

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

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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 crabs, *Chionoecetes bairdi* and *C. opilio*. Soft-shell female red king crab were consumed during spring in Bristol Bay. Estimates of percentages of female red king crab standing stock consumed by the Pacific cod population were 3.8%, 2.8% and 1.4% 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. Predation mortality of *C. bairdi* by cod was estimated to be about 84%, 95%, and 94% of the population of age 1 crab during 1981, 1984, and 1985, respectively. Annual predation removal 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. Although these calculations indicated that cod may consume large proportions of the age 1 snow crab populations, the estimates are tentative partly because of uncertainties in reconstructing the population numbers of age 1 crab.

The results also indicate that *C. bairdi* are more vulnerable to cod predation because of their high spatial overlap with cod populations, whereas an unknown fraction of the *C. opilio* juvenile population is north of the main survey area and does not overlap with cod. Results from this study suggest that predation by cod may be an important factor influencing survival of ages 1 and 2 snow crab in the eastern Bering Sea.

Pacific cod, *Gadus macrocephalus*, biomass in the eastern Bering Sea has increased by about 800,000 t over the last decade primarily because of two strong year classes spawned in 1978 and 1979. Stock biomass levels have been about 1 million metric tons since 1982 and a growing domestic fishery for this species is responsible

for most of the catch (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; Blau 1986; Livingston et al. 1986), 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 decreased by an order of magnitude from a maximum of 365 million crab in 1977. Otto (1986) suggested reasons for the decline including 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. Pacific cod may also be implicated in the decline of red king crab abundance in the Kodiak region of the Gulf of Alaska (Blau 1986) and in the disappearance of certain year classes of *C. opilio* snow crab in the eastern Bering Sea (Incze and Schumacher 1986). Although circumstantial evidence has implicated Pacific cod predation in these crab population declines, direct evidence is so far lacking.

The regulation of prey population size by a predator requires that prey mortality rate increase with prey population size (direct density-dependent mortality, Holling 1959). Thus examination of changes in Pacific cod diet with changes in crab population abundance is necessary to determine whether the rate of cod predation on crab changes when crab abundance changes. Total removals of crab by cod need to be estimated and compared with crab population size. If percentage of removal of crab by cod alters with changes in crab density, then cod predation is a likely density-dependent factor regulating crab population size.

I examined the interannual trends in Pacific cod predation on three commercially important crab species in the eastern Bering Sea: red king crab, *C. opilio*, and *C. bairdi*. Three years of Pacific cod food habits data from 1981, 1984, and 1985 were analyzed to determine 1) the areas

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where crab predation occurred, and whether this changed with time in response to environmental variables; 2) changes in the percentage 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 were compared with the size distribution and population levels of crab estimated from annual research surveys to determine whether cod exerted density-dependent control over crab population size.

METHODS

Sample Collection and Laboratory Analysis

Stomachs were collected from 4,023 Pacific cod (30–107 cm fork length (FL)) during the three years (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 occurred throughout the 24 h day in 1984 and 1985 and from 0600 to 2000 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

later 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. If carapaces were intact, 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 ≥ 60 cm FL. Previous studies (Livingston et al. 1986) 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 ≥ 60 cm in length. Thus, the food habits and daily ration need to be examined separately for the two size groups of cod.

Logistic regression, using the BMDPLR routine in the BMDP statistical software package (Dixon 1983), was performed to determine which major factors (predator size and year) were important in describing variation in predation by cod on a particular crab species. The dependent variable was the presence or absence of a crab species in cod stomachs from two cod size groups (Size 1 = 30–59 cm, Size 2 = ≥ 60 cm) during the three sampling years (1981, 1984, and 1985). The most parsimonious model was chosen for describing predation on each crab species using the criteria that 1) only factors that resulted in a significant improvement ($P < 0.05$) in model fit be added and, 2) the overall model goodness of fit chi-square be nonsignificant ($P > 0.05$), indicating that the model provided a good fit to the data. In addition, BMDPLR permitted

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) ¹	Number of stomachs			Sampling platform
				30–59 cm	≥ 60 cm	Total	
1981	5/23–8/3	145	0600–2000	1,130	527	1,657	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	1,576	research vessels foreign commercial vessels

¹ADT is Alaska daylight time.

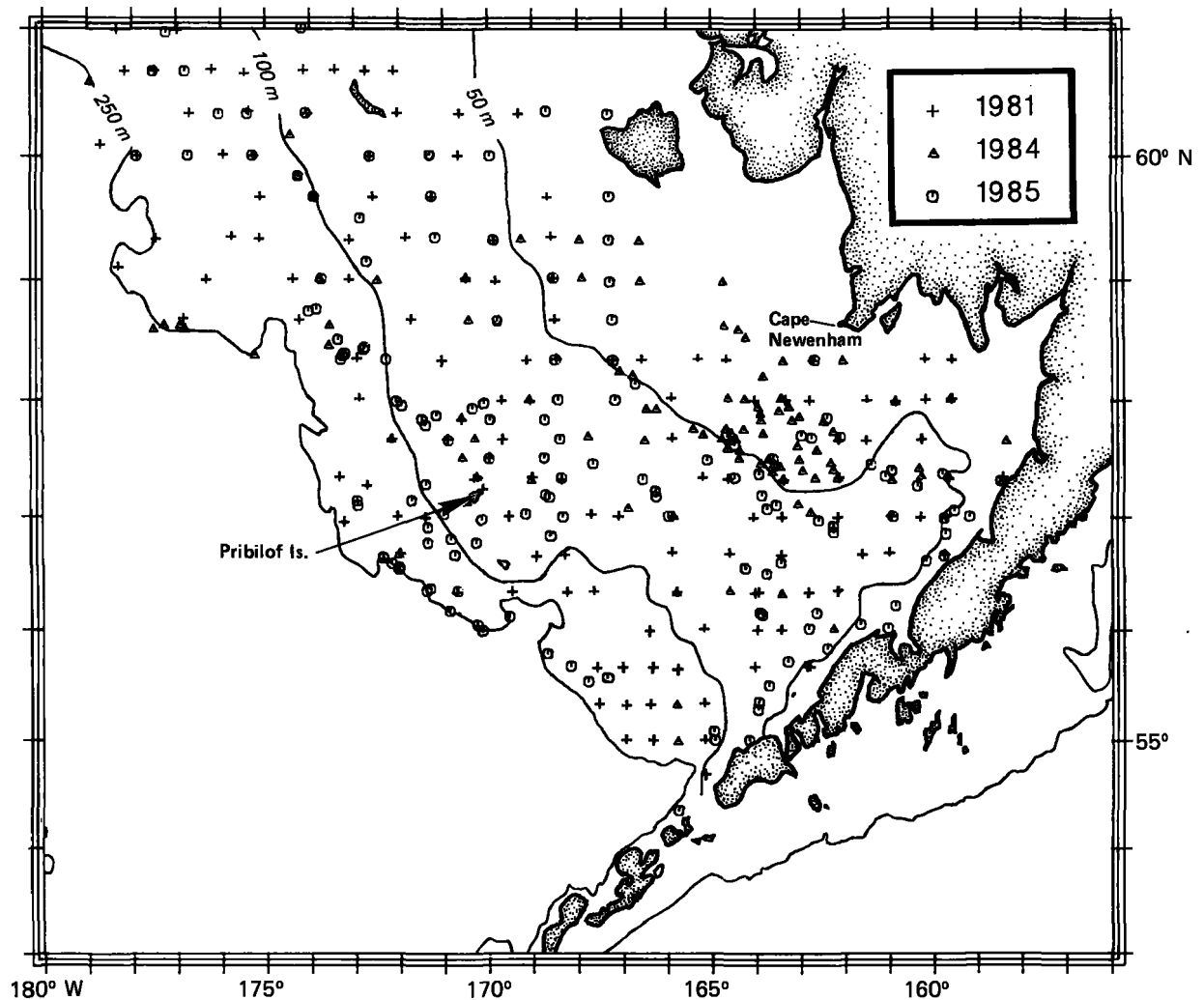


FIGURE 1.—Haul locations where Pacific cod, *Gadus macrocephalus*, stomach samples were taken during 1981, 1984, and 1985 in the eastern Bering Sea.

significance tests of the relationship between levels of each factor, so that a description of which predator sizes and sampling years had higher occurrences of crab predation could be presented.

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):

$$C_i = DR_i \cdot D \cdot B_i \cdot P_i \quad (1)$$

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 proportion of body weight daily, BWD) of cod size group i , D is the number of days in the sampling period of May through Sep-

tember when crab were vulnerable to predation, 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 .

The areas of crab consumption by cod were derived by plotting the areal distribution of the percentage 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 (P) 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 percentage 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. Since cod sometimes consume only the legs of red king crab, these stomachs were not included in the estimation of P because this behavior may not contribute to predation mortality.

Because recent studies indicate that individual prey size or weight is a more important factor influencing gastric evacuation rates in fish than prey type (Ursin et al. 1985; Jobling 1987), 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 mean individual prey weight (w) in grams, and bottom temperature (T) in °C:

$$R = aS \quad (2)$$

where $a = a_0 w^{a_1}$ and $a_0 = a_{00} e^{0.096T}$ and where $a_0 = 0.61 d^{-1}$, $a_{00} = 0.33$, and $a_1 = -0.36$ for North Sea temperatures were adjusted for the Bering Sea using the average bottom temperature for Pacific cod stations sampled in each year from expendable bathythermographs obtained at most stations.

The number of days (D) when snow crab were vulnerable to predation was considered to be the whole sampling period of May through September (153 days) because predation on hard-shell juveniles of both species has been shown to occur throughout this period (Livingston et al. 1986). Although the Pacific cod's diet contains large amounts of snow crab during other times of year, geographic distribution of samples taken in other periods was not sufficient to include in the current study. Because red king crab in the hard-shell state are very spiny, cod probably consume adults only when they are in the soft-shell state. During the period sampled in this study, only female red king crab are molting (males molt earlier in the year), and their molt extends only through May of the study period ($D = 30$).

Pacific cod biomass was estimated using data collected simultaneously with stomach collections 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/nmi² 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 length-frequency information from resource assessment surveys. Total biomass for each cod size group could then be calculated as the sum of the CPUEs multiplied by the area of 20 nmi wide square (400 nmi²).

Population estimates and size distributions of crab from assessment surveys were provided by Robert Otto¹. 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. Reeves²).

Age	Carapace width (mm)	
	<i>C. opilio</i>	<i>C. bairdi</i>
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+	≥95	≥105

Ice edge locations were taken from ice edge atlases (Joint Ice Center 1981, 1984, and 1985). These data come principally from satellite imagery. In each year, I chose the last observed southernmost ice edge extent during spring before the permanent ice retreat.

RESULTS

Geographic Distribution of Crab Consumption by Year

In all three years, red king crab were consumed by cod in the crab consumption-area bounded by long. 165°00'W in the west and lat. 58°30'N at depths of 31-100 m (Fig. 2). Red king crab were found in stomachs from May through

¹R. Otto, Kodiak Laboratory, RACE, Northwest Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Kodiak, AK 99615, pers. commun. 1986.

²J. Reeves, Northwest Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98115, pers. commun. May 1988.

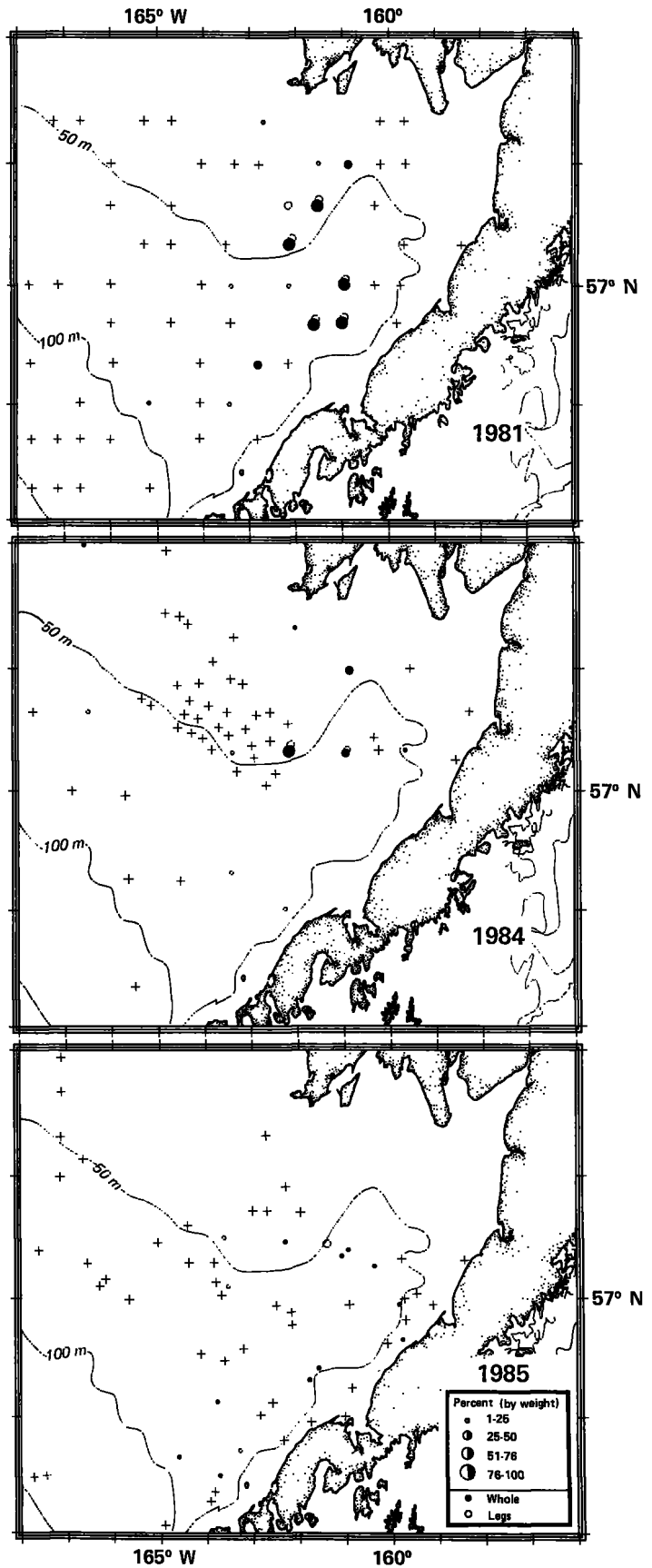


FIGURE 2.—Percentage by weight of red king crab, *Paralithodes camtschatica*, in Pacific cod stomachs by geographic location in 1981, 1984, and 1985. (Open circles denote percentage by weight of red king crab legs and black circles denote percentage by weight of whole red king crab. +'s are locations where cod were sampled but no red king crab were eaten.)

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 years. 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* in Pacific cod stomachs during 1981, 1984, and 1985 are shown in Figure 3. The figure also shows 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. In contrast, this species was consumed over a much broader area of the southeastern Bering Sea shelf during 1984 and 1985. *Chionoecetes 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 50–100 m. In 1981, high percentages by weight of *C. opilio* appeared in cod 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

Results of logistic regression of the frequencies of occurrence for each crab species in the two Pacific cod size groups for 1981, 1984, and 1985 are presented in Table 2. The most significant 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 30–59 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. Percentages by weight and frequency of occurrence of red king crab in cod stomachs followed similar year and size trends (Fig. 4).

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	Main factors chosen ¹	df	Improvement		Relationship among factor levels ²
			Chi-square	P value	
<i>Paralithodes camtschatica</i>	Size	1	29.549	0.000	Size 2 > Size 1
	Year	2	11.960	0.003	1981 > 1984 ≥ 1985
	Residual (goodness of fit)	2	(3.578)	(0.167)	
<i>Chionoecetes bairdi</i>	Size	1	14.832	0.000	Size 1 > Size 2
	Residual (goodness of fit)	4	(23.378)	(0.000) ³	
<i>C. opilio</i>	Year	2	81.699	0.000	1985 > 1984 > 1981
	Size	1	10.341	0.001	Size 2 > Size 1
	Residual (goodness of fit)	2	(2.379)	(0.304)	

¹Main factors chosen ($P < 0.05$) are shown in order of entry into the model.

²Determined from significance and sign of between-level contrasts.

³Chosen model has poor fit due to one anomalous cell: Size 2 in 1981 had much lower frequency of occurrence of *C. bairdi* than other cells. (Year was not significant.)

LIVINGSTON: PACIFIC COD PREDATION ON THREE CRAB SPECIES

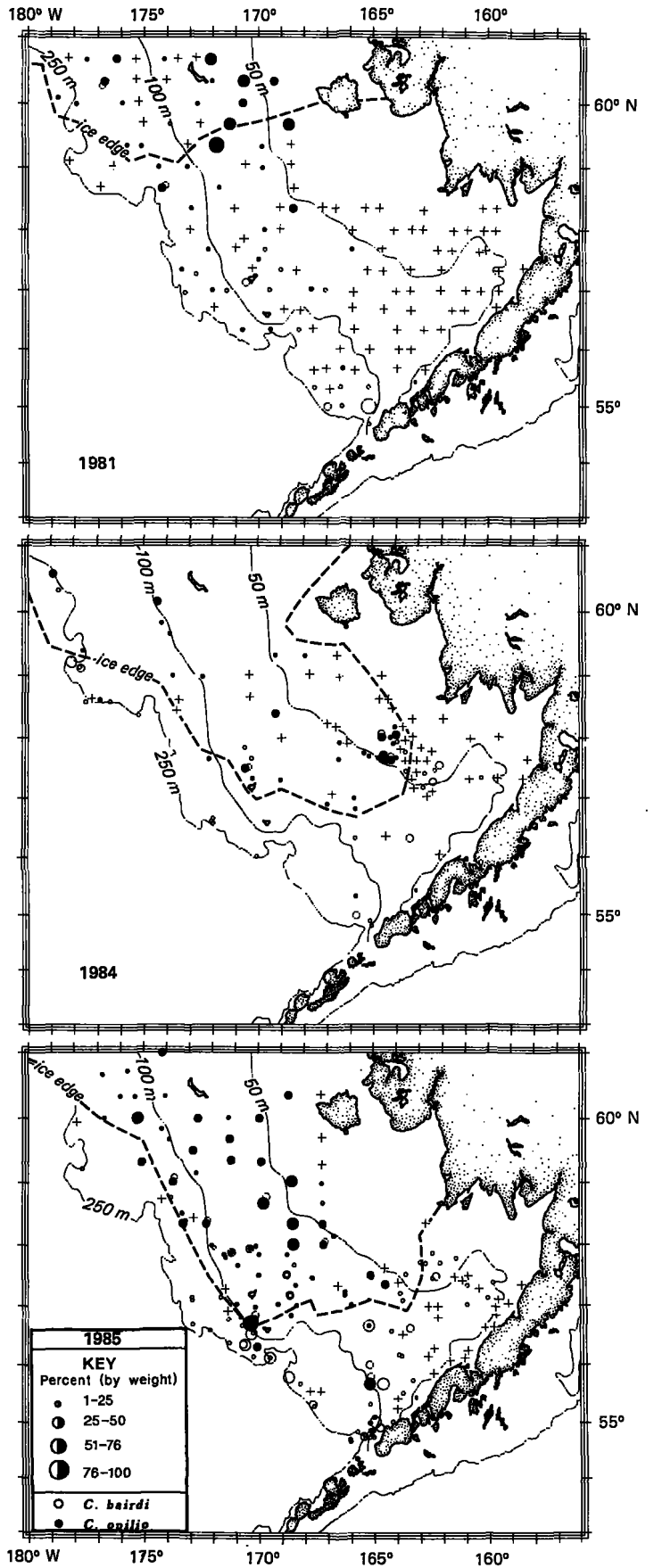


FIGURE 3.—Percentage by weight of *Chionoecetes bairdi* (open circles) and *C. opilio* (black circles) in Pacific cod stomachs by geographic location in relation to the ice edge before its last retreat in 1981, 1984, and 1985.

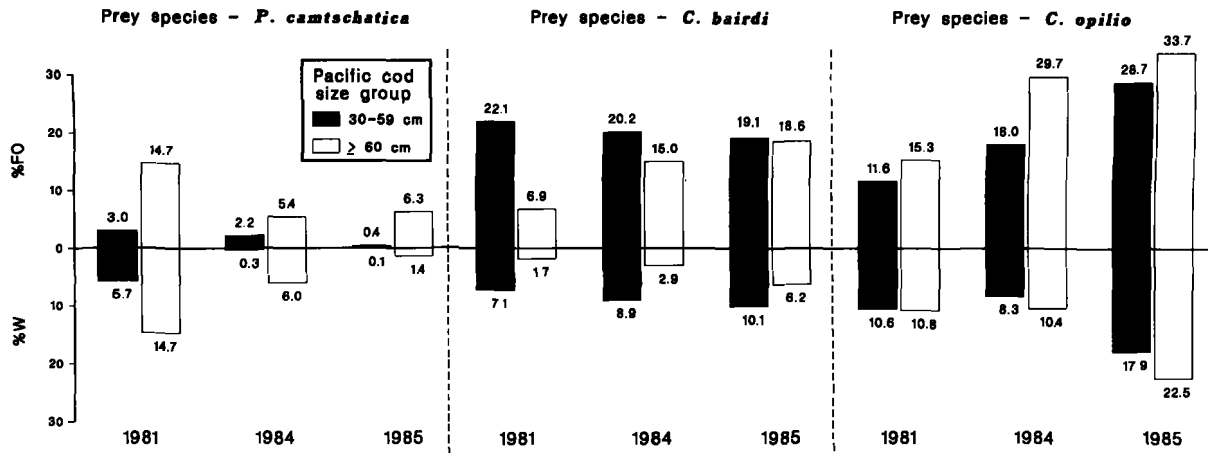


FIGURE 4.—Percentage of frequency of occurrence (%FO) and percentage by weight (%W) of red king crab, *Paralithodes camtschatica*, and two species of snow crab, *Chionoecetes bairdi* and *C. opilio*, in stomachs of two Pacific cod size groups in the respective crab consumption area during 1981, 1984, and 1985.

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 ≥ 60 cm. The chosen model fits these data poorly because of the presence of one anomalous cell; cod ≥ 60 cm in 1981 contained *C. bairdi* much less frequently than any other group. The anomalous value produces a size-year interaction wherein small cod do not show inter-annual 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; 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 CL measurements were taken over all three years because of the advanced state of digestion of most of these crabs found in Pacific cod stomachs. Carapace lengths ranged from 53 to 160 mm with an average of 106 mm. Nine out of 10 crabs were larger than 90

mm. Sex was determined for only one specimen; it was a female.

The Kolmogorov-Smirnov test (Zar 1974) showed that there was no significant difference ($P > 0.05$) between *C. bairdi* size distributions (Fig. 5) consumed by cod 30–59 cm in 1984 and 1985, and no significant size difference between *C. bairdi* consumed by cod ≥ 60 cm 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 only size-frequency distributions of *C. opilio* (Fig. 6) that 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 were very different from size distributions for the other 2 years. Smaller cod during that year ate more crabs 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 proportions of female snow crabs in Pacific cod stomachs and in resource assessment trawl surveys were determined (Table 3). In cod stom-

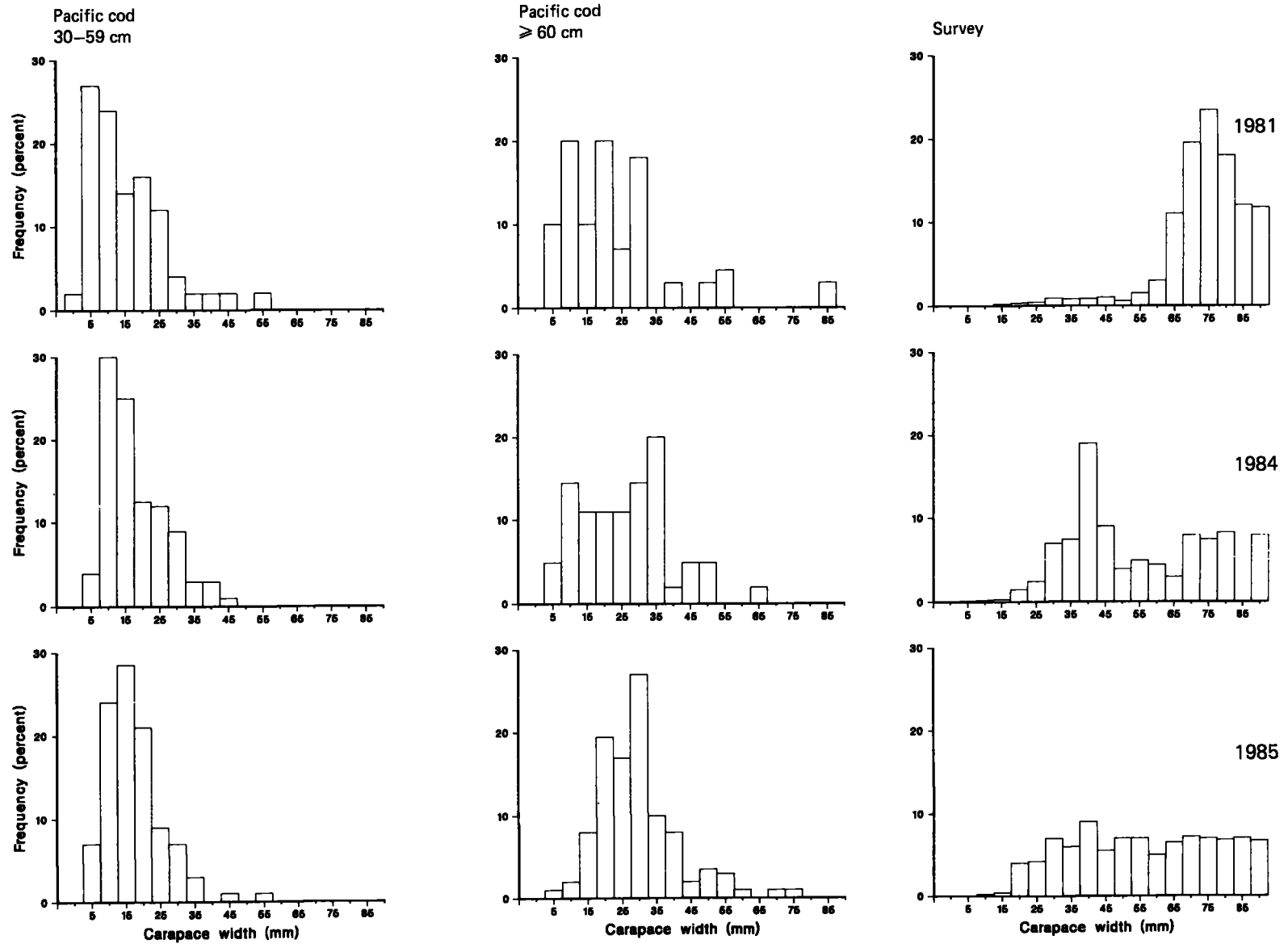


FIGURE 5.—Relative size-frequency distribution of *Chionoecetes bairdi* in stomachs of two Pacific cod size groups and in the resource assessment survey during 1981, 1984, and 1985.

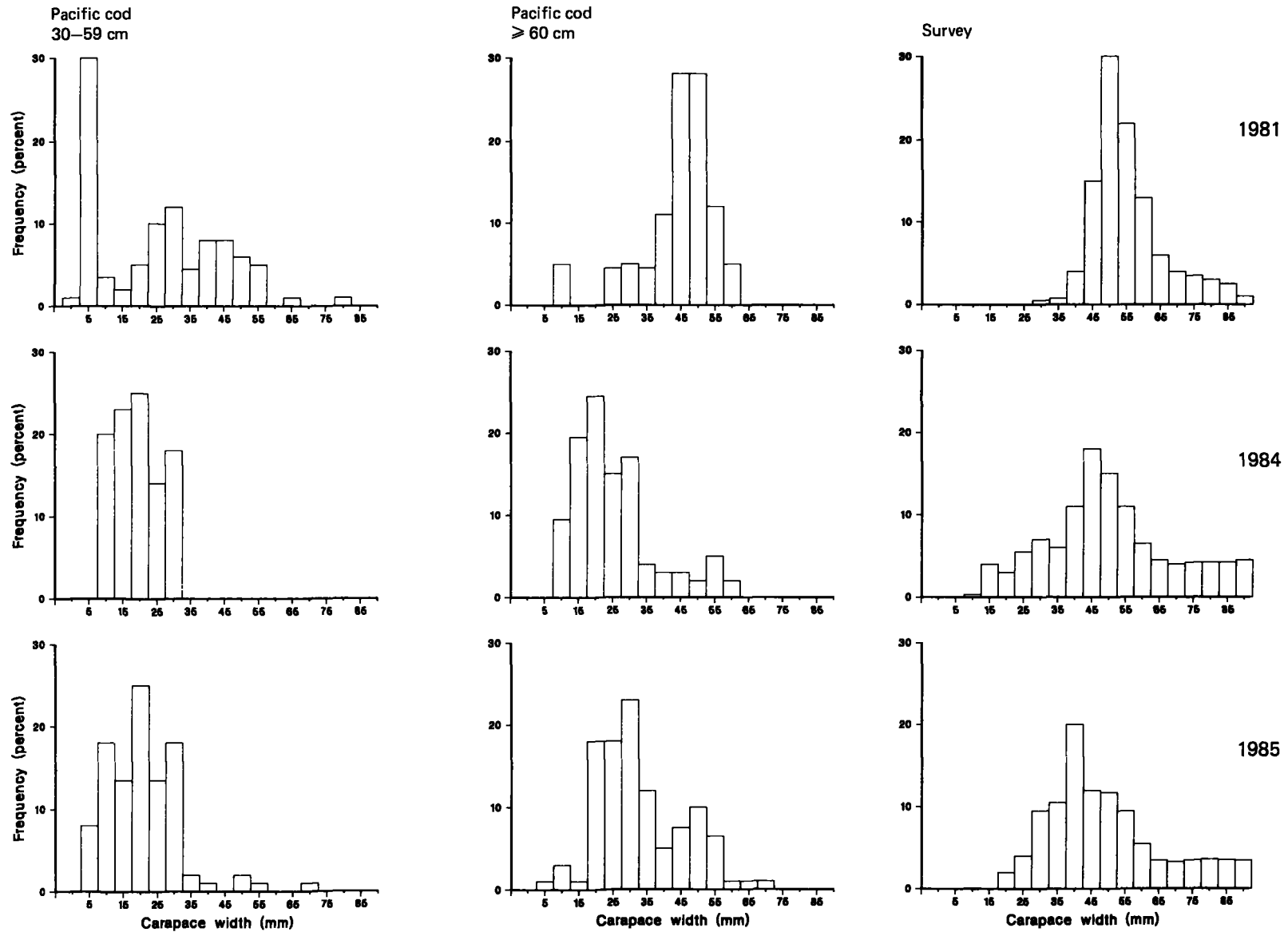


FIGURE 6.—Relative size-frequency distribution of *Chionoectes opilio* in stomachs of two Pacific cod size groups and in the resource assessment survey during 1981, 1984, and 1985.

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.

Crab species	Year	Stomachs		Survey ¹	
		<i>N</i>	PF	<i>N</i>	PF
<i>C. bairdi</i>	1981	248	² 0.935	6,774	0.675
	1984	180	³ 0.567	5,770	0.645
	1985	817	0.557	2,664	0.567
<i>C. opilio</i>	1981	77	² 0.857	22,728	0.640
	1984	165	³ 0.557	19,709	0.510
	1985	512	0.607	12,125	0.426

¹Sex ratios and number of crab sexed provided by Resource Assessment and Conservation Engineering Division, Kodiak Laboratory for crab <95 mm CW.

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

³Observed proportion was not significantly different from 0.5 ($P > 0.05$) using the normal approximation to the binomial test.

achs, the proportions of females for both species of snow crabs during 1981 were much larger than other years. In 1984 and 1985, the proportions of females in cod stomachs were fairly close to 0.5, although in the normal approximation to the binomial test (Zar 1974) only the proportions in 1984 were 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 trawl survey. No trends seem readily apparent except that trawl survey estimated proportions, and those proportions in Pacific cod stomach contents were 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.

The parameters necessary for calculating population consumption are the 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 (Tables 5–7). 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 days 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 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 5). The total amount of *C. bairdi* consumed by cod during the 153 d sampling period in each year, in terms of total weight and numbers, decreased slightly from 1981 to 1984 and increased about threefold from 1984 to 1985 (Table 6). Although the total biomass of *C. opilio* consumed by cod dropped dur-

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 percentage of body weight daily.)

Year	Cod size group	Average weight (g)			Bottom temperature (°C)	Daily ration (% BWD)
		Cod	Individual prey	Cod stomachs		
1981	30–59	1,340	1.02	25.1	3.7	0.86
	≥60	4,045	12.31	141.4	3.7	0.66
1984	30–59	1,095	0.48	16.7	3.1	0.87
	≥60	4,994	6.55	180.7	3.1	0.80
1985	30–59	1,217	1.00	18.7	2.3	0.63
	≥60	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 days of the study period.)

Year	Cod size (cm)	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	118	5.7	1.7	2.00
	≥60	39	14.7	1.1	2.00
	Total			2.8	4.00
1984	30–59	72	0.3	0.1	0.06
	≥60	127	6.0	1.8	2.00
	Total			1.9	2.06
1985	30–59	89	0	—	—
	≥60	103	1.4	0.2	0.20
	Total			0.2	0.20

TABLE 6.—Parameters used to obtain cod population consumption estimates for *Chionoecetes bairdi* 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 days of the study period.)

Year	Cod size (cm)	Cod biomass (1,000 t)	Daily ration (%BWD)	Percent crab in diet (by weight)	Total biomass crab consumed (1,000 t)	Total number crab consumed (billions)
1981	30–59	122	0.86	7.1	11.4	2.71
	≥60	140	0.66	1.7	2.4	0.10
	Total				13.8	2.81
1984	30–59	51	0.87	8.9	6.0	0.91
	≥60	164	0.80	2.9	5.8	0.31
	Total				11.8	1.22
1985	30–59	224	0.63	10.1	21.8	3.87
	≥60	246	0.47	6.2	11.0	0.51
	Total				32.8	4.38

TABLE 7.—Parameters used to obtain cod population consumption estimates for *Chionoecetes opilio* 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 days of the study period.)

Year	Cod size (cm)	Cod biomass (1,000 t)	Daily ration (%BWD)	Percent crab in diet (by weight)	Total biomass crab consumed (1,000 t)	Total number crab consumed (billions)
1981	30–59	274	0.86	10.6	38.2	1.72
	≥60	136	0.66	10.8	14.8	0.28
	Total				53.0	2.00
1984	30–59	100	0.87	8.3	11.0	2.00
	≥60	164	0.80	10.4	20.9	1.29
	Total				31.9	3.29
1985	30–59	185	0.63	17.9	31.9	4.06
	≥60	173	0.47	22.5	28.0	1.03
	Total				59.9	5.09

ing 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 (Table 7).

Total numbers by age of *C. bairdi* and *C. opilio* consumed are shown in Figures 7 and 8. Most *C. bairdi* consumed are age 1, but 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 Pacific 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 >75 mm CL (Otto 1986) which is

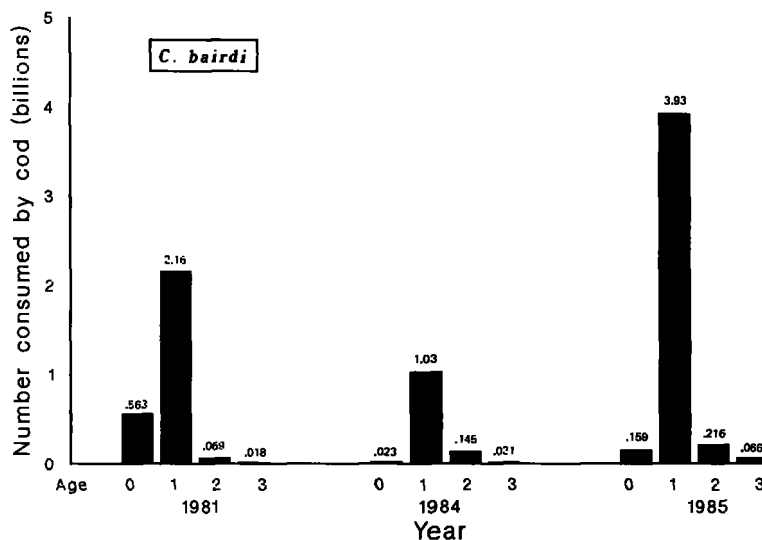


FIGURE 7.—Total number by age group of *Chionoectes bairdi* consumed by the Pacific cod population in 1981, 1984, and 1985.

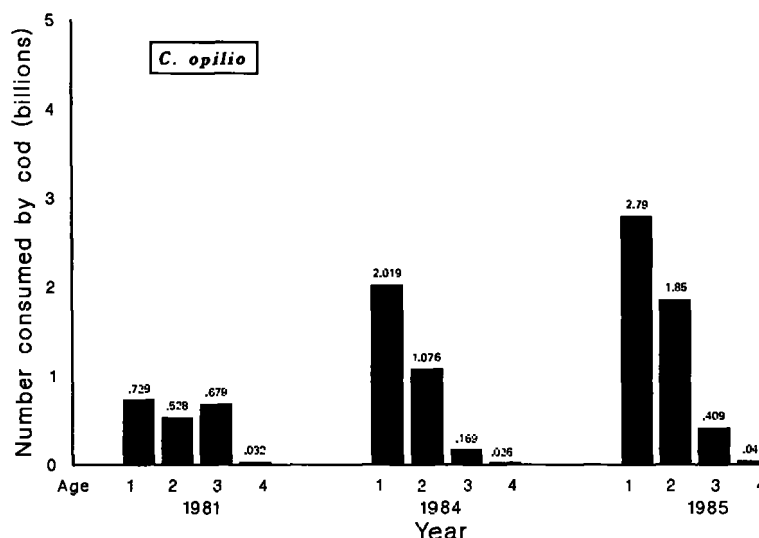


FIGURE 8.—Total number by age group of *Chionoectes opilio* consumed by the Pacific cod population in 1981, 1984, and 1985.

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 that does not match areas of adult abundance determined from NMFS trawl surveys, probably because the trawls used in these surveys do not catch small snow crabs <40 mm CW, which is the size consumed most by cod. Surveys showed most adult *C. bairdi* to be east and southeast of the Pribilof Islands in 1981, 1984, and 1985, while cod stomach contents showed 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 Pacific cod was very 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 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 those year classes that 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 of another environmental variable such as bottom temperature.

The average bottom temperature at stations where *C. opilio* were found in cod stomachs is compared (*t*-test) with bottom temperatures where no *C. opilio* were consumed during the three years of this study (Fig. 9). The average bottom temperatures ($\leq 3^{\circ}\text{C}$) were significantly lower ($P < 0.05$) for the locations where *C. opilio* were found than for locations where they were absent. Somerton (1981) reported the weighted average bottom temperatures at stations where *C. opilio* occurred in 1979 was less than 3°C when the weights used were crab abundance. In that year, juveniles <40 mm CW had the highest abundances per station, indicating that the temperatures apply mainly to the juvenile portion of the population. In the northwest Atlantic, Br  thes et al. (1987) found bottom temperatures $< 3^{\circ}\text{C}$ to be the most significant factor in determining the spatial distribution of juvenile *C. opilio* <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

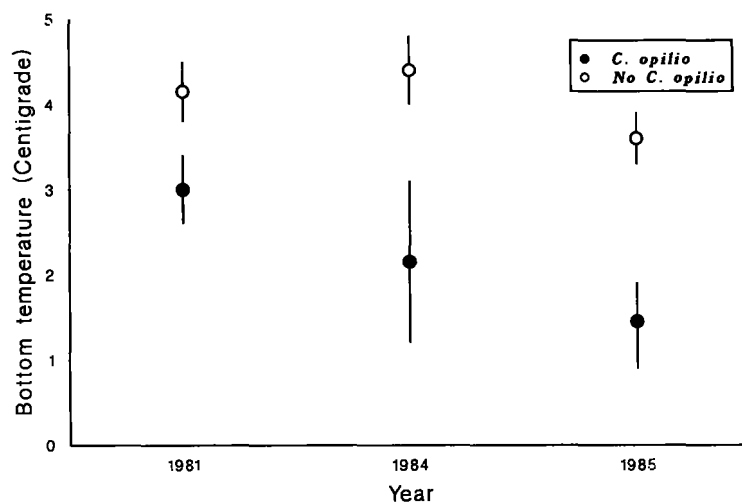


FIGURE 9.—Mean bottom temperature ($^{\circ}\text{C}$) and 95% confidence intervals at locations where Pacific cod consumed *Chionoecetes opilio* (black circles) and at locations where Pacific cod did not contain *C. opilio* (open circles) in 1981, 1984, and 1985.

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 Pacific 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. 4), 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. NMFS surveys are not able to provide precise estimates of crab < 40 mm CW, not only because of escapement through trawl meshes, but also because snow crab < 100 mm CW have a greater tendency to bury themselves in bottom sediments (Conan and Maynard 1987), reducing 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 < 40 mm CW over the three study years. The similarity of *C. bairdi* size distributions in cod stomachs for the three years 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 smaller cod). If the occurrence of juvenile crab < 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 have entered southeastern Bering Sea shelf waters and have become more available to cod. Of course, there is a limit to the distance juvenile crab can migrate in one year. 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 progressive southerly shifts in the geographic distribution of small juveniles in progressively colder years. More years of data need to be examined, however, to determine what happens to juvenile distributions over time, particularly between two consecutive years with very different climatic conditions.

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 consume 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. Because 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, which

molt during winter. However, our winter sampling coverage has been 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 were close to 0.5 and were 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. Brêthes et al. (1987) found sex ratios of *C. opilio* <30 mm CW in the north-west 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 were 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 that were 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 temperatures in the eastern Bering Sea. My 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. When compared with cod growth data, however, the rations for small cod were too small to account for growth, and rations for large cod were 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 in recent years have 95% confidence intervals of 12–18% of the mean biomass estimate (Thompson and Shimada 1987), a minimum confidence interval because of the assumptions of complete vulnerability and catchability of cod to bottom trawls. Cod also performed 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). I have attempted to reduce bias in diet composition estimates that 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, I have estimated consumption that occurred only during May through September, so the estimated numbers of snow crab consumed by cod apply only to that portion of the year. Livingston et al. (1986) has 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 the allocation of crab size groups to age classes should be considered approximate.

Impact on Crab Populations

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. 10). Both the female red king crab population and the estimated removals from the population by cod follow the

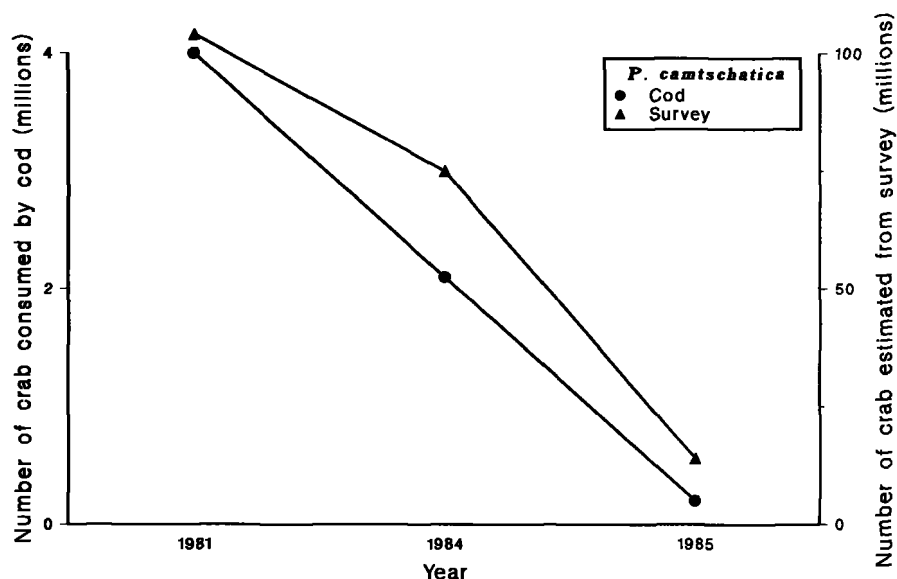


FIGURE 10.—Total number of red king crab, *Paralithodes camtschatica*, eaten by the Pacific cod population during 1981, 1984, and 1985 compared with resource assessment estimates of the total female red king crab population during the same years. (Note different y-axis scales.)

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. The declining percentages removed actually indicate weak compensatory 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 included only 30 out of a possible 60 days 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 percentage of removals in each year by a factor of two but would not change the seemingly compensatory 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 because cod consume 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 years later in NMFS research surveys, which should be more precise (Figs. 11, 12). Although the curves of age 1 crab consumed and the number of age 3 crab found 2 years later in the trawl surveys appear to be somewhat similar in shape for *C. bairdi* for the 3 years, 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 years later. This at least indicates that cod are responsible for removing large numbers of age 1 crab relative to the number that remain at age 3. The unequal ratios of prey removed to prey remaining among years could also indicate that density-dependent removals are occurring.

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. This assumes that cod predation is the major source of mortality for crab less than age 3 and that virtually all of this mortality occurs at age 1. If removals by cod are calculated as a percentage of the reconstructed population size, then the values obtained for 1981, 1984, and 1985 are 84%, 95%, and 94%, respectively. These percentages are substantial

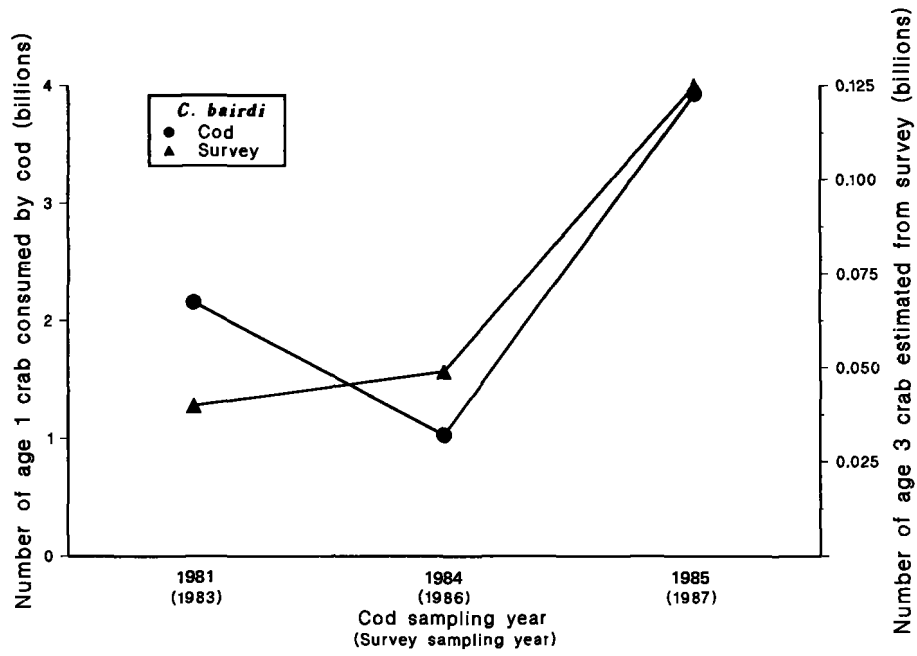


FIGURE 11.—Total number of age 1 *Chionoectes bairdi* snow crab eaten by the Pacific cod population during 1981, 1984, and 1985 compared with resource assessment estimates of the age 3 population in 1983, 1986, and 1987. (Note different y-axis scales.)

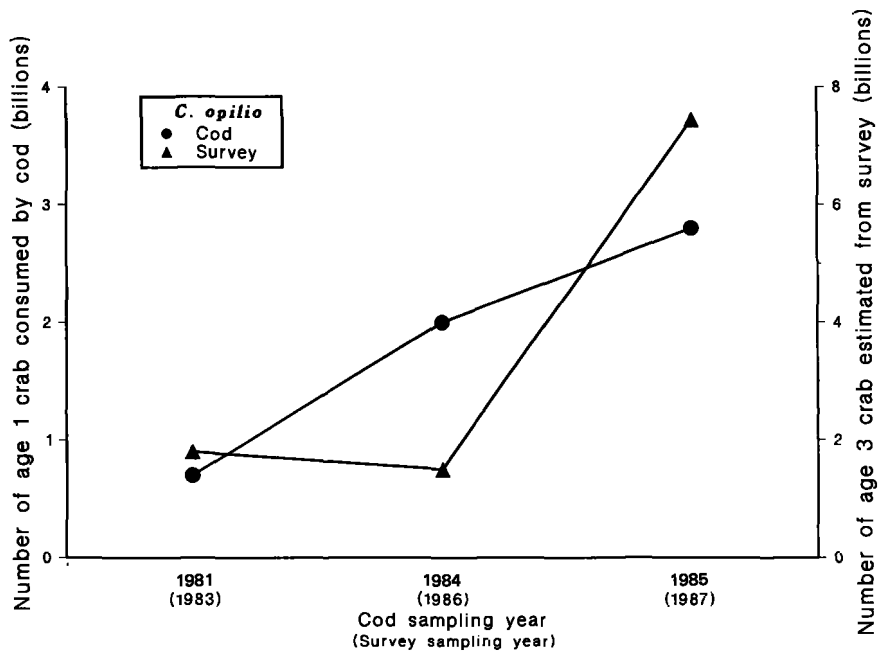


FIGURE 12.—Total number of age 1 *Chionoectes opilio* snow crab eaten by the Pacific cod population during 1981, 1984, and 1985 compared with NWAFC resource assessment estimates of the age 3 population in 1983, 1986, and 1987. (Note different y-axis scales.)

portions of the estimated age 1 population and could be an indication of overestimation of the population consumption by cod, underestimation of the age 1 population size because of unaccounted sources of mortality or underestimation of age 3 numbers by research trawl surveys. As mentioned earlier, cod have been shown to consume snow crab throughout the year in the eastern Bering Sea so the current estimate of 153 days for vulnerability to predation by cod is an underestimate. Further, the cod diet contained fair amounts of snow crab that could not be identified to the species level due to state of digestion and were not included in the estimates. This again leads to conservative estimates of the total number of snow crab consumed by cod.

A similar comparison of *C. opilio* removals at age 1 by cod 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 because substantial numbers of age 2 *C. opilio* are also eaten (Fig. 8) but not included in the reconstructed population estimate.

Although these estimates are subject to many sources of error, 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. *Chionoecetes bairdi* are also more vulnerable to cod predation because of their high spatial overlap with cod populations. In contrast, 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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