

DISTRIBUTION AND REPRODUCTIVE BIOLOGY OF THE GOLDEN KING CRAB, *LITHODES AEQUISPINA*, IN THE EASTERN BERING SEA

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ABSTRACT

The golden king crab is a large anomuran that supports a new, rapidly expanding fishery in the eastern Bering Sea and Aleutian Islands. Based on size, sex, and abundance data collected by U.S. observers aboard foreign trawlers and by National Marine Fisheries Service personnel aboard research vessels, we examined latitudinal and depth variation in mean size (carapace length), size at maturity, weight at size, and relative abundance. Mean size decreases by 6.2 mm for males and 4.6 mm for females with each 1 degree increase in latitude. Size at maturity decreases with increasing latitude from 130 mm for males and 111 mm for females in the southern area to 92 mm and 98 mm in the northern area. These decreases may be due to a temperature induced decrease in growth rate. Weight at size increases by 10% from the southern to the northern area owing to a latitudinal change in body shape. Mean size and relative abundance of both sexes increase with a decrease in depth, suggesting that an onshore ontogenetic migration occurs and that adult males migrate into somewhat shallower water than adult females. Fecundity (number of uneyed embryos) of northern females increases with size according to $-24815 + 323 \text{ CL}$, where CL is carapace length. This relationship changes with latitude and southern females carry about 1,330 fewer eggs than equal-sized northern females. Mean length of uneyed eggs is 2.2 mm. Based on the lack of a clear seasonal change in the occurrence of eyed and uneyed clutches, golden king crab appear to have protracted, or perhaps year-round, breeding.

The golden king crab, *Lithodes aequispina*, is a large anomuran that inhabits the upper continental slope from southern British Columbia, Canada, northward to the Bering Sea and westward to Suruga Bay, Japan (Butler and Hart 1962; Suzuki and Sawada 1978). Although similar in size to red king crab, *Paralithodes camtschatica*, and blue king crab, *P. platypus*, the traditional species harvested by Alaskan crab fisheries, golden king crab have not been intensively harvested because they live in deeper water than red and blue king crabs and are therefore more difficult and expensive to capture (McNair 1983). Since 1980, however, precipitous declines in abundance of red and blue king crabs have stimulated growth of directed fisheries for golden king crab. These fisheries expanded rapidly in the eastern Bering Sea and Aleutian Islands, and between 1981 and 1983 the catch of golden king crab increased from 50 t to 4900 t or 44% of the total king crab catch from these areas.

The fisheries for golden king crab have been managed according to regulations designed for red and blue king crabs (Alaska Department of Fish and Game 1983; Miller 1976) because little biological information was available to establish more specific regulations. Although golden king crab have been studied before, published reports either concern Asian stocks (Hiramoto and Sato 1970; Suzuki and Sawada 1978; Rodin 1970) or are restricted to taxonomy (Benedict 1895; Makarov 1938), distribution (Butler and Hart 1962; Slizkin 1974), or early life history (Haynes 1981).

In 1981, the National Marine Fisheries Service (NMFS) began collecting biological data on golden king crab necessary for establishing minimum size limits and fishing seasons. We summarize these data here, focusing our attention on latitudinal and depth gradients in mean size, size at maturity, weight at size, and sex ratio as well as various aspects of the reproductive biology. We then examine the management implications of our findings.

MATERIALS AND METHODS

Data Sources

Golden king crab were sampled by NMFS re-

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search personnel on stock assessment and tagging cruises and by NMFS observers aboard foreign fishing vessels. In the following we distinguish between survey data and observer data because the sampling designs differed considerably. In both cases, however, crabs were measured with calipers to the nearest millimeter according to the descriptions in Wallace et al. (1949).

Survey Data

From 1981 to 1983, NMFS conducted 10 survey cruises sampling the eastern Bering Sea population of golden king crab with either bottom trawls or commercial king crab pots (Table 1). All crabs were measured for carapace length, and females were classified into one of four categories of reproductive condition:

- 1) Non-ovigerous - no embryos or empty egg cases attached to the pleopod setae.
- 2) uneyed embryos - embryos without conspicuous dark eyes.
- 3) eyed embryos - embryos with dark eyes.
- 4) empty egg cases - empty egg cases and funiculi attached to the pleopod setae.

When opportunity occurred, one or more of the following were also collected:

- 1) height of the right chela of males (excluding males with partially regenerated right chela).
- 2) Total wet body weight of males, measured to the nearest gram on a triple beam balance or to the nearest 5 g on a handheld spring scale (excluding males with damaged exoskeletons or missing appendages).
- 3) egg masses from females (stored in Formalin³ diluted to 10% with seawater).

Observer Data

Golden king crab, like most of the other large Alaskan crabs, is classified as a prohibited species and, as such, may not be retained if captured by foreign fisheries. Because of this status, NMFS fishery observers routinely record the carapace length, sex, and number of golden king crab that are incidentally caught by foreign vessels during their normal fishing operations for other species (Nelson et al. 1981). To delineate the distribution

TABLE 1.—Inclusive dates, latitude and depth ranges, number of crabs sampled and type of sampling gear are shown for each of the 10 golden king crab research cruises conducted by the National Marine Fisheries Service.

Year	Dates	Latitude (degrees N)	Depth (m)	Number		Gear
				males	females	
1981	2/12-2/23	54.4-55.1	346-472	4	6	trawl
1982	7/12-8/4	58.3-60.9	168-849	292	341	trawl
1983	1/31-2/8	52.3-52.5	183-366	188	123	pot
	2/22-2/24	54.4-55.7	362-461	24	17	trawl
	5/9-5/10	56.0-56.1	365-421	288	1,114	pot
	5/12-5/15	57.8-58.5	329-365	489	1,753	pot
	7/8-7/10	57.7-57.7	347-365	1,073	741	pot
	7/14-7/18	55.9-56.3	311-384	1,285	1,012	pot
	10/2-10/4	56.2-56.2	347-365	596	1,035	pot
	11/15-11/21	52.4-52.6	110-283	376	404	pot

of golden king crab in the eastern Bering Sea, we chose to examine the 1981 and 1982 observer data obtained from Japanese small stern trawlers that fish for turbot (*Reinhardtius hippoglossoides*) because 1) these vessels use trawls designed to remain in direct contact with the bottom and are therefore likely to catch crabs, 2) these vessels operate year-round along nearly the entire length of the continental slope of the eastern Bering Sea, and 3) turbot have a depth distribution similar to that of golden king crab. Although these data are not necessarily a random sample of the golden king crab population, they are the most extensive data available and include samples from the entire depth range of golden king crab during all four seasons. The number of crabs measured and the number of trawl hauls sampled are summarized by year, month, latitude, and depth (Table 2). Due to a lack of Japanese fishing effort for turbot, observer data were unavailable for areas south of lat. 54°15'N.

Both survey and observer data, in some instances, were partitioned into three latitudinal strata or subareas (Fig. 1): northern (north of lat. 58°30'N), central (between lat. 58°30'N and 54°15'N), southern (south of lat. 54°15'N and east of long. 173°00'W), which correspond approximately to the crab management districts used by the Alaska Department of Fish and Game. In addition, the observer data were partitioned into two depth strata separated at the approximate median depth (500 m) of the samples (nearly the entire depth range of golden king crab is bounded by the 200 m and 1,000 m isobaths).

Methods of Analysis

Size-frequency distributions by sex were constructed from the combined 1981 and 1982 observer

³Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Number of trawl hauls sampled (excluding hauls without crabs) and number of crabs sexed and measured by U.S. observers aboard Japanese small trawlers within the study area during 1981 and 1982. Data are summarized by depth, latitude and month.

	1981		1982	
	Hauls	Crabs	Hauls	Crabs
Depth (m)				
100	0	0	3	3
200	7	81	23	86
300	30	323	33	848
400	217	2,475	339	3,551
500	456	6,885	548	4,380
600	201	2,065	192	1,112
700	16	97	27	81
800	6	24	1	2
900	2	13	0	0
1,000	1	6	0	0
Latitude (degrees N)				
53	12	18	0	0
54	7	135	132	678
55	34	455	43	184
56	165	1,582	163	879
57	59	376	75	552
58	284	3,936	151	899
59	175	2,995	166	2,019
60	200	2,472	436	4,852
Month				
1	18	55	19	125
2	65	443	19	79
3	75	977	66	528
4	114	1,688	41	73
5	104	1,398	102	332
6	112	2,027	136	1,681
7	72	1,528	75	306
8	89	1,121	124	1,215
9	106	927	192	992
10	99	814	194	2,436
11	68	931	150	1,654
12	14	60	48	654
Total	936	11,969	1,166	10,063

data for each of the two depth strata within the northern and central subareas to help illustrate depth and latitude trends in the size distributions (see Figure 2). Potential bias because of the variation of fishing effort with depth was minimized by first partitioning the data into 100 m depth intervals. Within each depth interval, a size-frequency distribution and an average catch per hour (CPH) were calculated. Size-frequency distributions, weighted by the appropriate mean CPH, were then summed over all 100 m depth intervals within each of the two depth strata.

Variations in mean size, CPH, and proportion male with latitude and depth were also examined using multiple regression. Two normalizing transformations were used: 1) CPH was transformed to the natural log scale and 2) proportion male was transformed to the arcsine-square root scale after replacing 0 with $0.25/N$ and 1 with $(N - 0.25)/N$,

where N is the number of crabs within each trawl haul (Bartlett 1947).

Egg size was estimated by randomly selecting 10 eggs from each preserved egg mass and measuring their maximum lengths (eggs are oval) to the nearest 0.1 mm with an ocular micrometer. The remainder of each egg mass was air dried and, after separating the eggs from the pleopods and setae, weighed to the nearest 0.1 mg. Two subsamples of about 200 eggs each were randomly selected from each dried egg mass and then weighed and counted. Fecundity was then estimated by dividing the total weight of an egg mass by the average of the two estimates of individual egg weight that were obtained from that egg mass.

Male size at maturity was estimated from the allometric growth of the right chela. When king crab chela measurements are plotted against carapace measurements on log-log axes, the data conform to two straight lines that intersect at the average carapace length at maturity (see Figure 3) (Somerton 1980; Somerton and MacIntosh 1983). To estimate this size, we used the computer method described in Somerton and MacIntosh (1983) which fits a pair of intersecting straight lines by iteratively varying the carapace length at the intersection point until the residual sum of squares about the lines is minimized. Variance of the male size at maturity was estimated using a computer technique known as bootstrapping (Efron and Gong 1983). In our application, the method consisted of randomly choosing, with replacement, 50 subsamples equal in size to the original data set. For each subsample, the size at maturity was estimated by fitting the two line model. Variance of the estimated size at maturity was then computed as the variance among the 50 independent estimates.

Although we attempted to detect and exclude partially regenerated chelae in the field, we were not always successful. Measurements from partially regenerated chelae can increase the variance of estimates of male size at maturity; therefore, these measurements were removed from the data set before analysis using a sequential outlier elimination technique described in Somerton and MacIntosh (1983).

Golden king crab females were considered to be mature, if they had eggs or empty egg cases attached to the pleopod setae. Although we are not certain that this is always true, for red and blue king crabs, adult females extrude eggs soon after every molt and the empty egg cases remain attached to the pleopod setae until the next molt (Somerton and MacIntosh 1985).

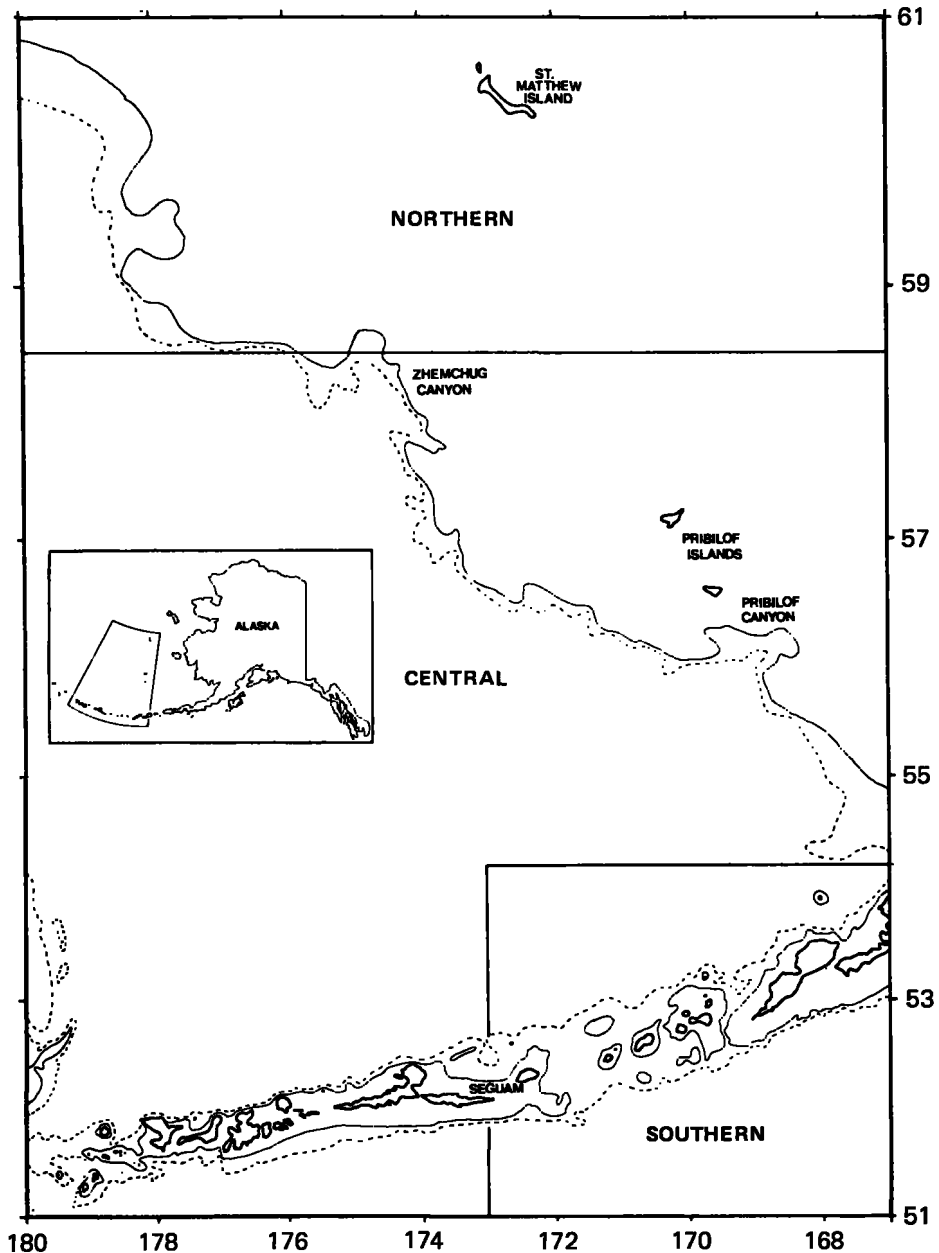


FIGURE 1.—Areas of the Bering Sea and eastern Aleutian Islands where golden king crab were sampled by U.S. fishery observers and National Marine Fisheries Service research cruises. Golden king crab occur primarily in a region bounded by the 200 m (solid line) and 1,000 m (dashed line) isobaths. The dark lines indicate the separation of this region into the three latitudinal strata discussed in the text.

Female size at maturity was estimated as the size at which 50% of the crabs were mature. Weighted nonlinear regression (weights equal to the inverse of the binomial variance at each size) was used to fit a logistic equation to the percentage mature

within 5 mm size intervals. The fitted logistic equation was then evaluated to determine the carapace length corresponding to 50% maturity. Variance of this size was estimated using the formula provided in Somerton (1980).

BIOLOGICAL VARIATION WITH DEPTH AND LATITUDE

Mean Size

Size-frequency distributions of golden king crab, based on the combined 1981 and 1982 observer data, are shown by sex, area, and depth strata in Figure 2. Linear trends in mean size with depth and latitude were examined statistically using multiple regression. For each sex in each year, when carapace length was regressed against latitude and depth simultaneously, ignoring interaction, both the latitude coefficient and the depth coefficient were negative and highly significant ($P < 0.001$). Aver-

aged over both years, mean size decreased by 6.2 mm for males and by 4.6 mm for females for each 1 degree increase in latitude, and mean size decreased by 7.9 mm for males and by 6.2 mm for females with each 100 m increase in depth.

The latitudinal decrease in size probably reflects a latitudinal decrease in growth rate. Two shallow-water Bering Sea crabs, *Chionoecetes bairdi* and *C. opilio*, also show a latitudinal decrease in size, and this decrease was correlated with a latitudinal decrease in maximum summer water temperature (Somerton 1981a). Although we lack sufficient temperature data from the depths inhabited by golden king crab to allow a statistical test, it is likely that mean annual bottom temperature also decreases

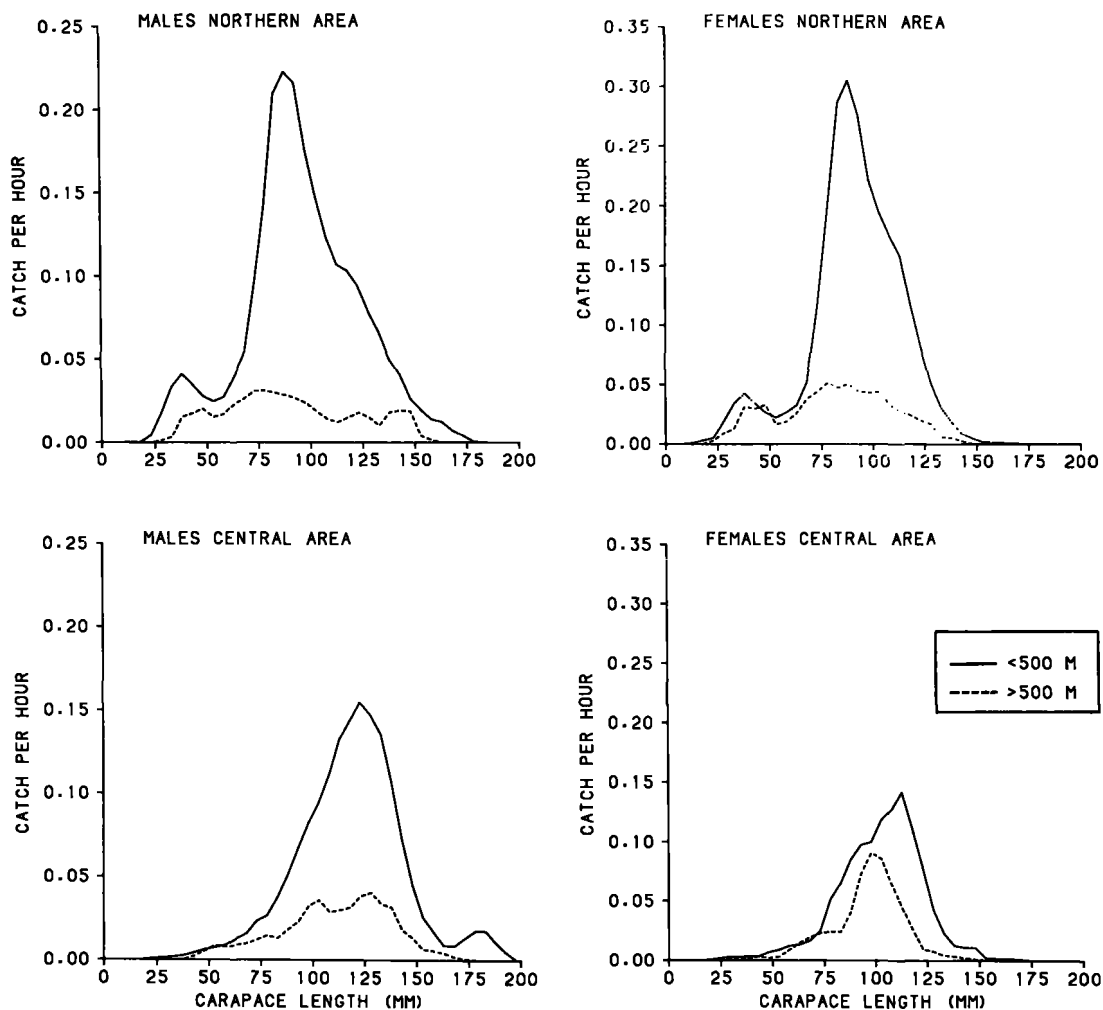


FIGURE 2.—Size-frequency histograms for males and females of golden king crab, by depth strata and subarea. Due to differences in the sampling intensity with depth (Table 2), frequencies have been standardized to catch per hour of trawling.

with increasing latitude along the slope. If this is true, then it is reasonable to assume that growth rates are lower in higher latitudes. Part of the latitudinal decrease in mean size, however, is due to the greater relative abundance of small (25-50 mm) crabs in the northern area (Fig. 2). Since we have only two years of data, we do not know if the greater abundance of small crabs in the northern area is a persistent feature of the distribution. But if it is, it may indicate that greater larval settlement occurs in the northern area because of the advection of larvae by the northwesterly currents over the continental slope (Kinder and Schumacher 1981).

The decrease in size with depth may reflect an ontogenetic upslope migration. Another slope dwelling crab, *Chionoecetes tanneri*, also displays a decrease in size with depth, and this was attributed to an offshore advection of pelagic larvae followed by an onshore migration of juveniles (Pereyra 1968). Although an onshore migration might explain the size variation with depth of golden king crab in the eastern Bering Sea, offshore advection depends on local oceanographic conditions and may not occur everywhere ovigerous golden king crab occur. For example, studies of golden king crab in other areas indicated that adults could be found in shallower water than juveniles (Hiromoto and Sato 1970), or at similar depths as juveniles but in different areas (Rodin 1970) or in deeper water than juveniles (N. Sloan⁴).

Size at Maturity

The change in the relative growth of a male's chela which occurs at maturity is more pronounced for golden king crab than it is for either blue king crab (Somerton and MacIntosh 1983) or red king crab (Somerton 1980), and this allows greater precision in the estimates of size at maturity (Fig. 3). Nevertheless, the estimates of male size at maturity are less precise than those for females (Fig. 4). For both sexes, however, the estimated sizes at maturity differ significantly between areas and progressively decrease with increasing latitude (Fig. 4).

The decrease in the size at maturity is consistent with a latitudinal decrease in growth rate; however, the decrease is greater for males than it is for females (Fig. 4). If golden king crab are similar to red king crab (Weber 1967) in that males and females grow identically while they are immature,

then the greater latitudinal decrease in male size at maturity implies that female age at maturity increases, relative to that of males, with latitude. This could occur if females and males have different life history strategies to maximize their reproductive values (Bell 1980). The reproductive value of a female is largely determined by her lifetime fecundity. Since fecundity increases markedly with size and somatic growth decreases abruptly at maturity, under conditions of reduced growth, female reproductive value might be increased by delaying maturity until some optimum size is reached. The reproductive value of a male, however, is largely determined by the number of females he is able to mate with over his lifetime. Unless access to females is strictly limited to the largest males, male reproductive value is unlikely to be increased by delaying maturity. Along a gradient of decreasing growth rate, such strategies would lead to a divergence between male and female sizes and ages at maturity.

Weight at Size

Weight-size relationships of males were determined for each of the three subareas by regressing body weight on carapace length after transforming both variables to natural logarithms. Analysis of covariance showed that the slopes of the regression lines were not significantly different ($F = 0.49$, $df = 2, 1,079$, $P = 0.613$), but that the intercepts were significantly different between areas ($F = 19.03$, $df = 2, 1,081$, $P < 0.001$). Pairwise t -tests further showed that the intercept for each area differed significantly from the other two (Bonferroni critical values; maximum $P < 0.05$) and that the intercepts progressively increased with increasing latitude. Males in higher latitudes are therefore proportionately heavier than equal-sized males from lower latitudes.

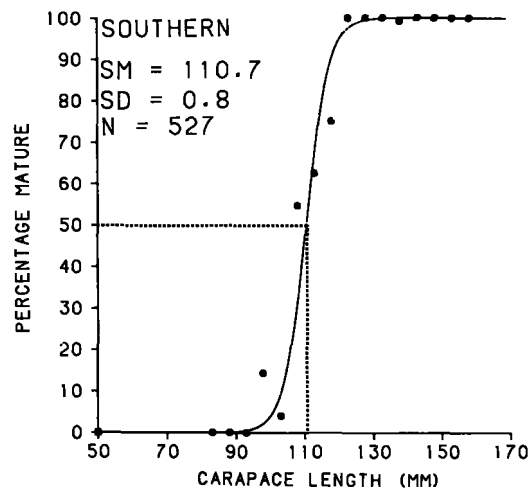
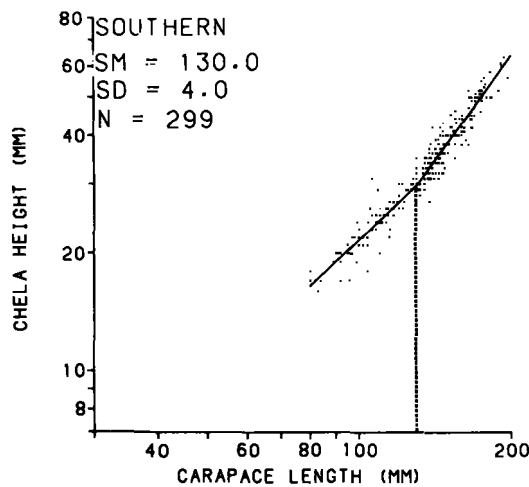
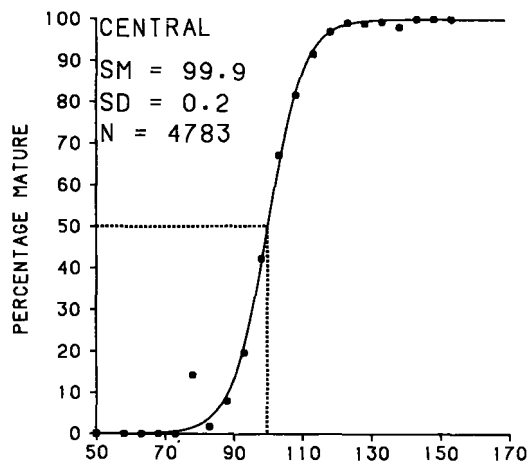
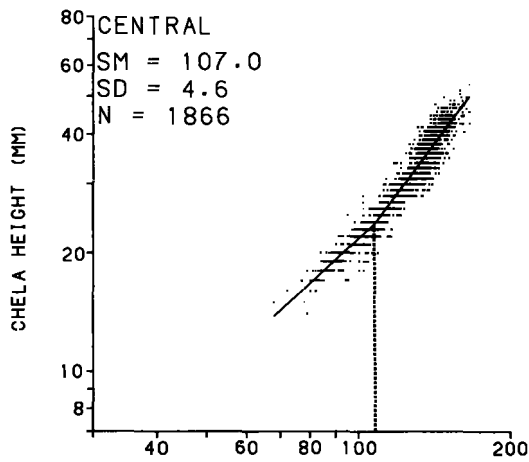
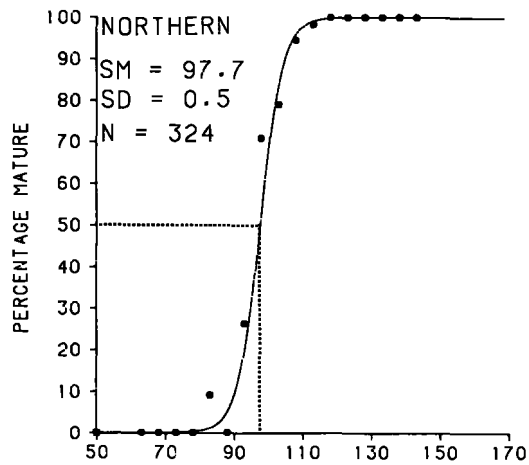
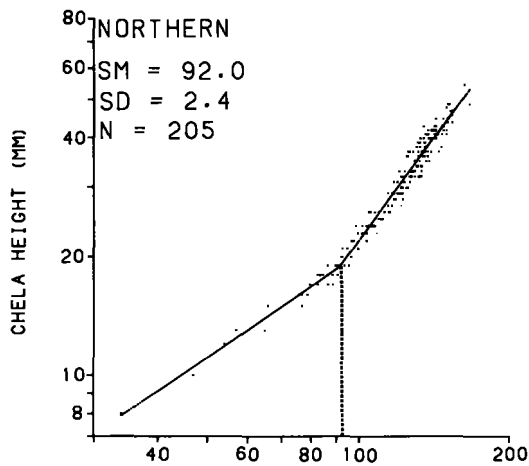
This proportionate change in weight with latitude might be due to changes in body shape, such as the relative size of the chelae, that are coincident with the onset of maturity. Since the rate of chela growth increases, relative to carapace growth, at maturity, and since the size at maturity decreases with latitude, mature males in northern areas should have larger chelae than equal-sized males in southern

FIGURE 3.—For the golden king crab males, chela heights, carapace lengths, and the best fitting two line model are shown for each subarea. For the females, percentage mature, within 5 mm size intervals, and the fitted logistic equation are shown for each subarea. Estimated sizes (carapace length) at maturity are indicated by dotted lines.

⁴N. Sloan, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, V9R 5K6, Canada, pers. commun. 1984.

MALE

FEMALE



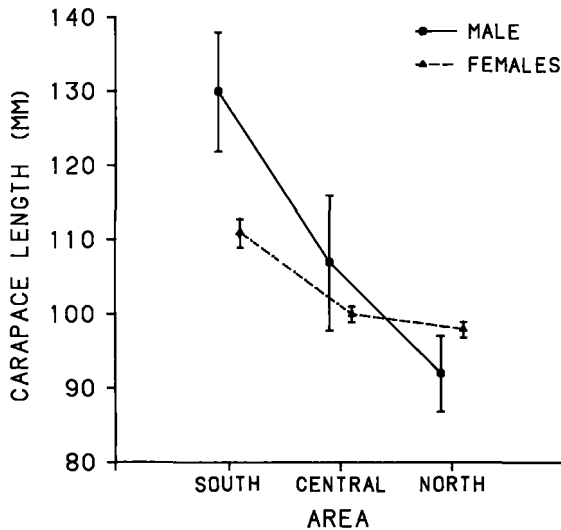


FIGURE 4.—For both sexes of golden king crab, estimated sizes at maturity, and their 95% confidence intervals, are plotted against area.

areas. To test whether this is true, chela height and carapace length relationships for adult males were compared between areas. Analysis of covariance showed that the slopes did not differ ($F = 0.14$, $df = 2, 1,998$, $P = 0.87$), but the intercepts differed significantly ($F = 146.7$, $df = 2, 2,000$, $P < 0.001$). Pairwise t -tests further showed that each intercept differed significantly (Bonferroni critical values; maximum $P < 0.05$) from the other two and, similar to the weight-size relationships, that the intercepts progressively increased with latitude. Thus northern males, which are the heaviest, have the largest chelae.

By itself, chela size is unlikely to be responsible for latitudinal differences in weight because chela weight is only a small proportion of total body weight. However, chela size may be correlated with other body dimensions (for example, length of walking legs) that also increase relative to carapace length at maturity. We therefore used chela height as a proxy for these dimensions and examined whether the difference in chela height could account for the difference in weight-size relationships. This was done by comparing the weight-size relationships between areas including the logarithm of chela height as a covariate. Two additional modifications of the previous weight-size comparison were made. First, since weights and chela measurements were not obtained from the same crabs in the southern area, the comparison was restricted to the northern and central areas. Second, since chela height and

carapace length are linearly related only over the adult (or juvenile) size range, the comparison was restricted to males greater than the size at maturity in each area. When the northern ($N = 129$) and central ($N = 614$) areas were compared considering only carapace length as a covariate, the slopes were not significantly different ($F = 0.06$, $df = 2, 739$, $P = 0.81$), but the intercepts were significantly different ($F = 7.36$, $df = 1, 740$, $P = 0.007$). When chela height was included as a covariate, however, neither the slopes ($P = 0.316$) nor the intercepts ($P = 0.430$) differed significantly between areas. This indicates that latitudinal changes in chela size, and perhaps other body measurements that also increase at maturity, account for the observed latitudinal increase in body weight.

Juvenile weight-size relationships were also compared between the northern ($N = 10$) and central ($N = 207$) areas and neither the slopes ($F = 0.06$, $df = 1, 213$, $P = 0.938$) nor the intercepts ($F = 0.19$, $df = 1, 214$, $P = 0.664$) were significantly different. The weight-size relationship for male golden king crabs is therefore described by one equation for juveniles and three equations for adults. Transformed back to a linear scale, these relationships are

Juveniles	$W = 0.000365 CL^{3.099}$	($N = 217$, $R^2 = 0.88$)
Adults		
Northern	$W = 0.000225 CL^{3.206}$	($N = 139$, $R^2 = 0.93$)
Central	$W = 0.000219 CL^{3.206}$	($N = 632$, $R^2 = 0.91$)
Southern	$W = 0.000204 CL^{3.206}$	($N = 100$, $R^2 = 0.91$)

where W is body weight in grams and CL is carapace length in millimeters. Within the adult size range, males from the northern area are 10.3% heavier and males from the central area are 9.8% heavier than equal-sized males from the southern area.

Relative Abundance and Proportion Male

Relative abundance, or catch per hour (CPH), based on combined 1981 and 1982 observer data, is shown by sex, latitude, and depth in Figure 5. Linear trends in CPH with depth and latitude were examined statistically using multiple regression (depth and latitude were considered simultaneously; interaction was ignored). The latitude coefficient for males was not significant ($P > 0.05$) in either year, but the latitude coefficient for females was positive and highly significant ($P < 0.01$) in both years. The depth coefficient for males was negative

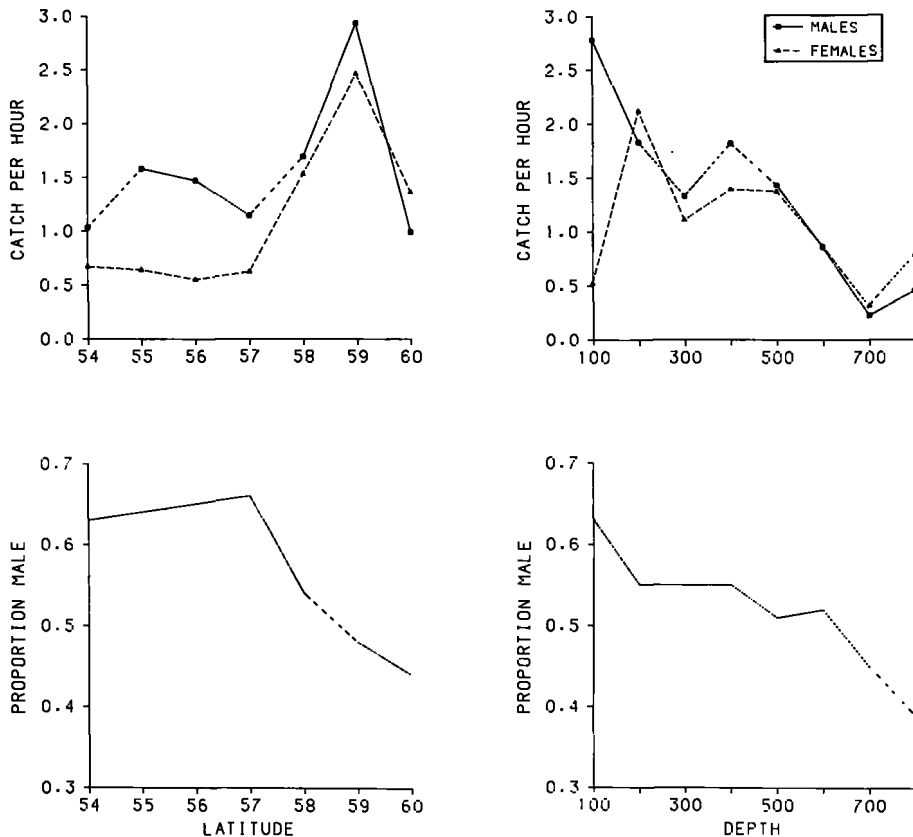


FIGURE 5.—Catch per hour, by sex, and the proportion of males of golden king crab are shown as a function of latitude (left panels) and depth (right panels).

and highly significant in both years ($P < 0.01$), but the depth coefficient for females, although negative in both years, was significant ($P < 0.05$) in only one. Although male CPH decreases significantly with depth whereas female CPH decreases significantly with latitude, CPH is not a strict linear function of depth and latitude; therefore, linear approximations mask aspects of the variability. The important point is that both male and female CPH generally increase with an increase in latitude or a decrease in depth, but at more southerly latitudes or at the shallowest depth, male CPH is considerably higher than female CPH (Fig. 5).

Different trends in CPH between sexes suggested that the sex ratio of golden king crab varied spatially. To investigate this further we examined the variation in proportion of males within trawl hauls having at least five crabs. The proportion of males, based on combined 1981 and 1982 observer data, is shown by latitude and depth in Figure 5. When the proportion of males was regressed against

latitude and depth (using weights equal to the number of crabs within each trawl haul), the latitude coefficient was negative and highly significant ($P < 0.01$) in both years; and the depth coefficient, although negative in both years, was significant ($P < 0.05$) in only one.

From a biological perspective, the latitudinal decrease in the proportion of males is difficult to explain; therefore, we considered possible sampling bias that could lead to an apparent change in the proportion of males. Since males are considerably larger than females in the central area but nearly the same size as females in the northern area, the proportion of males might vary with latitude due to size selectivity of the trawls. This hypothesis was tested by comparing the proportion of males between the northern and central areas considering only crabs within an equal size range. To eliminate a possible confounding effect due to a sexual difference in growth rate that begins at maturity, we restricted the comparison to crabs < 90 mm. Based

on the combined 1981 and 1982 observer data, the proportion of males was 0.51 ($N = 1,375$) in the central area and 0.43 ($N = 8,271$) in the northern area. Since the proportion of males still differed significantly between areas (2×2 contingency table, $\chi^2 = 30.7$, $df = 1$, $P < 0.001$), it is unlikely that the change in the proportion of males was due to size selectivity. Furthermore, since the difference in the proportion of males appears to be established before maturity, biological explanations such as sexual differences in migratory behavior or natural mortality are also unlikely.

Although we cannot explain the latitudinal variation in the proportion of males, we believe that the depth variation, especially the abrupt increase in the proportion of males in the shallowest depth zone, is due to sexual segregation. Sexual segregation by depth has been observed for another slope-dwelling crab, *C. tanneri* (Pereyra 1966). Adult female *C. tanneri* occur within a rather narrow depth zone throughout the year while adult males undergo a seasonal migration from relatively shallow water in summer to the deeper water occupied by females during the winter mating period. To determine if golden king crab have a similar seasonal migration, we examined the proportion of males from the northern area at depths < 400 m (the northern area had nearly equal sampling in all four seasons). Using pooled 1981 and 1982 data, analysis of variance showed that the proportion of males did not vary significantly between seasons ($F = 0.13$, $df = 3$, 179 , $P > 0.05$). Although adult males of golden king crab probably congregate in somewhat shallower water than adult females, unlike *C. tanneri* this segregation appears to be maintained throughout the year.

REPRODUCTIVE BIOLOGY

Fecundity

Fecundity-size relationships for golden king crab were estimated stagewise by examining 1) the form of the relationship, 2) whether the relationships varied with stage of embryo development, and 3) whether the relationships varied between areas.

The fecundity of king crabs has been reported to increase as either a linear (Haynes 1968) or a curvilinear (Somerton 1981b) function of carapace length. To determine which form was more appropriate for golden king crab, a second degree polynomial was fitted to the fecundity and size data from the northern area (all clutches contained uneyed embryos) and the coefficient of the quadratic term was tested for

significance. Since the coefficient was not significantly different from zero ($F = 3.85$, $df = 1$, 57 , $P = 0.06$), we chose a linear relationship to describe the data.

Fecundity-size relationships for females with uneyed embryos ($N = 46$) and eyed embryos ($N = 19$) from the central area were compared to determine whether the relationships changed with stage of embryo development. Analysis of covariance showed that the slopes did not differ ($F = 0.77$, $df = 1$, 61 , $P = 0.38$) but that the intercept for eyed embryos was significantly less ($F = 4.89$, $df = 1$, 62 , $P = 0.03$) than that for uneyed embryos. At 114 mm, the median size of adult females in all areas combined, uneyed clutches were 18% greater than eyed clutches. Similar to other crab species (Wear 1974), golden king crab lose a significant number of embryos between egg extrusion and the appearance of embryonic eyes.

Fecundity-size relationships were then compared between the northern ($N = 59$), central ($N = 46$), and southern ($N = 24$) areas considering only those clutches with uneyed eggs. Analysis of covariance showed that the slopes did not differ ($F = 0.74$, $df = 2$, 123 , $P = 0.48$), but the intercepts differed significantly between areas ($F = 4.38$, $df = 2$, 125 , $P = 0.01$). Pairwise t -tests indicated that southern and central intercepts did not differ ($P = 0.99$) from each other, but that both differed significantly ($P = 0.01$, $P = 0.04$) from the northern intercept. Data from the southern and central areas were therefore pooled and compared with those from the northern area. Again, the slopes did not differ ($F = 1.25$, $df = 1$, 125 , $P = 0.27$), but the northern intercept was significantly greater ($F = 8.83$, $df = 1$, 126 , $P = 0.004$) than the pooled central and southern intercept. Assuming equal slopes, the resulting fecundity-size relationships are

Northern	$E = -24815 + 323 CL$ ($N = 59$, $R^2 = 0.79$)
Central-southern	$E = -26145 + 323 CL$ ($N = 68$, $R^2 = 0.74$)

where E is number of uneyed eggs and CL is carapace length in millimeters. Females from the northern area carry, on average, 1,330 more eggs than equal-sized females from the central and southern areas. For 114 mm females, this represents a 12.6% difference in fecundity.

Northern females may be more fecund than equal-sized central and southern females because they are older and size-specific fecundity often increases with age (Pianka and Parker 1975). But, it is also likely

that the observed difference in fecundity is an artifact due to a difference in mean embryo age. We attempted to eliminate the effect of embryo age by considering only clutches with uneyed embryos, but this may not have been a sufficiently sensitive criterion of age and northern females could have had more embryos simply because they had younger embryos. Considering that for equal-sized females the percent difference in clutch size between eyed and uneyed stages was greater than the percent difference in clutch size between areas, it is possible that the loss of embryos within the uneyed stage is sufficient to account for between-area differences. More precise embryo aging techniques are needed to clarify this.

Egg Size

To estimate the size of golden king crab eggs, we considered 1) whether egg size varied with stage of embryo development and 2) whether egg size varied between areas. When mean lengths of uneyed eggs ($N = 42$) and eyed eggs ($N = 26$) from the central area were compared, eyed eggs were found to be significantly larger than uneyed eggs (two sample t -test, $P < 0.001$). Golden king crab eggs therefore appear to increase in size, as has been reported for other crab species (Wear 1974), during embryonic development. When mean length of uneyed eggs from the southern ($N = 25$) and central ($N = 42$) areas (no egg length data was collected from the northern area) were compared, no significant difference was found (two sample t -test, $P = 0.25$). Mean length of uneyed eggs, based on the pooled central and southern data, is 2.2 mm (SD = 0.1).

Our estimate of egg length is similar to those reported for Asian populations of golden king crab (2.38 mm, Hiramoto and Sato 1970; 2.30 mm, Suzuki and Sawada 1978), and it is also similar to egg lengths reported for other *Lithodes* species (*L. antarctica*, 2.2 mm, Guzman and Campodonico 1972; *L. couesi*, 2.3 mm, Somerton 1981b). However, this size is more than twice as large as the egg lengths reported for *Paralithodes* species (*P. camtschatica*, 1.0 mm, Haynes 1968; *P. platypus*, 1.2 mm, Sasaki 1975). The larger eggs of golden king crab are, in turn, reflected in the relatively large size of their first stage zoea (*L. aequispina*, 7.3 mm TL, Haynes 1981; *P. camtschatica*, 4.6 mm TL, Sato and Tanaka 1949; *P. platypus*, 4.9 mm TL, Hoffman 1968). The larger size of *L. aequispina* larvae may allow them to withstand starvation for a longer period or may allow them to capture a wider size range of prey

than *Paralithodes* larvae. If this is true, golden king crab larvae may not need to ascend to the photic zone but instead stay at greater depths. Evidence supporting this hypothesis is provided by a study on crab larvae that sampled the upper 50 m near the edge of the eastern Bering sea continental shelf (Fig. 1). Although both *P. platypus* and *P. camtschatica* larvae were found, *L. aequispina* larvae were not (D. Armstrong⁵).

Seasonality of Reproduction

King crabs either can be synchronous and seasonal in their egg extrusion and embryo hatching, as reported for *P. camtschatica* (Powell et al. 1973), or they can be asynchronous and lack seasonal periodicity, as reported for *L. couesi* (Somerton 1981b). To determine which pattern better characterizes golden king crab, we tabulated the percentage of mature females in each of the three reproductive conditions by area and by quarter (Table 3). If the reproductive cycle were synchronous and seasonal, then each of the three categories of reproductive condition should predominate sequentially over the course of a year, but such a pattern is not evident. Regardless of the area or the season in which a sample was collected, all three reproductive categories were always obtained. This suggests that golden king crab have an asynchronous reproductive cycle lacking distinct seasonal variation.

TABLE 3.—Percentage of adult females in each of three categories of reproductive condition: 1) uneyed embryos, 2) eyed embryos, and 3) empty egg cases, and total sample size (N) by subarea and quarter.

Quarter	South				Central				North			
	1	2	3	N	1	2	3	N	1	2	3	N
1	55	33	12	67	50	8	42	12				
2					28	63	9	1,307				
3					14	36	50	1,399	78	3	19	224
4	28	67	5	384	61	16	23	859				

The apparent lack of seasonality conflicts with previous studies of golden king crab reproduction. Hiramoto and Sato (1970) reported that egg extrusion occurs from July to October and embryo hatching occurs from February to July along central Japan. However, Hiramoto and Sato found embryos in late stages of development throughout the year,

⁵D. Armstrong, College of Fisheries, University of Washington, Seattle, WA 98195, pers. commun. 1984.

indicating that embryo hatching was probably occurring at times other than the peak season. Rodin (1970) reported that egg extrusion occurs from August to September based on the relatively high incidence of recently molted females with new embryos. However, Rodin based this on only one summer sample and some of our samples, especially those from the northern area, if examined alone would have also incorrectly led to the same conclusion. Our findings, however, are consistent with those for other deep water crabs (*L. couesi*, Somerton 1981b; *Geryon quinquedens*, Haefner 1978) which have asynchronous or protracted spawning.

Asynchronous spawning is also consistent with two of our other observations. First, the larvae of golden king crab, due to their large size and presumably deep habitat, should be relatively insensitive to seasonal changes in primary production. Second, adult males and females of golden king crab appear to segregate by depth and this segregation appears to be maintained throughout the year. Such year-round sexual segregation is unlikely for a seasonally reproducing species; however, it is consistent with an asynchronous reproducing species if only the reproductively active individuals migrate between depth zones.

IMPLICATIONS FOR FISHERY MANAGEMENT

Two of our findings, the latitudinal decrease in the size at maturity and the asynchronous reproductive cycle, pertain to regulations used to manage the golden king crab fisheries in Alaska.

Commercial harvest of king crabs is restricted to males larger than a minimum legal size (maximum carapace width including spines) which is specified for each species in each management area. These minimum sizes are set at the average size of a male three years after reaching maturity based on the rationale that such a size would preserve sufficient males for breeding even when the exploitation rate is high (North Pacific Fishery Management Council 1981). Thus, to establish a minimum size limit that conforms to this rule, both an estimate of the size at maturity and an estimate of male growth rate are needed. Unfortunately, we lack sufficient data to estimate the growth rates of golden king crab in any of the three management areas considered here and therefore cannot determine appropriate minimum size limits. However, our estimates of male size at maturity can be used to judge, in a qualitative sense, the adequacy of the current minimum size limits. These size limits and the estimated sizes at matur-

ity, expressed in terms of carapace length, are as follows:

	<i>Minimum size limit</i> (mm CL)	<i>Size at maturity</i> (mm CL)
Northern area	123	92
Central area	123	107
Southern area	134	130

The current minimum size limits decrease with increasing latitude, but not in proportion to the estimated sizes at maturity. Based solely on the relative magnitude of our estimates, we believe that the current minimum size limit in the southern area, and perhaps in the central area as well, is too low. However, we believe that the prolonged or year-round breeding of golden king crab would allow males more opportunities for mating than would be possible with a short breeding season; therefore, relative to seasonally breeding king crabs, fewer males would be sufficient for the breeding needs of the population. If this is true, then minimum size limits based on the criteria established for red and blue king crabs may be unnecessarily conservative for golden king crab.

Commercial harvest of king crabs is also restricted to a legal fishing season specified for each species in each area. Although economic or logistic factors are considered when fishing seasons are established, of primary importance is the timing of the breeding and molting seasons. During the breeding season, females molt while aggregated together with the males (Powell et al. 1973); and if fishing were permitted at this time, not only would females be caught in greater numbers, they would also be injured by the fishing gear. During and soon after the male molting season, the recovery rate (ratio of recoverable meat to total body weight) is low; and if fishing were permitted at this time, the value of the crabs would also be low. Since the breeding seasons tend to occur in the late winter and early spring and the male molting seasons occur in late spring, the fishing seasons usually begin in the fall. For golden king crab, however, there is no clear seasonality in breeding; and adult males and females appear to be spatially segregated throughout the year. Although we lack sufficient data to determine if there is any seasonality in male molting, it appears that there is no compelling biological reason to restrict the golden king crab fisheries to any particular time of the year. Therefore, we believe that, at present, fishing seasons should be determined primarily by what is most convenient or beneficial to fishermen and processors.

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