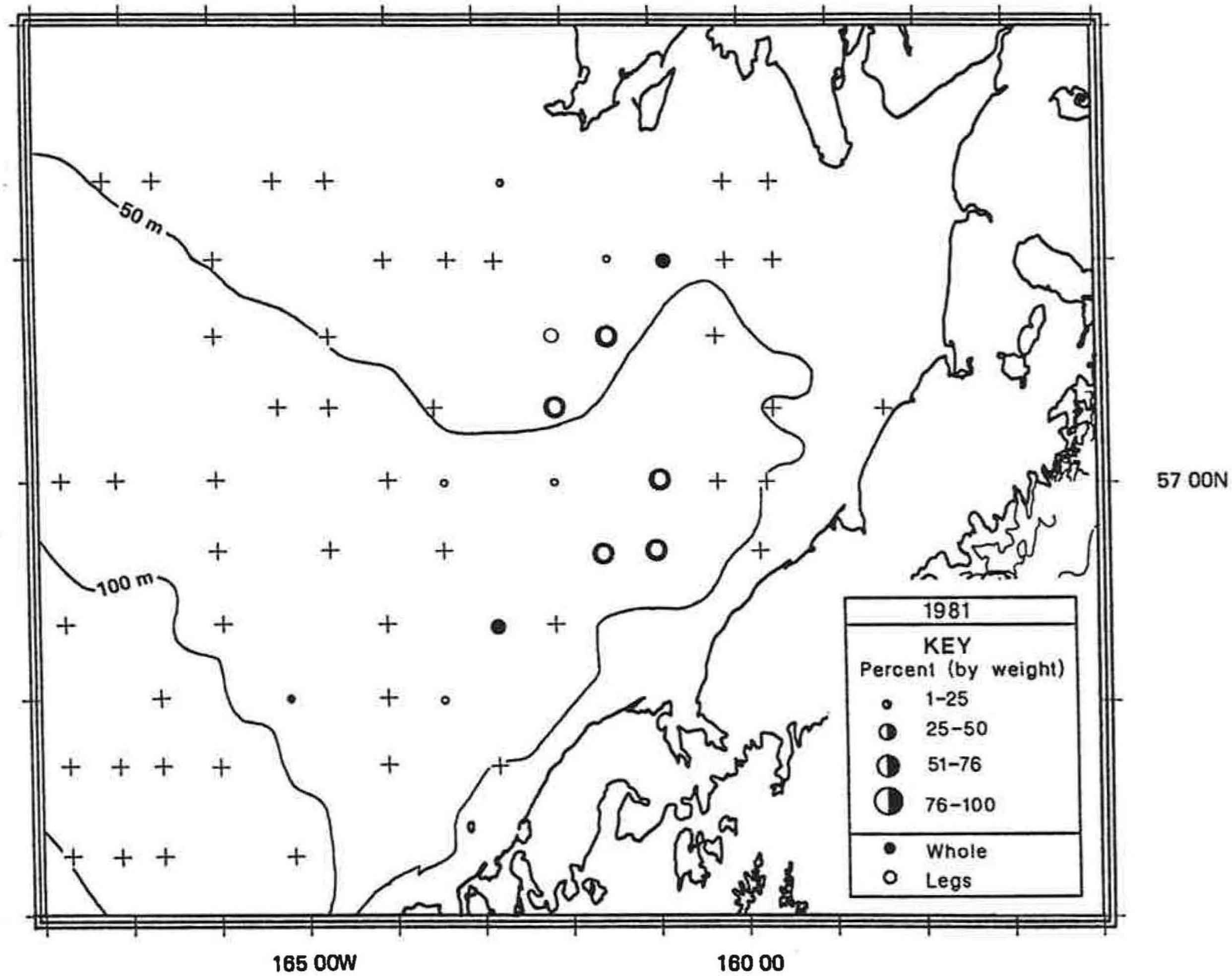

Figure 2.--Percent by weight of red king crab, Paralithodes camtschatica, in Pacific cod stomachs by geographic location in 1981. (Open circles denote percentage by weight of red king crab legs and black circles denote percentage by weight of whole red king crab. +'s are locations where cod were sampled but no red king crab were eaten.)

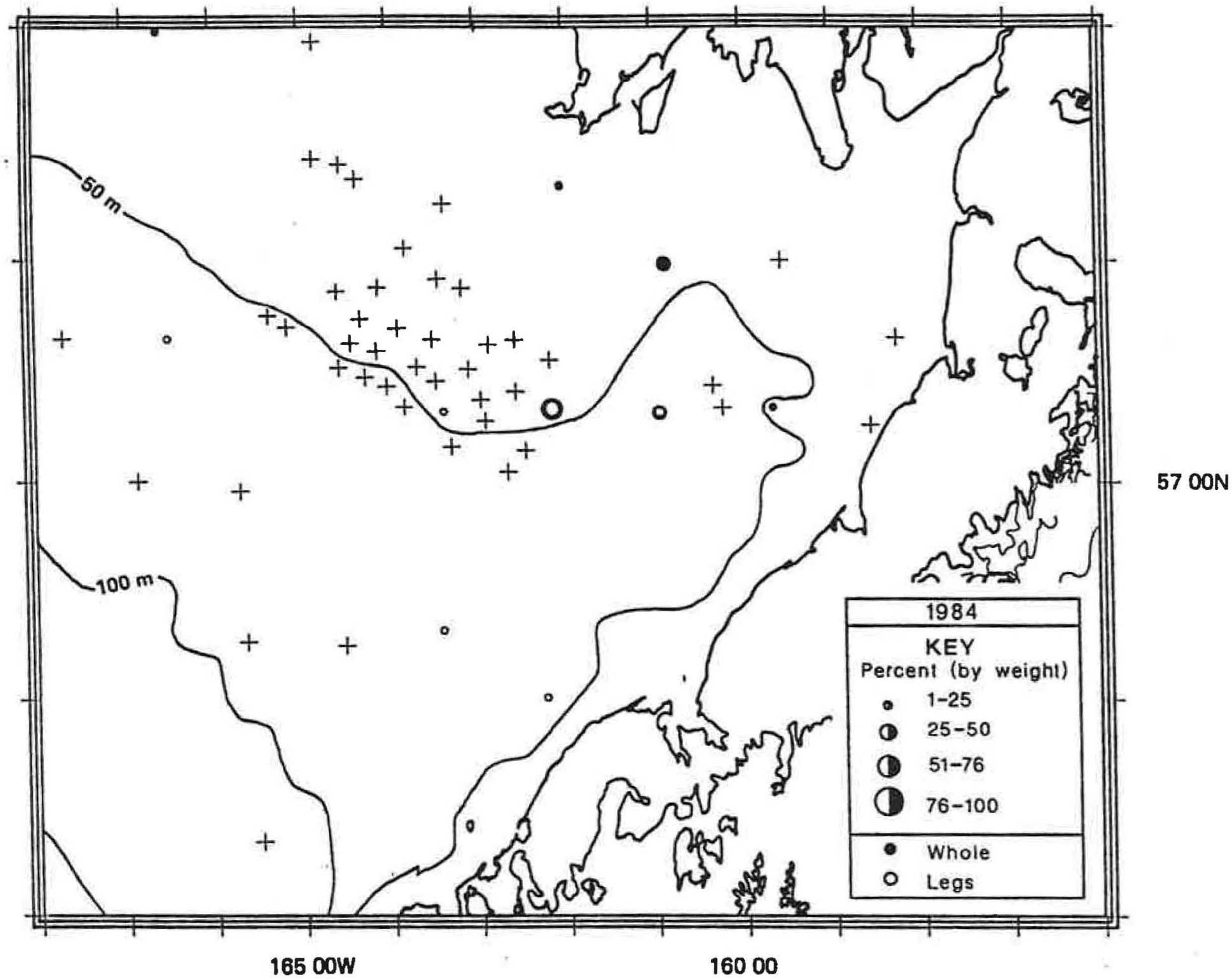

Figure 3.--Percent by weight of red king crab, *Paralithodes camtschatica*, in Pacific cod stomachs by geographic location in 1984. (Open circles denote percentage by weight of red king crab legs and black circles denote percentage by weight of whole red king crab. +'s are locations where cod were sampled but no red king crab were eaten.)

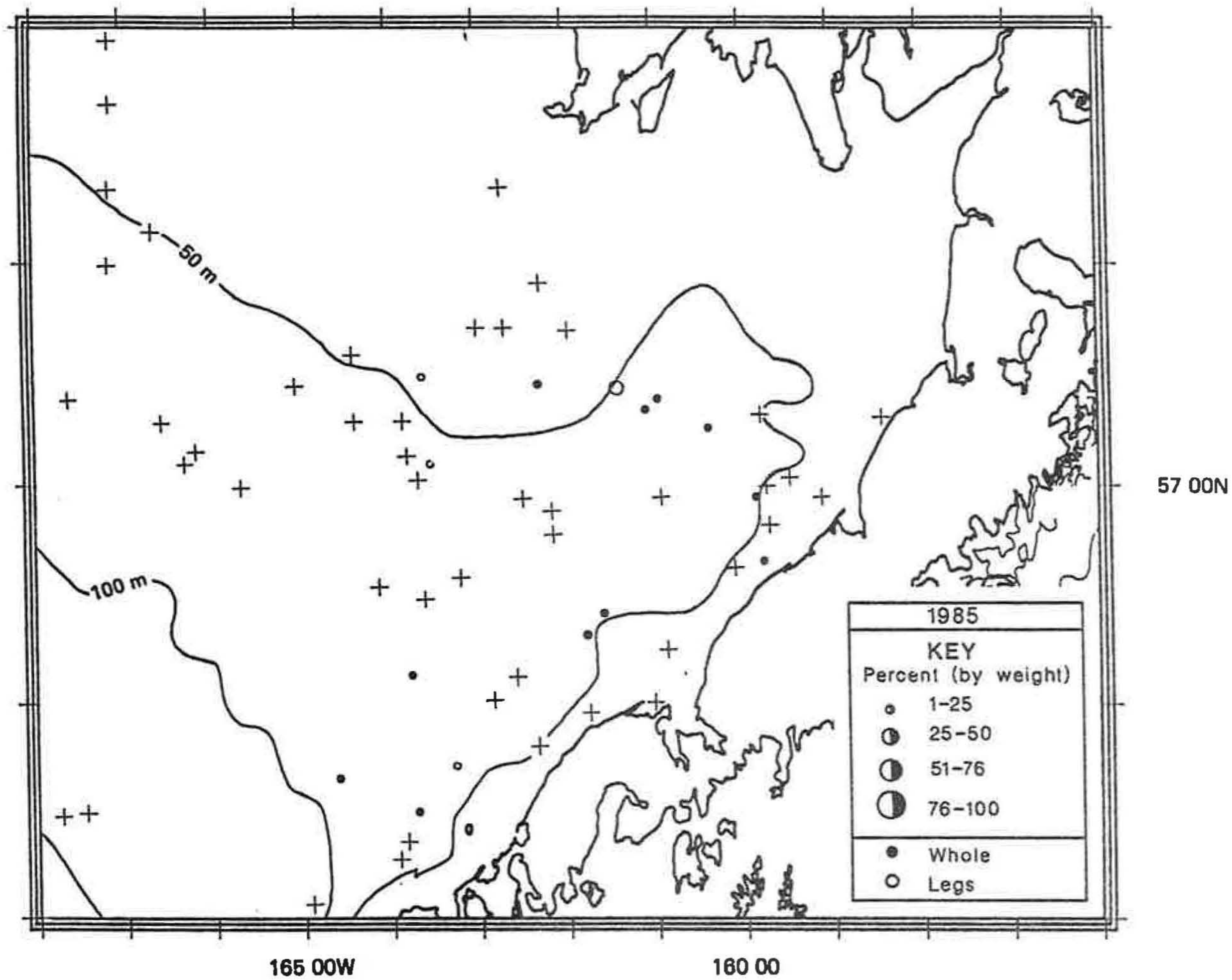

Figure 4.--Percent by weight of red king crab, *Paralithodes camtschatica*, in Pacific cod stomachs by geographic location in 1985. (Open circles denote percentage by weight of red king crab legs and black circles denote percentages by weight of whole red king crab. +'s are locations where cod were sampled but not red king crab were eaten.)

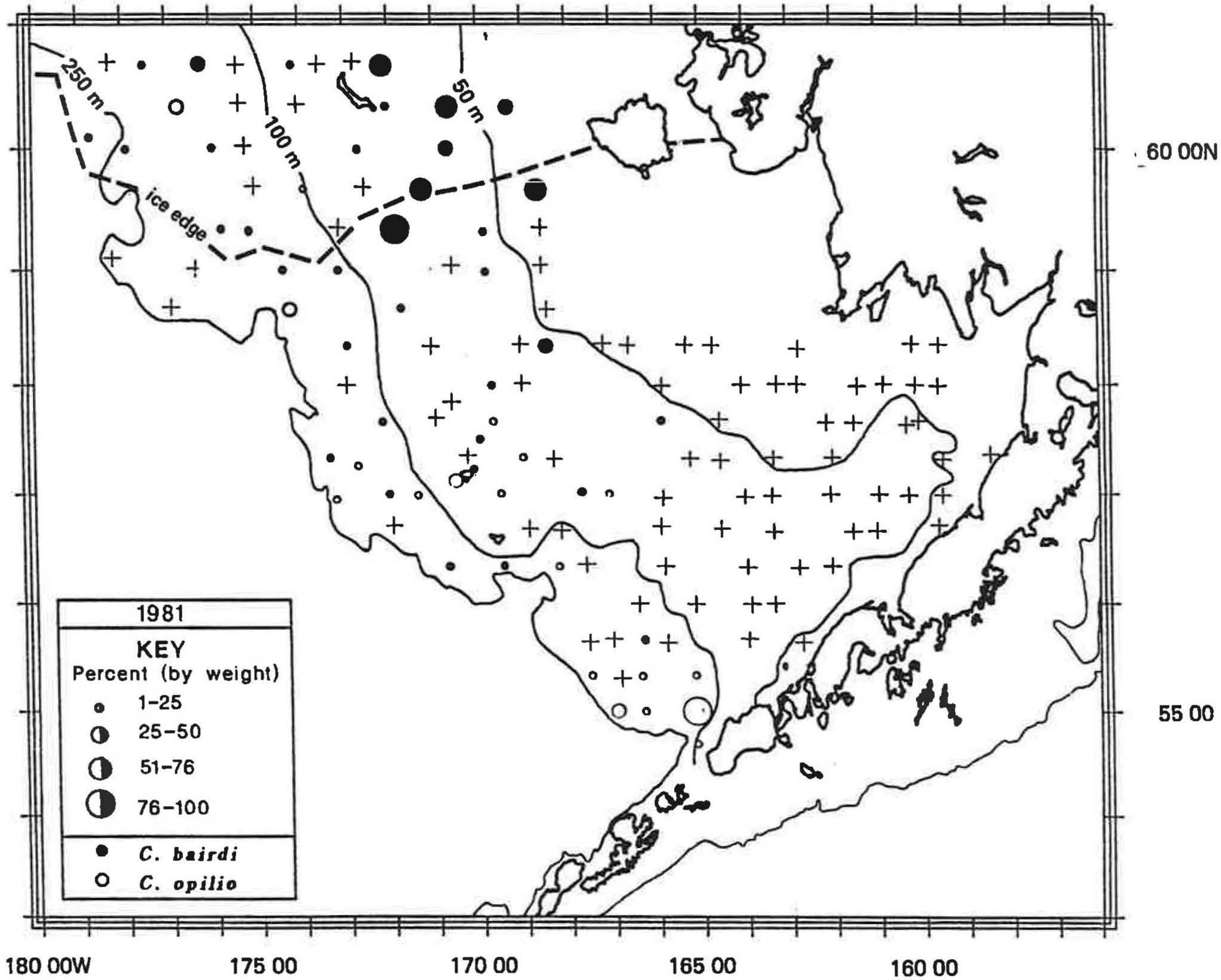

Figure 5.--Percent by weight of Chionoecetes bairdi (open circles) and C. opilio (black circles) in Pacific cod stomachs by geographic location in relation to the ice edge before its last retreat in 1981.

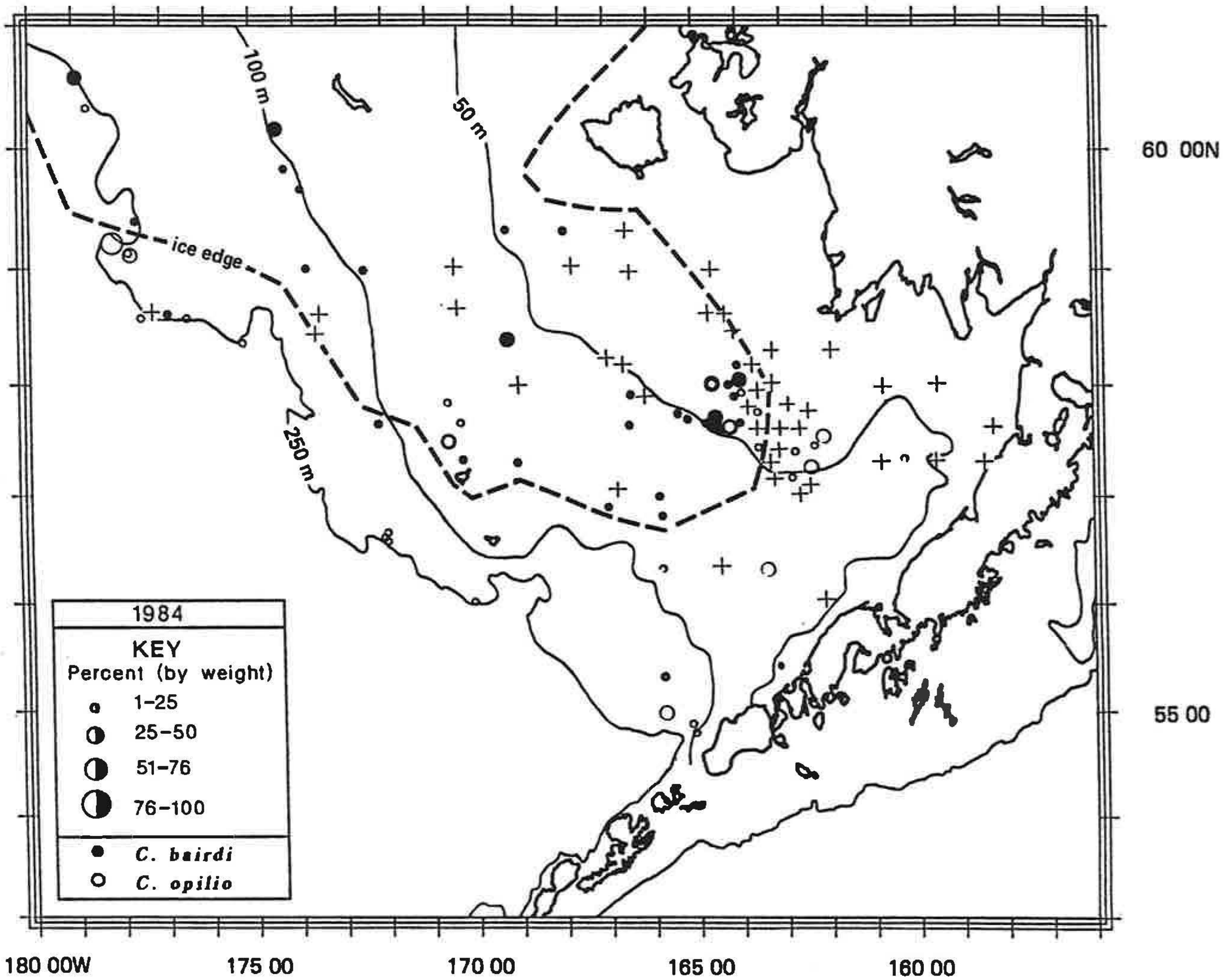

Figure 6.--Percent by weight of Chionoecetes bairdi (open circles) and C. opilio (black circles) in Pacific cod stomachs by geographic location in relation to the ice edge before its last retreat in 1984.

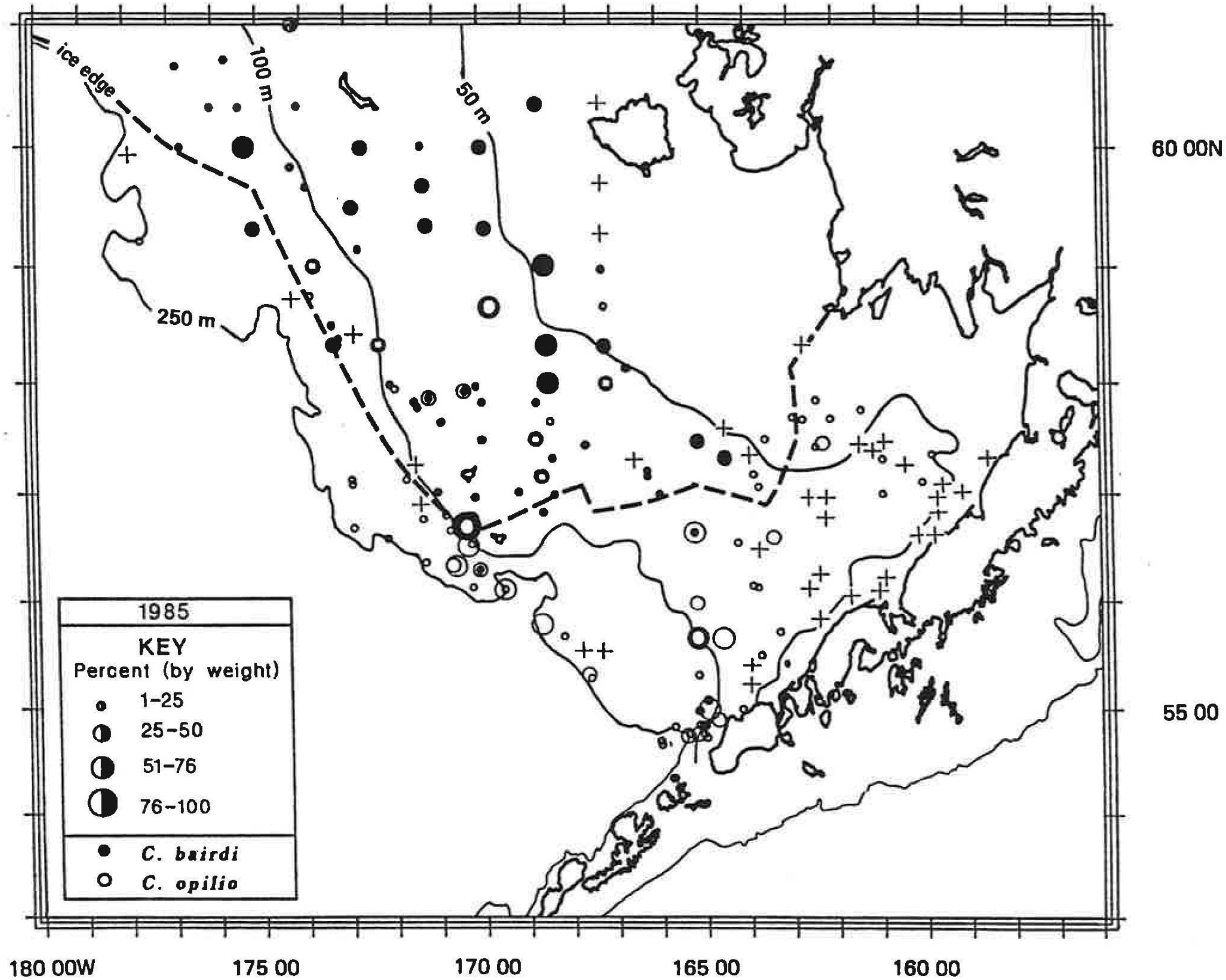

Figure 7.--Percent by weight of Chionoecetes bairdi (open circles) and C. opilio (black circles) in Pacific cod stomachs by geographic location in relation to the ice edge before its last retreat in 1985.

Table 2.--Results from logistic regression of frequencies of occurrence of each crab species against year (1981, 1984, and 1985) and Pacific cod size group (Size 1 = 30-59 cm, Size 2 = ≥60 cm).

Crab species	Chosen model 1/	Model relationship	Goodness of fit Chi-square	Goodness of fit p-value
Paralithodes camtschatica	Size	Size 2 > Size 1	3.58	0.167
	Year	1981 > 1984 >1985		
Chionoecetes bairdi	Size	Size 1 > Size 2	23.378	0.000 2/
C. opilio	Year	1985 > 1984 > 1981	2.379	0.304
	Size	Size 2 > Size 1		

1/ Model chosen at significance level p = 0.05.

2/ Chosen model has a poor fit mainly due to outlier value. Size 2 in 1981 had much lower frequency of occurrence of *C. bairdi* than other cells.

relationship for describing Pacific cod consumption of whole red king crab was Pacific cod size: cod larger than 60 cm contained whole red king crab more frequently than cod 30 to 59 cm in length. Interannual differences in frequency of occurrence of red king crab in stomachs were also significant, showing a decrease in occurrence from 1981 to 1985. Figure 8 shows that the percentages by weight of red king crab in cod stomachs follow similar year and size trends as the percent frequencies of occurrence.

The only significant relationship for the occurrence of *C. bairdi* was fish size; cod 30-59 cm in length contained this crab species more frequently than cod $\geq$60 cm. The chosen model fits these data poorly due to the presence of one anomalous cell: cod $\geq$60 cm in 1981 contained *C. bairdi* much less frequently than any other group. Figure 9 displays the relationship: the anomalous value produces a size-year interaction wherein small cod do not show interannual differences in the occurrence of *C. bairdi* while large cod seem to have an increase in occurrence over time. The percentages by weight also show a size-related difference in *C. bairdi* consumption.

Year was the most important variable describing differences in occurrence of *C. opilio* in cod stomachs: occurrence increased from 1981 to 1985. Size was also significant, with large cod consuming this species more frequently than did small cod. Percentages by weight of *C. opilio* do not show the same trends as strongly as do the frequency of occurrence data (Fig. 10): 1981 and 1984 appear similar and the size-related differences do not look as strong.

Size Frequencies and Sex Ratios of Crab Species

Only 10 red king crab carapace length measurements were taken over all 3 yr due to the advanced digestion state of most of these crabs found in Pacific cod stomachs. Carapace lengths ranged from 53 to 160 mm with

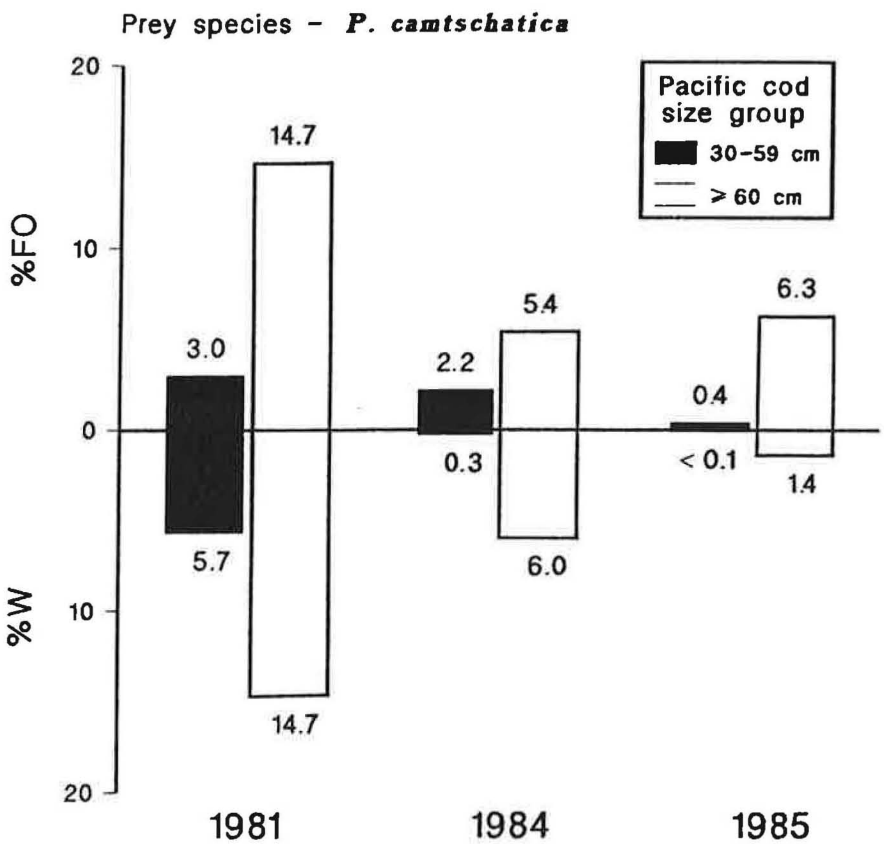

Figure 8.--Percent frequency of occurrence (%FO) and percent by weight (%W) of red king crab, Paralithodes camtschatica, in stomachs of two Pacific cod size groups in the red king crab consumption area during 1981, 1984, and 1985.

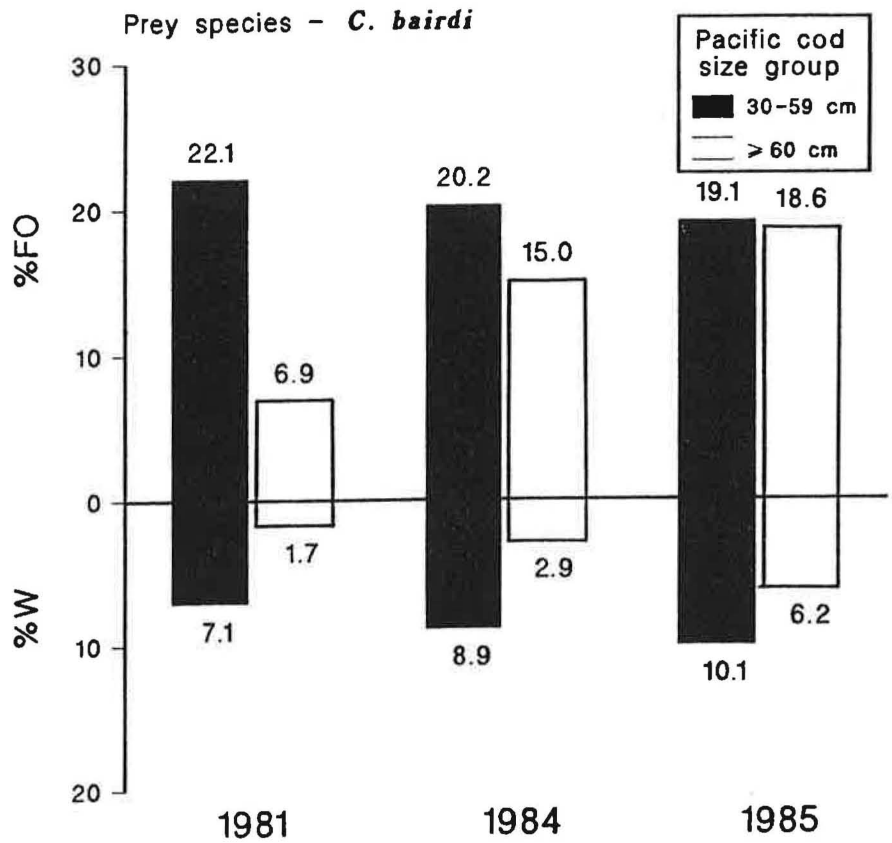

Figure 9.--Percent frequency of occurrence (%FO) and percent by weight (%W) of snow crab, Chionoecetes bairdi, in stomachs of two Pacific cod size groups in the C. bairdi crab consumption area during 1981, 1984, and 1985.

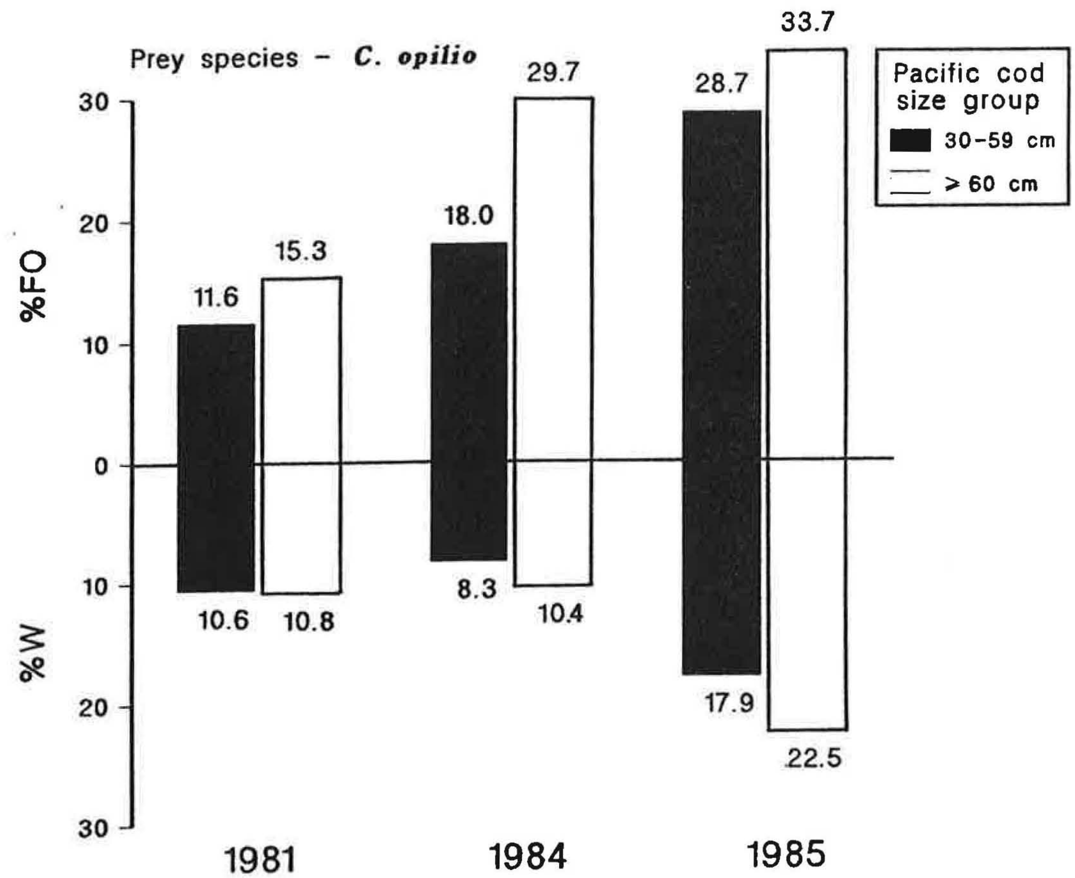

Figure 10.--Percent frequency of occurrence (%FO) and percent by weight (%W) of snow crab, *Chionoecetes opilio*, in stomachs of two Pacific cod size groups in the *C. opilio* crab consumption area during 1981, 1984, and 1985.

an average of 106 mm. Nine out of 10 crabs were larger than 90 mm. Sex was determined for only one specimen which was a female.

Figure 11 shows the size frequency composition of C. bairdi measured from stomachs of the two size groups of Pacific cod for all 3 yr. The Kolmogorov-Smirnov test (Zar 1974) which was used to compare the similarities in these carapace width distributions showed that there was no significant difference ($P > 0.05$) between C. bairdi size distributions consumed by cod 30-59 cm in 1984 and 1985, and no significant difference between C. bairdi consumed by large cod in 1981, 1984, and 1985. All other size frequency distribution comparisons, in particular comparisons between cod size groups within years, showed significant differences. Most C. bairdi in smaller cod (30-59 cm) were <20 mm CW, while large cod consumed crab in the 20-30 mm CW size range. Size distributions of crab <95 mm CW from survey results show size frequency modes at 40 mm CW or greater. In 1981, most crab in the survey were >60 mm CW.

The size frequency distributions of C. opilio measured from cod stomachs are shown in Figure 12. The only size frequency distributions which were not significantly different ($P > 0.05$) from each other were those for smaller cod (30-59 cm) in 1984 and 1985. The size distributions of C. opilio consumed during 1981 by both cod size groups look much different than size distributions for the other 2 yr. Smaller cod during that year ate more crab larger than 30 mm CW than in other years and the modal crab size consumed by large cod (≥60) was also greater (40-50 mm CW) compared to 1984 and 1985. Crab size distributions from the survey show size frequency modes at 40-50 mm CW.

The number of snow crabs sexed and the proportion of female crabs in Pacific cod stomachs and in resource assessment trawl surveys are shown in Table 3. In cod stomachs, the proportions of females for both species of

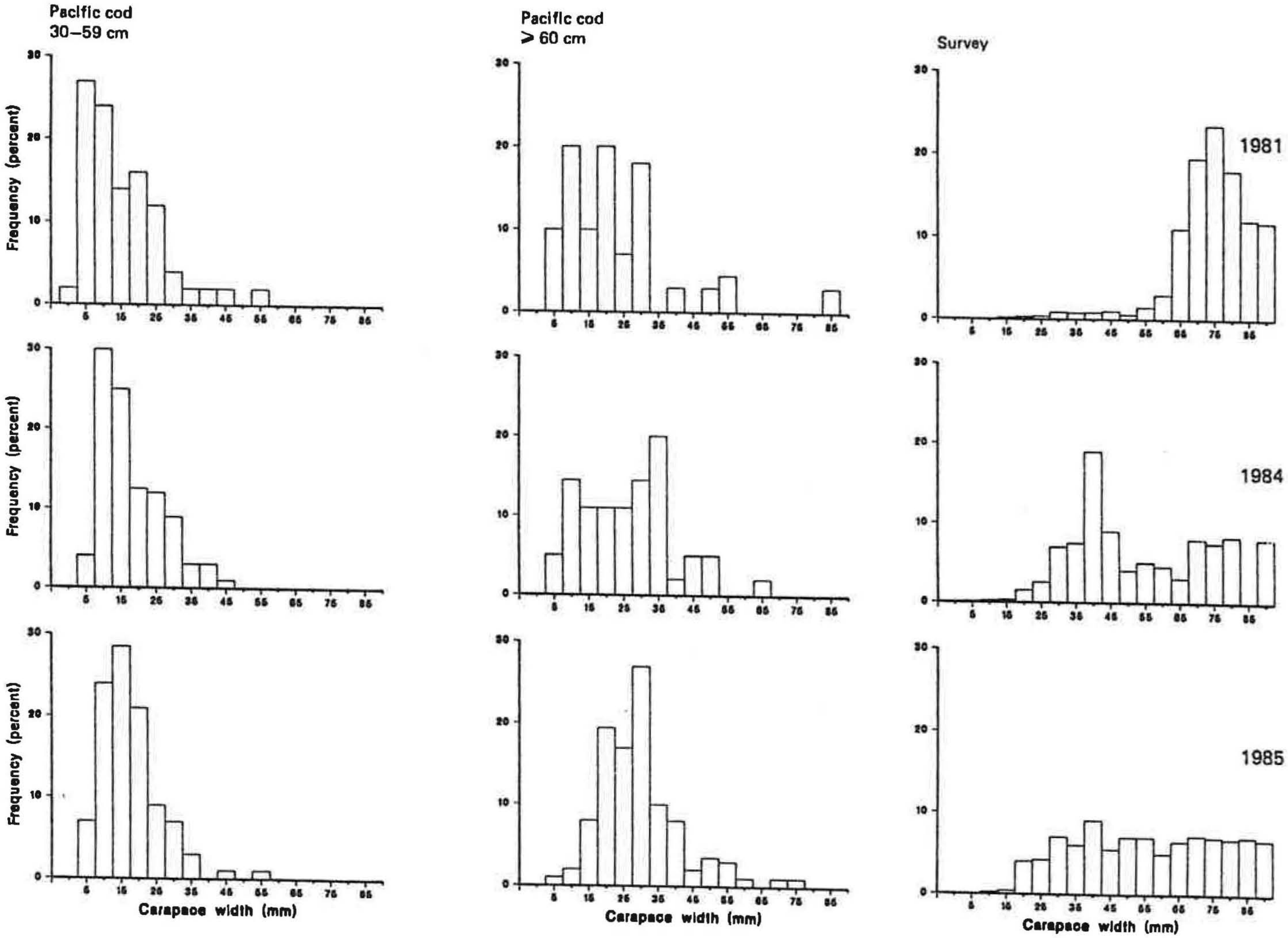

Figure 11.--Relative size frequency distribution of <u>Chionoecetes bairdi</u> in stomachs of two Pacific cod size groups and in the resource assessment survey during 1981, 1984, and 1985.

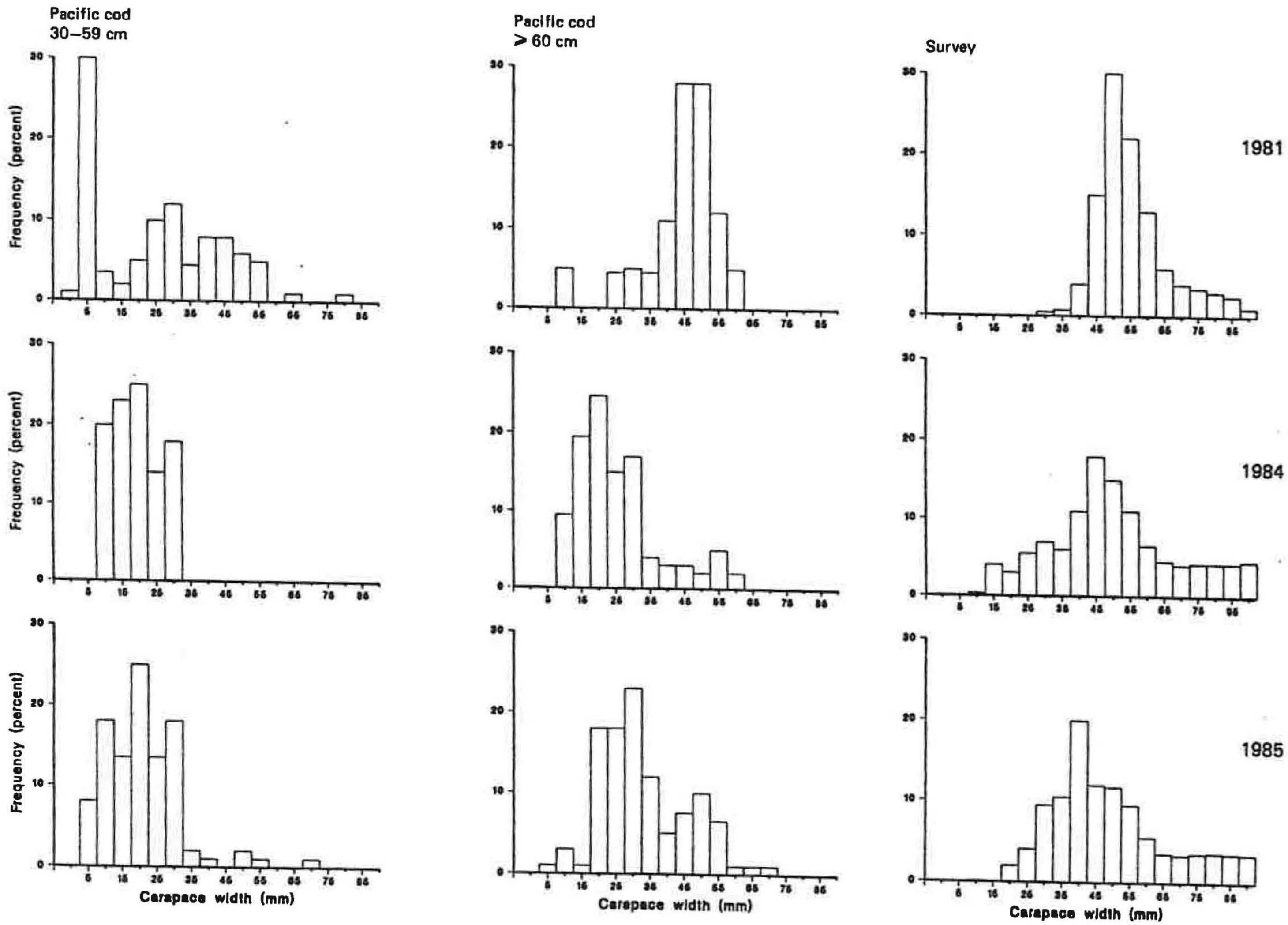

Figure 12.--Relative size frequency distribution of <u>Chionoecetes opilio</u> in stomachs of two Pacific cod size groups and in the resource assessment survey during 1981, 1984, and 1985.

snow crabs during 1981 are much larger than other years. In 1984 and 1985, the proportions of females in cod stomachs are fairly close to 0.5, although only the proportions in 1984 are not significantly different ($P > 0.05$) from 0.5; a test of an even sex ratio. Trawl survey estimates of the proportion of female snow crab <95 mm CW range from 0.43 to 0.67. In some cases the proportion of females observed in stomach contents differed from the proportion estimated from the survey. No trends seem readily apparent except that trawl survey estimated proportions and those in stomach contents are more similar in 1984 and 1985 than during 1981.

Pacific Cod Population Consumption of Crab

Daily ration estimates range from about 0.5 to 0.9% BWD with small cod consuming larger rations as a percentage of their body weight than large cod in a given year (Table 4). Rations for both cod groups were smaller in 1985 than in 1981 and 1984 because of the lower bottom temperature and the large individual prey weight for large cod in that year.

Parameters necessary for calculating population consumption: cod biomass in the prey area, the percentages by weight of each crab species in the diet, and the number of days the crab species is vulnerable to cod predation are presented in Tables 5-7. Total numbers of crab consumed are calculated using the size distribution of crab in cod stomachs previously shown in Figures 11 and 12 and the relationships of carapace width to individual weight for the given crab species.

The calculations for the total amount of red king crab consumed by cod assume that only female crabs are consumed and the period of predation vulnerability during the sampling period is 30 d in May when female crabs are in the soft-shell condition. Further, because of the small number of crabs measured from stomach contents in each year, the average carapace

Table 3.--Total number (N) and proportion of female snow crabs (PF), Chionoecetes bairdi and C. opilio, in Pacific cod stomachs and resource assessment trawl surveys for the years 1981, 1984, and 1985 in the eastern Bering Sea.

		Stomachs		Survey 1/	
Crab species	Year	N	PF	N	PF
C. bairdi	1981	248	.935 2/	651,387	.675
	1984	180	.567 3/	224,225	.645
	1985	817	.557	87,632	.567
C. opilio	1981	77	.857 2/	5,117,773	.640
	1984	165	.557 3/	2,338,571	.510
	1985	512	.607	896,155	.426

1/ Population estimates derived from Resource Assessment and Conservation Engineering Division, Kodiak Laboratory for crab <95 mm CW.

2/ Crab sex was not consistently recorded by stomach analysts during this year.

3/ Observed proportion was not significantly different from 0.5 ($P > 0.05$).

Table 4.--Parameters used to derive daily ration estimates and the estimated daily rations for two size groups of Pacific cod in 1981, 1984, and 1985 in the eastern Bering Sea. (% BWD is percent body weight daily.)

Year	Cod size group	Average weight (g)			Bottom temperature (°C)	Daily ration (%BWD)
		Cod	Individual prey	Cod stomachs		
1981						
	30-59 cm	1,340	1.02	25.1	3.7	0.86
	> 60 cm	4,045	12.31	141.4	3.7	0.66
1984						
	30-59 cm	1,095	0.48	16.7	3.1	0.87
	> 60 cm	4,994	6.55	180.7	3.1	0.80
1985						
	30-59 cm	1,217	1.00	18.7	2.3	0.63
	> 60 cm	5,383	18.67	180.0	2.3	0.47

Table 5.--Parameters used to obtain cod population consumption estimates for Paralithodes camtschatica and the estimated total biomass and numbers consumed by the cod population. (Assuming this species of crab is vulnerable to cod predation for only 30 d of the study period.)

Year	Cod size	Cod biomass (1,000 t)	Percent crab in diet (by weight)	Total biomass crab consumed (1,000 t)	Total number crab consumed (millions)
1981	30-59 cm	118	5.7	1.7	2.00
	> 60 cm	39	14.7	1.1	2.00
				2.8	4.00
1984	30-59 cm	72	0.3	0.1	0.06
	> 60 cm	127	6.0	1.8	2.00
				1.9	2.06
1985	30-59 cm	89	0	-	-
	> 60 cm	103	1.4	0.2	0.20
				0.2	0.20

length of all red king crab measured in a year was used to calculate the total number of crab consumed (1981 = 104 mm CL and 1984-85 = 111 mm CL; corresponding to about age 6 for females). Both total biomass and numbers of red king crab consumed by cod declined from 1981 to 1985 by a factor of 10.

Table 6 shows the total amount of *C. bairdi* consumed by cod during the 153-d sampling period in each year. Removals in terms of total weight and numbers of this species decreased slightly from 1981 to 1984 and increased about threefold from 1984 to 1985. Although the total biomass of *C. opilio* consumed by cod dropped during 1984 compared with 1981 and 1985, the total number of crab consumed increased over the whole time period, reflecting the smaller sizes of crab consumed in 1984 and 1985.

Total numbers by age of *C. bairdi* and *C. opilio* consumed are shown in Figures 13 and 14. Most *C. bairdi* consumed are age 1, and ages 0, 2, and 3 are also represented. This figure does not show the small amount (3 million) of age 5 crab eaten in 1981 or the 5 million age 4 crab eaten during 1985. Cod consumption of *C. opilio* is mainly directed at crab of ages 1-2. More *C. opilio* of ages 3-4 are eaten than *C. bairdi*.

DISCUSSION

The geographic distribution of cod predation on red king crab corresponds to the main area of red king crab abundance from NMFS resource assessment trawl surveys. These surveys produce relatively precise abundance estimates for crab greater than 75 mm CL (Otto 1986) which is the size range of red king crab consumed by cod in this study. However, the areas of cod predation on snow crab show interannual variation which does not match areas of adult abundance determined from NMFS trawl surveys, probably because the trawls used in these surveys do not catch the small crabs (<40 mm CW) which are the sizes

Table 6.--Parameters used to obtain cod population consumption estimates for <u>Chionoecetes bairdi</u> and the estimated total biomass and numbers consumed by the cod population. (Assuming this species of crab is vulnerable to cod predation during the whole 153 d of the study period.)

Year	Cod size	Cod biomass (1,000 t)	Percent crab in diet (by weight)	Total biomass crab consumed (1,000 t)	Total number crab consumed (billions)
1981	30-59 cm	122	7.1	11.4	2.71
	> 60 cm	140	1.7	2.4	0.10
				13.8	2.81
1984	30-59 cm	51	8.9	6.0	0.91
	> 60 cm	164	2.9	5.8	0.31
				11.8	1.22
1985	30-59 cm	224	10.1	21.8	3.87
	> 60 cm	246	6.2	11.0	0.51
				32.8	4.38

Table 7.--Parameters used to obtain cod population consumption estimates for <u>Chionoecetes opilio</u> and the estimated total biomass and numbers consumed by the cod population. (Assuming this species of crab is vulnerable to cod predation during the whole 153-d of the study period.)

Year	Cod size	Cod biomass (1,000 t)	Percent crab in diet (by weight)	Total biomass crab consumed (1,000 t)	Total number crab consumed (billions)
1981	30-59 cm	274	10.6	38.2	1.72
	> 60 cm	136	10.8	14.8	0.28
				53.0	2.00
1984	30-59 cm	100	8.3	11.0	2.00
	> 60 cm	164	10.4	20.9	1.29
				31.9	3.29
1985	30-59 cm	185	17.9	31.9	4.06
	> 60 cm	173	22.5	28.0	1.03
				59.9	5.09

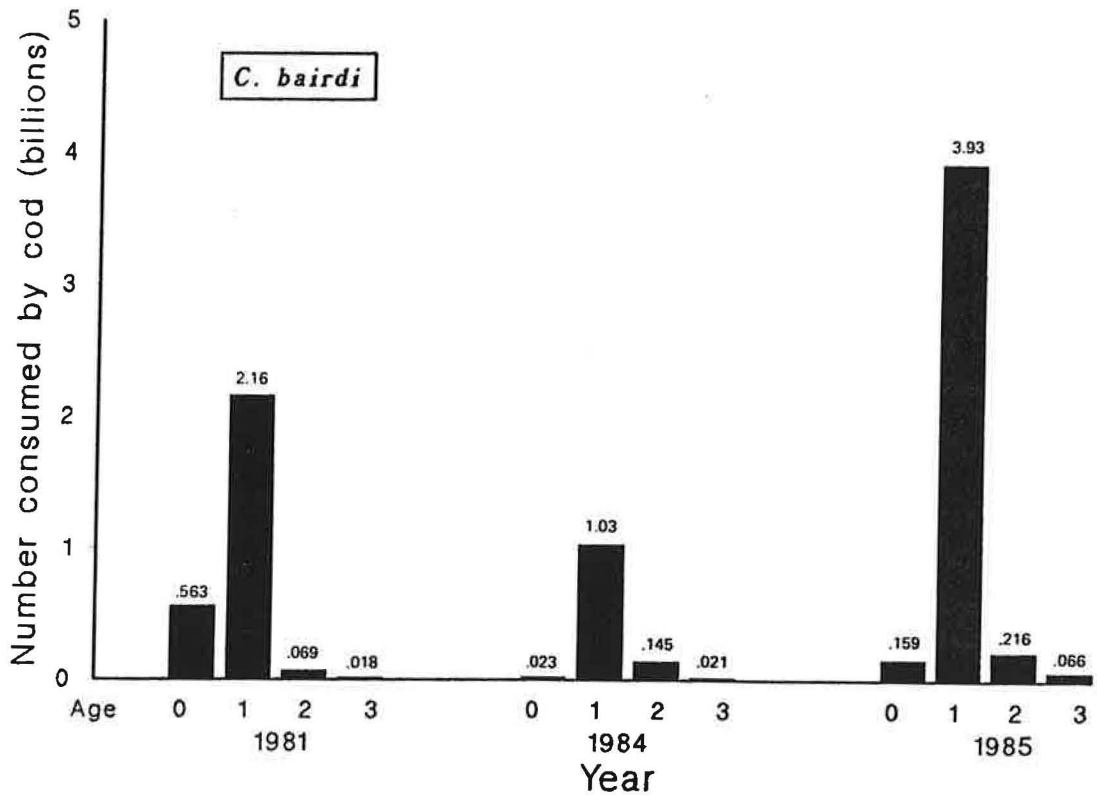

Figure 13.--Total number by age group of Chionoecetes bairdi consumed by the Pacific cod population in 1981, 1984, and 1985.

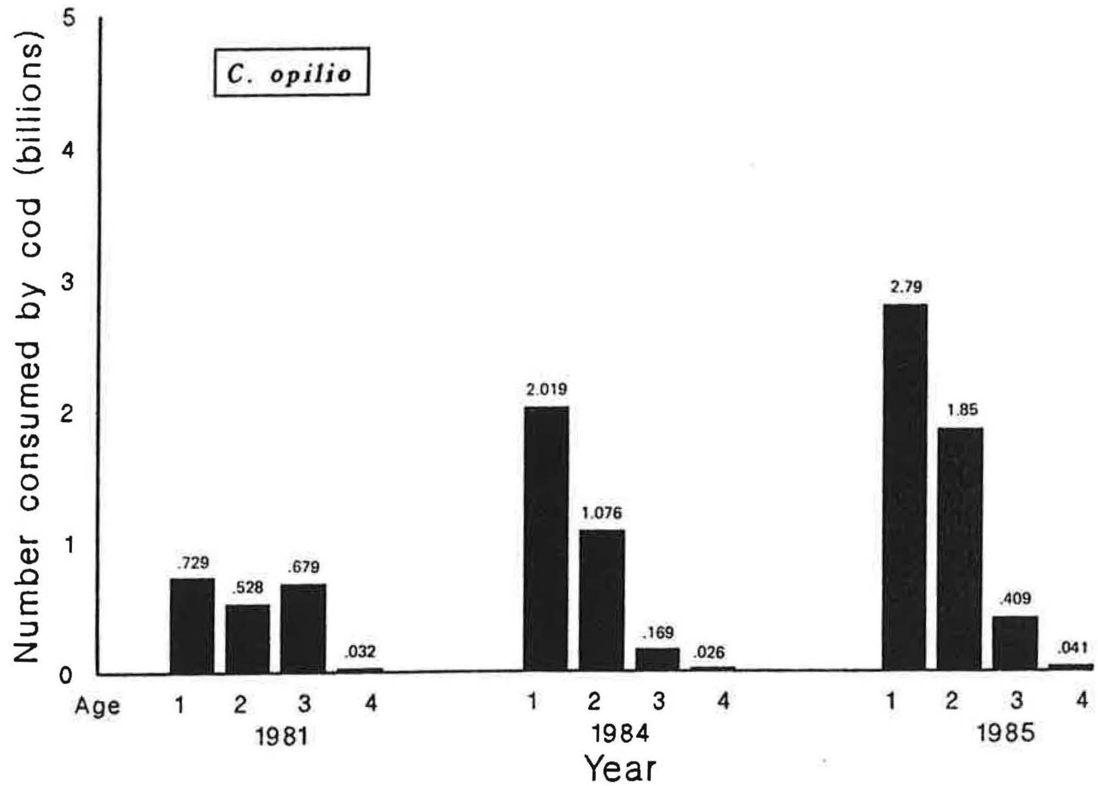

Figure 14.--Total number by age group of Chionoecetes opilio consumed by the Pacific cod population in 1981, 1984, and 1985.

consumed most by cod (Figs. 11-12). Surveys show most adult C. bairdi to be east and southeast of the Pribilof Islands in 1981, 1984, and 1985, while cod stomach contents show no small C. bairdi east of 165°00'W in 1981. Similarly, surveys showed high densities of C. opilio >95 mm CW as far south as the Pribilofs in 1981, whereas most small C. opilio eaten by cod were much farther north in that year. The geographic distribution of snow crab predation by cod was much different in 1981 than in the other two years and the more northerly location of the ice edge in that year relative to 1984 and 1985 (Figs. 5-7) suggests an environmental relationship between C. opilio distribution and physical factors. Somerton (1981, 1982) postulated a direct relationship between spring ice cover and planktonic larval survival of C. opilio in order to explain observed high recruitment to the adult population of yearclasses which may have been in the plankton and benefited from the associated ice edge production during 1971 and 1972 in the eastern Bering Sea. Instead of a relationship between ice cover and planktonic survival, however, our data suggest that ice cover in a given year may also indicate the areal extent of juvenile C. opilio in the same year. Since benthic dwelling juveniles would not benefit directly from an ice edge bloom, the ice edge in a particular year may be an indicator for another environmental variable such as bottom temperature. Figure 15 shows the average bottom temperature at stations where C. opilio and C. bairdi were found in cod stomachs during the 3 yr of this study. The average bottom temperatures were significantly different ($P < 0.05$) for the locations where the two species were found for all 3 yr and C. opilio were found in areas where the bottom temperature was about 3°C or less. Somerton (1981) reported the weighted average bottom temperature at stations where C. opilio occurred in 1979 was less than 3°C when the weights used were crab abundance. In that

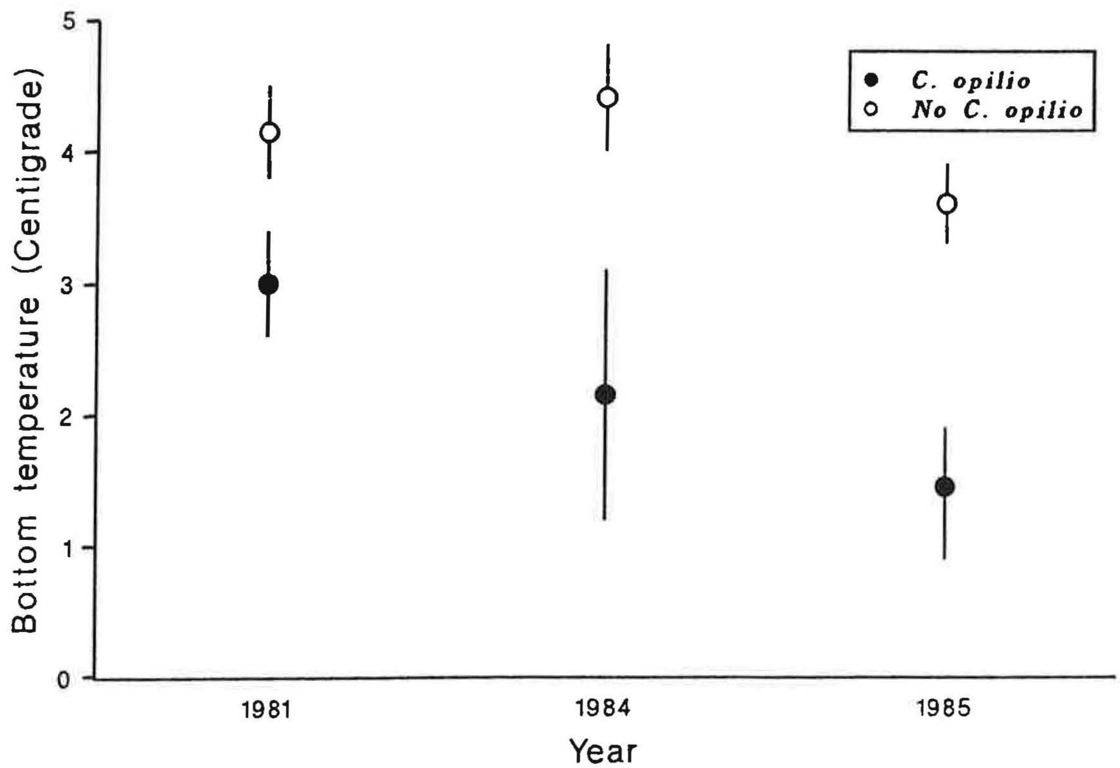

Figure 15.--Mean bottom temperature (°C) and 95% confidence intervals at locations where Pacific cod consumed Chionoecetes opilio (black circles) and at locations where Pacific cod did not contain C. opilio (open circles) in 1981, 1984, and 1985.

year, juveniles less than 40 mm CW had that highest abundances per station, indicating that the temperatures really apply to the juvenile portion of the population. In the northwest Atlantic, Brethes et al. (1987) found bottom temperatures less than 3°C to be the most significant factor in determining the spatial distribution of juvenile C. opilio less than 40 mm CW in the Gulf of St. Lawrence. Thus, the geographic distribution of juvenile C. opilio appears to depend mostly on bottom temperature; highest densities are found in areas where bottom temperatures are less than 3°C and those areas may be a significant portion of the eastern Bering Sea shelf in cooler years.

Diet Composition by Year and Cod Size

Analysis of frequencies of occurrence of red king crab in cod stomachs through logistic regression shows that cod size is the most important factor in determining consumption of whole red king crab; the frequency of occurrence was significantly greater in cod larger than 60 cm FL. Blau (1986) found that Pacific cod which presumably had consumed soft-shell female king crabs in the Kodiak region of the Gulf of Alaska ranged in size from 45 to 79 cm FL. That study, however, did not examine differences in frequency of occurrence within that size range and none of the crab eaten were whole. Interannual differences in red king crab consumption were significant in our study, decreasing from 1981 to 1985. NWAFC abundance estimates for the female portion of the red king crab population show a corresponding trend with a decrease in numbers from 103.6 million in 1981 to 13.7 million in 1985. This suggests that individual cod predators responded to decreases in crab density by consuming less crab.

Although logistic regression of C. bairdi frequencies of occurrence showed cod size as an important variable, the model fit was poor due to the low frequency of crab occurrence in cod >60 cm FL in 1981. If the percentages by weight are examined (Fig. 9), the size relationship looks clearer; smaller cod consistently ate more than large cod and the interannual changes within size groups showed consistent small increases across years. This interannual trend opposes population estimates of C. bairdi less than 95 mm CW from NMFS surveys which show a decrease in abundance from 651 million in 1981 to 87.6 million in 1985. However, the surveys are not able to provide precise estimates of crab less than 40 mm CW not only due to escapement through trawl meshes but also because snow crab less than 100 mm CW have a greater tendency to bury themselves in bottom sediments (Conan and Maynard 1987), which would reduce their vulnerability to trawl capture. If cod respond to changes in C. bairdi density as they appear to do for red king crab density, then our data suggest the possibility of stable or slight increases in juvenile C. bairdi population numbers for crab less than 40 mm CW over the 3 study years. The similarity of C. bairdi size distributions in cod stomachs for the 3 yr within each cod size group further supports the suggestion of stable juvenile (<40 mm CW) C. bairdi population size distributions over time.

The model which best explains C. opilio consumption by cod shows year as the most important variable (with consumption increasing over years) and size as the next important variable (with larger cod consuming C. opilio more frequently than small cod). Again, NMFS survey estimates of C. opilio population size for crab less than 95 mm CW show an inverse trend of numbers with year: decreasing from 5 billion in 1981 to 896 million in 1985. If the occurrence of juvenile crab less than 40 mm CW in cod diets can be used as a measure of juvenile crab abundance in the survey area, then our data show a probable increase in juvenile C. opilio abundance from 1981 to 1985. Waiwood and Elner (1982) similarly suggested that the increase in Atlantic cod (Gadus morhua) predation on snow crab observed in 1980 and 1981 in the Gulf of St. Lawrence in the northwest Atlantic was due to increased availability of small crabs. The size frequency distributions of C. opilio in cod stomachs also indicate more C. opilio <35 mm CW in 1984 and 1985 than in 1981 at least in the survey area. Somerton (1981) showed that large numbers of C. opilio juveniles exist north of 61°00'N, an area which was not sampled in this study. It is possible that in colder years such as 1984 and 1985, an influx of juvenile C. opilio from these northern areas could enter southeastern Bering Sea shelf waters and become more available to cod. Thus, the observed downward shift in mean size and increased numbers of C. opilio in cod stomachs may not be the result of actual increases in juvenile C. opilio abundance but might be the result of southerly shifts in the geographic distribution of small juveniles in colder years.

Because of the large carapace lengths of red king crab consumed by cod (50-160 mm CL), the well-digested nature of red king crab in stomachs, the usual occurrence of whole crab only around May, and the fact that one red king crab's sex was determined to be female, we have assumed that Pacific cod are consuming soft-shell females which molt in Bristol Bay around April to May (Hayes 1983). It seems highly unlikely that cod could consume whole crab of those carapace lengths in a hard-shell condition. Blau (1986) also found cod consuming red king crab during the king crab molting period in the Gulf of Alaska. Since male red king crab molt in winter while migrating to the mating grounds (Powell and Nickerson 1965), our assumption that only soft-shell females are consumed in spring seems supportable. This does not rule out the possibility that cod may consume soft-shell males during winter. However, our winter sampling coverage is limited and has not detected this type of occurrence.

With the exception of 1981, when stomach analysts did not consistently record snow crab sex, the proportions of female juvenile snow crabs in stomach contents are close to 0.5 and are not significantly different from a 1:1 ratio of females to males in 1984. Adams (1979) reviewed the literature on C. opilio and found that the early life history of males and females are similar with respect to size, growth, distribution, and habitat. Brethes et al. (1987) found sex ratios of C. opilio <30 mm CW in the northwest Atlantic to be 1:1 with no spatial segregation of sexes. The proportions of female snow crabs <95 mm CW in the NMFS assessment surveys are close to 0.5 in most years. Thus, cod do not appear to be selecting snow crab on the basis of sex and are probably preying randomly on individuals on the basis of crab size.

Pacific Cod Population Consumption of Crab

Daily rations derived using the Ursin et al. (1985) model for incorporating prey size effects on gastric evacuation rate appear reasonable compared with estimates of daily ration for Atlantic cod from areas with bottom temperatures higher than the eastern Bering Sea; our estimates ranged from 0.47 to 0.86 %BWD and estimates for Atlantic cod of similar sizes range from 0.5 to 1.0 %BWD in the North Sea (Daan 1973), 1.6 to 2.0 %BWD in the Faroe plateau (Jones 1978), and 0.5 to 1.9 %BWD on Georges Bank (Durbin et al. 1983). Livingston et al. (1986) calculated daily ration for Pacific cod using the Elliott and Persson (1978) model without correction for prey size effects using a subset of the data presented in this paper and obtained values of 0.31 %BWD for cod <55 cm FL and 1.30 %BWD for cod >55 cm FL which, when compared by those researchers with approximate growth data, indicated that rations for small cod were too small to account for growth and rations for large cod were seemingly too large. The current approach seems to correct for the deficiencies in the previous estimates and produces ration values which are not so divergent for the two cod size groups.

Other parameters involved in estimating population consumption are also subject to error: predator biomass estimates, the percentage of prey items in the predator's diet, and the number of days the crab species is vulnerable to predation. NMFS survey estimates of cod biomass have 95% confidence intervals in recent years of 12-18% of the mean biomass estimate (Thompson and Shimada 1987), a minimum confidence interval due to the assumptions of complete vulnerability and catchability of cod to bottom trawls. Cod also perform seasonal onshore-offshore migrations (Wespestad and Shimada 1984), a factor not taken into consideration here that could change the biomass of cod in a particular area over the time period in this study. Errors in diet composition parameters can arise from insufficient sample sizes, uneven spatial distribution of samples, and possible diet changes over space and time scales not considered in this study. Sampling effort for cod stomachs was widely distributed over the whole shelf area during 1981 and 1985 but some areas were not sampled well during 1984 (Fig. 1). We have attempted to reduce bias in diet composition estimates (which may arise from uneven stomach sample sizes within areas) by averaging diet percentages estimated for each 20 nmi wide square where stomachs were sampled within a crab consumption area. A similar practice has been adopted in the North Sea stomach sampling program which provides diet composition estimates for a multispecies virtual population analysis model (Mehl 1986). In this study we have estimated consumption which occurred only during May through September, so the estimated numbers of snow crab consumed by cod only apply to that portion of the year. Livingston et al. (1986) have shown that Pacific cod in the eastern Bering Sea consume snow crab throughout the whole year; therefore, the estimates presented in this paper can be considered mainly as indexes of the total numbers consumed by cod. There is also great uncertainty about the size at age for crabs and our allocation of crab size groups to age classes should be considered approximate.

Impact on Crab Populations

As mentioned in the Introduction, predation mortality rate of a prey population must increase with prey population size in order to demonstrate that a predator population is regulating the size of the prey population (Holling 1959). NMFS resource assessment surveys provide annual estimates of female red king crab abundance which can be compared with the total cod population removals of female red king crab in the same year (Fig. 16). Both the female red king crab population and the estimated removals by cod from the population follow the same pattern of linear decline. Removals, expressed as a percentage of the population, are 3.8%, 2.8%, and 1.4% for the years 1981, 1984, and 1985, respectively; this indicates that direct density-dependent mortality is not occurring over the time period. The declining percentages removed actually indicate indirect density-dependent mortality over time which appears to be mainly due to the functional response of individual cod to declining prey populations (i.e., a decline in the average amount of crab per predator with a decline in crab population). Thus, at least over the range of female red king crab population sizes considered here, it appears that cod predation is not responsible for the observed declines in female red king crab populations from 1981 to 1985. The percentages removed by cod form a small and declining part of the total population decline. Since the period of red king crab vulnerability to cod predation for the present study only included 30 out of a possible 60 days

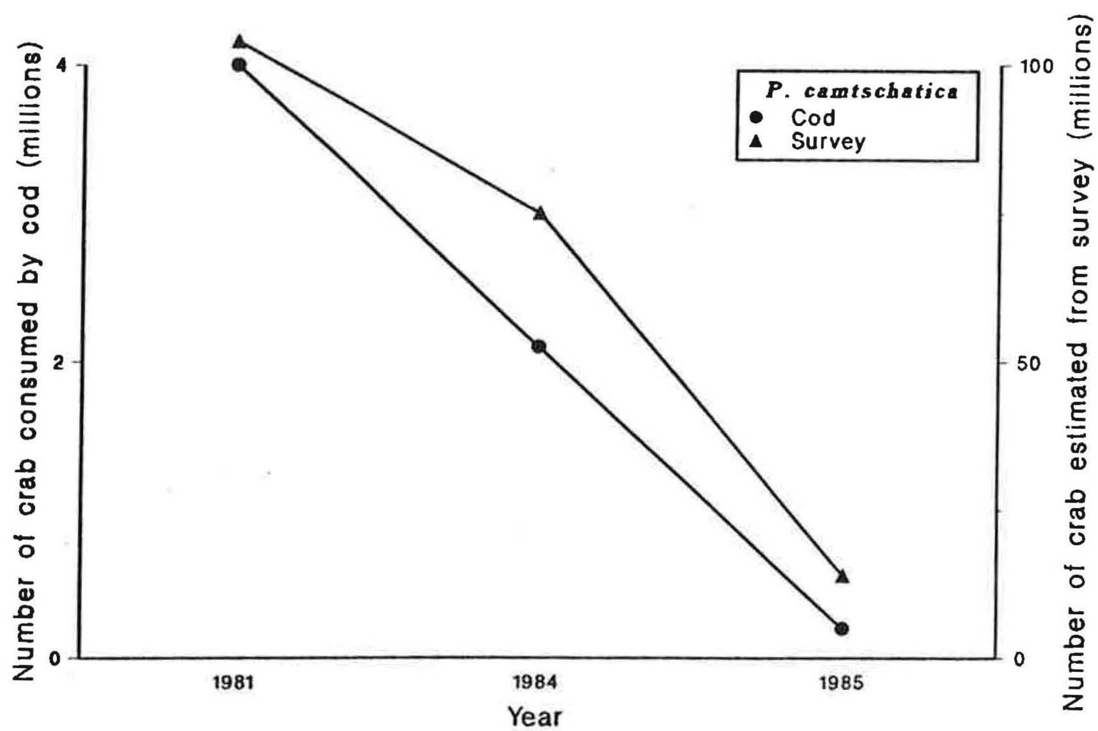

Figure 16.--Total number of red king crab, Paralithodes camtschatica, eaten by the Pacific cod population during 1981, 1984, and 1985 compared with resource assessment estimates of the total female red king crab population during the same years., (Note different y-axis scales.)

when red king crab females are in the soft-shell condition, the estimated removals could be doubled to approximate total annual amounts removed by cod. This would affect the percent removals in each year by a factor of two but would not change the seemingly indirect density-dependent relationship between crab removals and crab population size.

A similar comparison cannot be made directly for cod consumption of the two snow crab species since cod are consuming mostly age 1 crab which are not well estimated in NMFS research surveys. However, the numbers of age 1 snow crab eaten in a particular year can be compared to the number of age 3 crab collected 2 yr later in NMFS research surveys which should be more precise (Figs. 17 and 18). Although the curves of age 1 crab consumed and number of age 3 crab found 2 yr later in the trawl surveys appear to be somewhat similar in shape for C. bairdi for the 3 yr, the estimated numbers of age 1 crab consumed in a particular year are about two orders of magnitude greater than the numbers of age 3 crab found 2 yr later. The numbers of age 1 crab in the population can be reconstructed as in Forney (1977) by adding the number remaining at age 3 to the number of age 1 eaten by cod. If removals by cod are calculated as a percent of the reconstructed population size then the values obtained for 1981, 1984, and 1985 are 84.4%, 95%, and 94%, respectively. These are substantial portions of the estimated age 1 population and could be an indication of overestimation of the population consumption by cod or underestimation of age 3 numbers by research trawl surveys. A similar comparison with C. opilio removals by cod at age 1 with trawl survey estimates of numbers remaining at age 3 shows that numbers remaining at age 3 are greater than those eaten at age 1 during 1981 and 1985. Percentages removed of the reconstructed age 1 cohort would be 28%, 57%, and 27% for 1981, 1984, and 1985, respectively. These percentages are overestimates since substantial

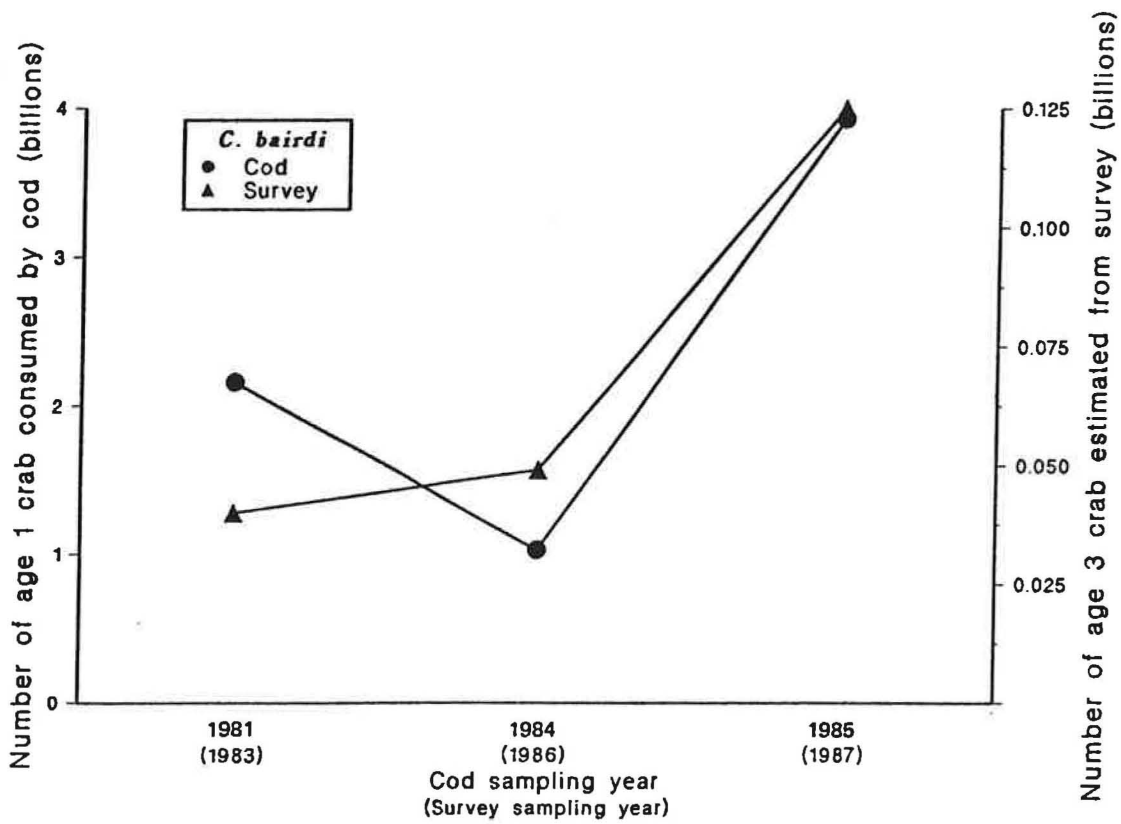

Figure 17.--Total number of age 1 Chionoecetes bairdi snow crab eaten by the Pacific cod population during 1981, 1984, and 1985 compared with resource assessment estimates of the age 3 population in 1983, 1986, and 1987. (Note different y-axis scales.)

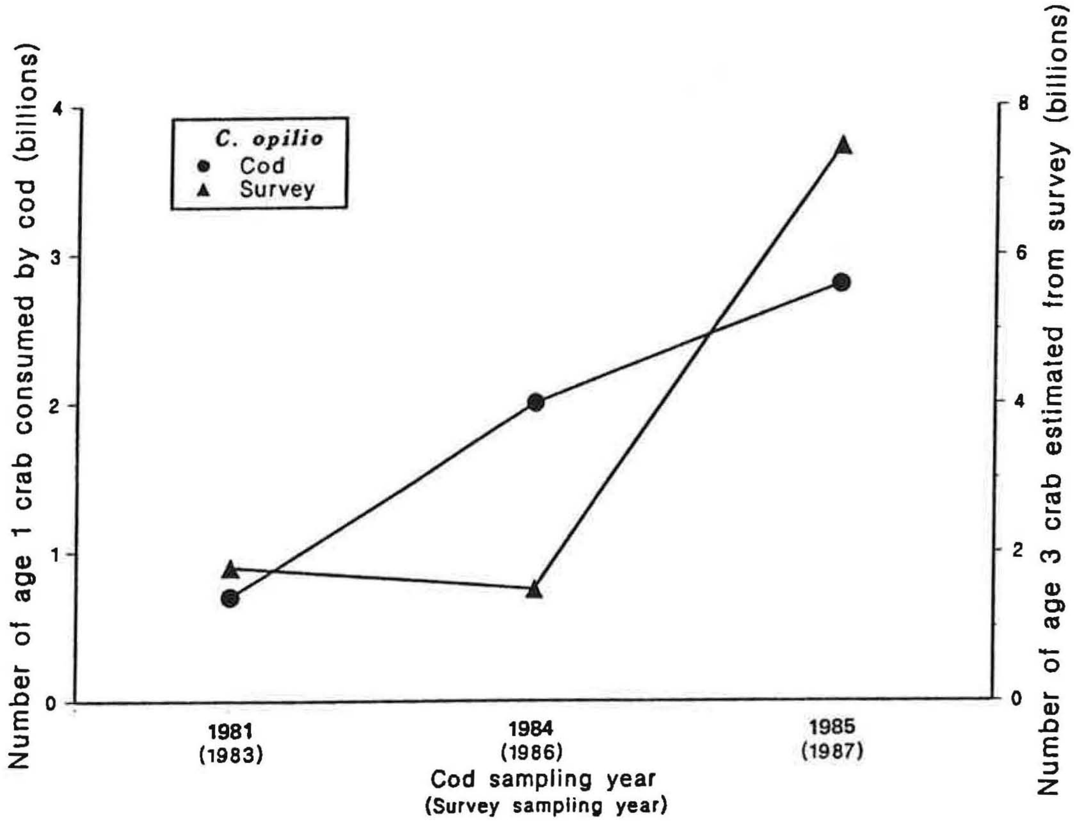

Figure 18.--Total number of age 1 Chionoecetes opilio snow crab eaten by the Pacific cod population during 1981, 1984, and 1985 compared with NWAFC resource assessment estimates of the age 3 population in 1983, 1986, and 1987. (Note different y-axis scales.)

numbers of age 2 C. opilio are also eaten (Fig. 14) but not included in the reconstructed population estimate.

Although these estimates are subject to many sources of error as discussed above, the high predation mortality rates of juvenile crab found here may not be unrealistic. Using food habits data to quantify predation removals, multispecies virtual population analysis of North Sea fish stocks produced average annual instantaneous predation mortality coefficients ranging from 0.2 to 1.8 for age 1 fish in the model (Daan 1987). Large interannual differences in predation mortality coefficients were observed within fish species, suggesting that predator populations were exerting density dependent control on some year classes. Similarly, our study has shown the possibility of large predation removals of mostly age 1 snow crabs and some interannual variation in the percentages removed. The impact on C. bairdi seems greater than on C. opilio, at least for age 1 crab. C. bairdi are also more vulnerable to cod predation because of their high spatial overlap with cod populations whereas unknown portions of the C. opilio juvenile population are north of the main survey area and the main center of their distribution may shift south into areas populated by cod in some years. Analysis of a longer time series of cod predation data may help locate abundant crab year classes and allow us to track their numbers over time. There is uncertainty about the growth patterns of juvenile snow crabs, and following size class modes in cod stomach data in succeeding years may provide more clues to these growth patterns. Further, although this study does not attempt to explain factors influencing early life history survival it does suggest that predation is an important factor influencing survival of ages 1 and 2 snow crab.

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