

ABILITY OF MALE KING CRAB, *PARALITHODES CAMTSCHATICA*, TO MATE REPEATEDLY, KODIAK, ALASKA, 1973

GUY C. POWELL,¹ KENNETH E. JAMES,² AND CHARLES L. HURD³

ABSTRACT

An experiment to test abilities of male king crab to mate repeatedly in an environment approximating natural conditions was conducted during the spring of 1970. Twenty-four males of varying size and shell age were placed into separate undersea compartments for intervals up to 56 days with 222 females. The ability of males to mate repeatedly was determined by introducing females in mating condition to males at the rate of one every 5 days.

No difference in mating capabilities of males of different types was evident until after exposure to seven females. At this point egg fertility and relative fullness of brood chamber of the females mated to the small old-shell males decreased significantly. Large new-shell males showed a marked decline in mating ability after the ninth mating. One small new-shell male mated with 13 females.

Owing to declining stocks within the Kodiak Island fishery, commercial harvest of king crab has declined from 96 to 11 million pounds over the past seven years, 1965-1971. To determine the level of king crab brood stocks necessary for perpetuation of a maximum sustained yield fishery, the reproductive capabilities of the king crab are being studied in detail.

In 1964, biologists of the Alaska Department of Fish & Game determined experimentally that recently-molted sublegal (smaller than 146 mm carapace length) male king crabs were capable of mating. Eleven males ranging from 120 to 144 mm carapace length mated 51 females in 16 days (Powell and Nickerson, 1965). Observations on individual males were not obtained. In 1971, males as small as 85 mm carapace length were found to be capable of mating (Powell, Shafford, and Jones, 1972). Of 3,402 males observed mating in nature from 1963 to 1971, however, only two were smaller than 100 mm (Powell, Rothschild, and Buss⁴).

Several authors have reported old-shell males congregated with adult females during the mating season and indicated they may be capable breeders because new-shell males were separate from the females at the time (Gray and Powell, 1966; Miyahara and Shippen, 1965).

Currently the reproductive success or failure of any particular brood year is not readily apparent until approximately 8 yr later when males are entering the fishery. At this late date, it is doubtful that we can, with any precision, evaluate the degree to which each of the limiting factors contributes to the success or failure; consequently we are unable to determine if resultant abundance levels are attributable to initial magnitude of egg production, environment, or effects of commercial fishing.

Prior to 1970, managers assumed that any level of harvest of males was acceptable as long as the 7-inch size limit (carapace width outside spines) was observed.

In recent years, we observed that the proportion of adult females without eggs and with partial broods had increased and that some of the female population was not being serviced (unpublished Alaska Department of Fish & Game data). Large adult females have approximately nine times more eggs than small ones (Haynes, 1968) and initial examination of unpublished Department of Fish & Game data reveals that the incidence of adults without eggs and with partial broods is greater among the

¹ Alaska Dept. of Fish & Game, Commercial Fisheries Div., Box 686, Kodiak, AK 99615.

² Bio-Statistics Div., Dept. of Preventive Medicine, Stanford University Medical Center, Stanford, CA 94305.

³ Alaska Dept. of Fish & Game, Commercial Fisheries Div., Box 234, Homer, AK 99603.

⁴ Powell, Guy C., Brian J. Rothschild, and James A. Buss. 1972. A study of king, *Paralithodes camtschatica* (Tilesius) brook stocks, Kodiak Island, Alaska, 1963-1971. 30 p. (Processed)

larger individuals. In order to place more males on the mating grounds and to stabilize annual harvests, a quota system was initiated in 1970.

It is important to know whether that segment of the male population harvested by the commercial fishery, i.e., large males and old-shell males (Nickerson, Osslander, and Powell, 1966) possess greater mating capabilities than smaller protected males which molt during the mating season. Also of significance is the question of whether undersized males would be adequate in numbers and ability to mate all females if larger males were removed by the fishery. Recent increases in the numbers of adult females with broods of reduced size appear related to simultaneous increased exploitation rates and may result from matings with males which had mated several times previously. Our experiment was designed to gain insight into these phenomena and to obtain more complete data for individual males, especially comparative data on mating ability for old-shell males and recently molted new-shell males.

In this paper, mating refers to the actual fertilization of the eggs. Hence, the term "mating capability" refers to the ability of the male to fertilize the eggs of the females to which he is exposed.

METHODS AND MATERIALS

Experimental Equipment and Location

The experiment was conducted in undersea pens, the sides and top of which were covered with nylon mesh; the bottoms were open to allow crabs to dig in the substrate as they would do in nature. Each pen was 8' × 8' × 4' and each divided into four equal sized compartments. Compartments were numbered 1 through 28 and situated in 40 ft of water on a level stretch of muddy-sand bottom east of Near Island adjacent to an area where king crabs normally mate. The study location is one mile from the city of Kodiak, Alaska. Pens were designed and located to simulate natural conditions. Environmental factors such as daily tidal currents, pressures, light intensities, temperatures, and salinities were considered important in that they might influence mating. For this reason, undersea pens were considered superior to aquaria.

The mating study was conducted in compartments 1 through 24 while 25 through 28 were

used to store crabs. Females were held in storage prior to and after the completion of mating.

Fishery biologists and trained technicians utilizing scuba observed the crabs underwater every day. Individual crabs were identified by tagging with permanent "isthmus" loop tags (Gray, 1965) prior to being placed in the pens.

Experimental Procedures

The experiment was designed to compare mating capabilities of four size shell-age classes of male king crabs (small new-shell, small old-shell, large new-shell, and large old-shell) by studying the effects of repeated matings on the ability of these males to mate successfully with additional females. A 5-mm range, 145-149, was used as a dividing point between small and large males at the juncture of legal and under-size crabs. Those 144 mm or less (commercially under-size males) were classified as small while those 150 mm or larger were classified as large (Table 1). Small males averaged 140 mm, large males 167.

Most males used in the experiment were captured by scuba divers. A few of the males of required size, however, were not available by diving (the preferred method of collecting) and therefore were taken from the catches of commercial pots and trawls.

All females used in the study were in pre-molt condition and were in the pre-copulatory embrace (Powell and Nickerson, 1965): i.e., they had already been selected for mating by males in the natural environment. The use of these females (called "graspees") was our method of insuring that females were ready to mate with males when introduced into the pens. Females from natural mating areas near the pens were captured by scuba divers a day or two before they were needed and ranged in length from 104 to 181 mm, with an average size of 134 mm.

TABLE 1.—Size relationships of experimental crabs.

Male king crabs Class	No. of female partners	Carapace length (mm)				
		Range		Mean		
Number		Male	Female	Male	Female	
Small old-shell	4	29	136-144	107-181	142	133
Large old-shell	9	82	156-193	114-175	178	134
Small new-shell	4	35	136-142	115-150	139	135
Large new-shell	10	76	150-168	104-160	158	134
Total	27 ¹	222				

¹ Three extra males replaced three original males which died.

Females were separated from the males which held them and placed in storage ready for use in the experiment. The average length of females increased as the study progressed because older females mate later in the season.⁵ Females captured 15 March through 15 April averaged 128 mm, while those captured 20 April to 20 May averaged 140.

Twenty-four females were paired randomly with the 24 males in the pens at the beginning of each of the 14 separate 5-day periods beginning 16 March and continuing through 24 May. On days when a complete set of 24 females could not be captured, those which had been were introduced to males which previously had had the largest number of female partners. Incomplete sets of females exist for early and late spawning periods—1, 2, 3, 12, 13, and 14—when mating crabs were relatively scarce. In addition, 12 females escaped from six compartments on 9 May when two pens were accidentally lifted; as many as three females were lost from a single compartment. During the middle of the mating season, 31 March through 5 May, females were abundant; consequently each male received a female for each of the eight consecutive periods within this interval. Females were introduced to males as soon after capture as possible; none were held more than two days and many were introduced the same day.

Females were left with males until mating was completed and eggs were known to be fertilized; consequently males commonly shared their compartments with several females at a time. Approximately 10 days after eggs were deposited on the pleopods, a sample of approximately 1,000 was obtained from each female to determine success of fertilization. Each sample consisted of several separate groups of eggs taken from scattered locations within the egg mass. Samples were preserved in Bouin's solution. Fertilized eggs developing for 7 to 10 days at approximately 37°F showed cleavage when viewed microscopically. When eggs were known to be fertilized (i.e., advanced cleavage stages observed), females were separated from their experimental male partners and placed in storage compartments 25-28.

Divers made observations at daily intervals recording data on underwater slates. Observations included collecting and measuring shed exoskeletons to determine day of molting, examining recently-molted females to determine relative fullness of the brood chamber, and recording activities of mating and feeding.

RESULTS

Relative success of male copulation was measured in two ways. First, relative fullness of brood chamber was determined subjectively by visually deciding what proportion of the brood chamber was filled with eggs and recording same on a scale of zero to one hundred (Table 2). The second, percent of eggs fertilized, was determined in two steps; (1) a prompt microscopic viewing of several hundred eggs to obtain quick estimates, followed later by (2) a careful microscopic examination of 100 eggs (Table 3).

Both measures of mating success provided compatible results and revealed that infertile eggs are scattered throughout the egg mass rather than being grouped separately from fertile eggs.

The raw data, y , for each of the two measurement variables were transformed so that they would be more normally distributed, using the formula:⁶

$$z = \sqrt{n + 1/2} \sin \sqrt{\frac{-1}{n + 3/4} \frac{y + 3/8^*}{n + 3/4}}$$

In this case, n is equal to 100, since both methods of measurement are based on a scale of 100.

A covariance analysis was performed relating z to x , the number of females mated. This analysis fits a least squares regression line $z = a_i + b_i x$ for each of the four groups, where a_i , b_i represent the intercept and slope respectively for the i th group. The results of this analysis are presented in Table 4. Slopes for each group appear to be significantly different from zero, except for percent of eggs fertilized in large old-shell and small new-shell males. The more negative the slope of the regression line, the less the

⁵ Determined from 3,402 observations of grasping pairs of king crabs captured over a 9-year period, 1963-1971. See page 257 National Geographic Magazine, Vol. 139, No. 2, Feb. 1971 for photograph of grasping pairs.

⁶ Thoni, H. Transformation of variables used in the analysis of experimental and observational data, a review. Technical Report No. 7, Statistical Laboratory, Iowa State University, Ames, Iowa, July 1967.

TABLE 2.—Success of each mating as determined by the relative fullness of the brood chamber (percent).

Male class	Male carapace length (mm)	Number of successive matings														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	
		Relative fullness of brood chamber (percent)														
Small old-shell	144	100	100	100	90	—	—	—	—	—	—	—	—	—	—	
	136	100	100	100	0	80	80	50	0	0	—	—	—	—	—	
	144	100	100	100	100	80	85	60	50	0	—	—	—	—	—	
	142	100	90	90	10	85	90	100	—	—	—	—	—	—	—	
No. of observations	4	4	4	4	4	3	3	3	2	2	—	—	—	—	—	
Average	141.5	100	97.5	97.5	50	81.7	85.0	70.0	25.0	0	—	—	—	—	—	
Large old-shell	164	100	100	90	100	80	90	80	75	80	—	—	—	—	—	
	156	80	100	90	100	100	100	90	20	80	30	—	—	—	—	
	163	100	90	100	100	100	100	100	—	—	—	—	—	—	—	
	190	100	100	100	100	90	100	100	90	90	75	80	90	5	35	
	184	100	100	70	100	100	90	90	90	100	—	—	—	—	—	
	193	100	90	95	100	50	100	90	60	80	0	—	—	—	—	
	181	100	85	100	100	90	100	100	—	—	—	—	—	—	—	
	180	100	100	100	100	100	100	90	75	20	85	—	—	—	—	
	189	90	90	100	90	90	75	20	90	—	—	—	—	—	—	
No. of observations	9	9	9	9	9	9	9	8	7	5	4	1	1	1	1	
Average	177.8	96.7	95.0	93.9	98.9	88.9	95.0	82.5	72.9	70.0	47.5	80	90	5	35	
Small new-shell	140	60	100	100	80	100	100	90	100	100	60	60	50	—	—	
	136	100	75	80	100	75	60	—	—	—	—	—	—	—	—	
	142	100	80	60	90	75	90	50	75	25	—	—	—	—	—	
	138	100	100	90	100	100	90	90	—	—	—	—	—	—	—	
No. of observations	4	4	4	4	4	4	4	3	2	2	1	1	1	1	—	
Average	139.0	90	88.8	82.5	92.5	87.5	85.0	76.7	87.5	62.5	100	60	60	50	—	
Large new-shell	150	75	100	100	100	90	90	—	—	—	—	—	—	—	—	
	160	100	100	100	70	100	0	90	90	90	70	0	0	—	—	
	165	10	100	100	10	100	75	80	70	90	100	80	—	—	—	
	163	100	90	100	100	90	60	90	50	60	—	—	—	—	—	
	168	100	90	90	100	100	100	100	10	80	75	—	—	—	—	
	161	100	100	100	100	90	75	60	—	—	—	—	—	—	—	
	160	100	100	90	80	35	—	—	—	—	—	—	—	—	—	
	153	100	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	151	100	70	70	100	90	90	80	50	60	60	0	—	—	—	—
	151	100	85	80	100	—	—	—	—	—	—	—	—	—	—	—
No. of observations	10	10	9	9	9	8	7	6	5	5	4	3	1	—	—	
Average	158.2	88.5	92.8	92.2	84.4	86.9	70.0	83.3	54.0	76.0	76.2	26.7	0	—	—	

TABLE 3.—Success of each mating as determined by percent of egg mass fertilized.

Male class	Male carapace length (mm)	Number of successive matings													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
		Percent of eggs fertilized													
Small old-shell	136	100	100	100	0	97	79	99	0	0					
	142	100	100	100	87	96	90	99	—	—					
	144	100	100	100	100	100	100	82 ²	99 ²	0					
	144	100	100	100	90	—	—	—	—	—					
No. of observations	4	4	4	4	4	3	3	3	2	2					
Average	141.5	100	100	100	69.3	97.7	89.7	93.3	44.5	0					
Large old-shell	164	100	100	90	100	100	100	100	99	100	—	—	—	—	—
	156	100	100	95	100	100	100	99	91	100	92	—	—	—	—
	163	100	99	100	100	100	100	100	—	—	—	—	—	—	—
	190 ¹	100	100	100	100	100	100	97	98	100	100	100	100	100	100
	184	100	100	100	100	100	99	100	100	100	—	—	—	—	—
	193	99	98	97	100	100	100	100	99	100	100	0	—	—	—
	181	98	100	100	100	100	100	100	99	—	—	—	—	—	—
	180	99	99	100	100	100	100	100	100	100	100	100	—	—	—
	189	100	100	100	100	100	100	100	100	100	—	—	—	—	—
No. of observations	9	9	9	9	9	9	8	7	5	4	1	1	1	1	
Average	177.8	99.6	99.6	98.0	100	99.9	99.7	99.4	98.6	100	73	100	100	100	
Small new-shell	140	100 ²	100	100	100	100	100	100 ²	100	98 ²	95 ²	100	97	100 ²	—
	136	98	100	91 ²	94 ²	98 ²	86	—	—	—	—	—	—	—	—
	142	100	100	98	99	100	89	100	99 ²	99 ²	—	—	—	—	—
	138	100	100	100	100	100	100	100 ²	—	—	—	—	—	—	—
No. of observations	4	4	4	4	4	4	3	2	2	1	1	1	1	1	
Average	139.0	99.5	100	97.2	98.2	99.5	93.8	100	99.5	98.5	95	100	97	100	
Large new-shell	150	100	100	100	100	100	100	—	—	—	—	—	—	—	—
	160	100	100	100	100	100	0	97	100	100	91	0	0	—	—
	165	100	100	100	100	98	99	87	97	0	99	59	—	—	—
	163	100	100	100	100	100	100	100	98	100	98	100	—	—	—
	168	100	100	38	100	98	94	97	95	100	35	—	—	—	—
	161	100	100	100	100	99	98	100	—	—	—	—	—	—	—
	160	100	99	99	100	95	—	—	—	—	—	—	—	—	—
	153	100	—	—	—	—	—	—	—	—	—	—	—	—	—
	151	100	100	100	100	100	100	100	99	100	100 ²	0	—	—	—
151	100	98	100	100	—	—	—	—	—	—	—	—	—	—	
No. of observations	10	10	9	9	9	8	7	6	5	5	4	3	1	1	
Average	158.2	100	99.7	93	100	98.8	84.4	96.8	97.8	80.0	81.2	19.7	0	0	

¹ The last 2 females ovulated but escaped before egg samples were taken.

² Female larger than male.

TABLE 4.—Comparison of king crab mating ability, slopes and slope contrasts for relative fullness of brood chamber and percent of eggs fertilized.

Male class	Relative fullness of brood chamber			Percent of eggs fertilized		
	Slope	Standard deviation of slope	F Value for Test of slope = 0	Slope	Standard deviation of slope	F Value for Test of slope = 0
Small old-shell	$b_1 = -1.416$	0.234	$F = 36.5$ $P < .0001$	$b_1 = -1.171$	0.202	$F = 33.5$ $P < 0.0001$
Large old-shell	$b_2 = -0.616$	0.112	$F = 30.3$ $P < .0005$	$b_2 = -0.087$	0.107	$F = .7$ $P = .32$
Small new-shell	$b_3 = -0.328$	0.164	$F = 3.9$ $P = .05$	$b_3 = -0.036$	0.142	$F = .1$ $P = .75$
Large new-shell	$b_4 = -0.677$	0.116	$F = 33.9$ $P < .0001$	$b_4 = -0.637$	0.100	$F = 40.4$ $P < .0001$
Test for equality of slopes $b_1 = b_2 = b_3 = b_4$			$F = 4.07, P = 0.01$	$F = 11.74, P = .0001$		
Slope Contrasts						
Contrast estimate	Standard deviation of estimate	F Value for test of contrast = 0	Contrast estimate	Standard deviation of contrast	F Value for test of contrast = 0	
Old-shell vs. new-shell $b_1 + b_2 - b_3 - b_4$	-1.028	0.329	$F = 9.80$ $P = 0.001$	-0.585	0.287	$F = 4.1$ $P = 0.04$
Large vs. small $b_1 + b_3 - b_2 - b_4$	-0.450	0.329	$F = 1.9$ $P = 0.17$	-0.482	0.287	$F = 2.8$ $P = 0.10$

mating ability of the males in that particular group. A test of the hypothesis of equality of slopes ($b_1 = b_2 = b_3 = b_4$) yields an F ratio of 4.1 for relative fullness of brood chamber and 11.7 for percent of eggs fertilized, significant at the 1 and 0.01 percent level respectively. In order to determine the significance of the size shell-age classifications, contrasts of old-shell versus new-shell and small versus large were computed as shown in Table 4. These contrasts indicate that the major contribution to the inequality in slopes comes from the difference in shell age. Size did not appear to be a significant factor as is indicated by P values of 0.17 and 0.10 respectively for relative fullness of brood chamber and percent of eggs fertilized. Within the shell-age contrast, the small old-shell males contribute the most in the form of a more negative slope, indicating that these males have much less mating ability than the other three groups.

The data presented thus far give a comparison of the mating abilities of the four size shell-age groups. A linear approximation was assumed for each group and, although this procedure is not exact, it is sufficiently close for comparative purposes. Graphs of the curves for mating ability versus number of matings indicate that small old-shell and large new-shell males have the least linear relationship of the four groups. The points plotted in Figures 1 and 2 are the means

of the transformed variables for each successive mating. A point may represent as few as one or as many as ten observations, as shown in Tables 2 and 3. The original 0 to 100 scale is attached to the graphs to make them easier to read; thus after the means are computed, they are transformed back to the original scale.

The slopes of the functions were approximated by computing the means of the transformed measurement variables for each x and fitting empirical curves to the data points. Figures 1 and 2 show the relationship between percent of eggs fertilized and relative fullness of brood chamber respectively and are presented primarily as an aid to fisheries management. The results, however, are quite consistent with those given in Table 4. The graphs show a marked decline in the mating ability of small old-shell males after approximately the seventh mating and a decline in the ability of large new-shell males after the tenth mating. Figure 2 indicates that partial clutches result from mating with small old-shell and large new-shell males which had mated several times previously.

The least squares regression lines for large old-shell males and small new-shell males are also plotted in Figures 1 and 2. These groups show little decrease in mating ability as the number of matings increases, particularly for the percent of eggs fertilized. The slope of the

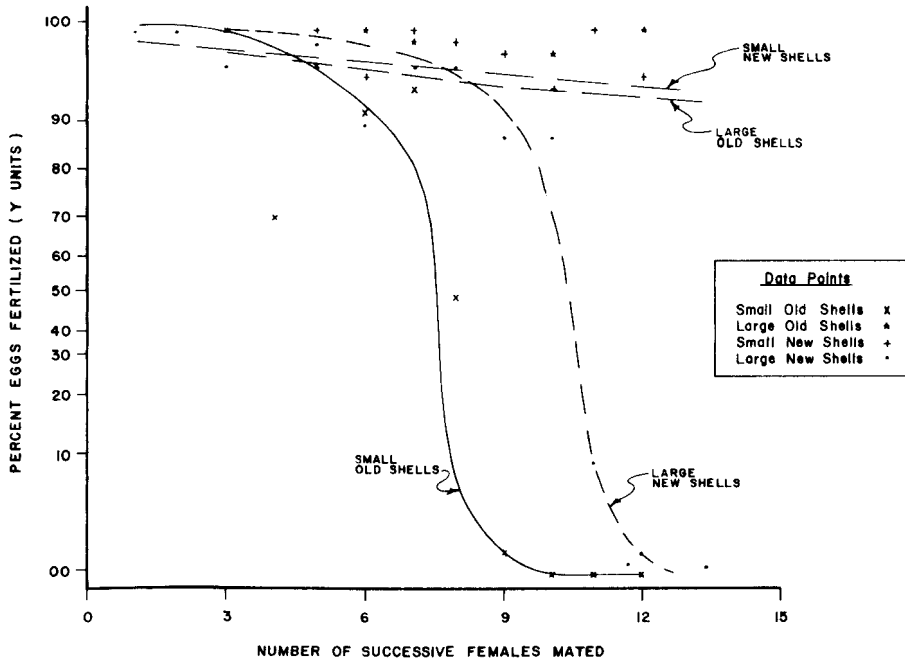


FIGURE 1.—Mating ability of male king crabs expressed as percentage of eggs fertilized.

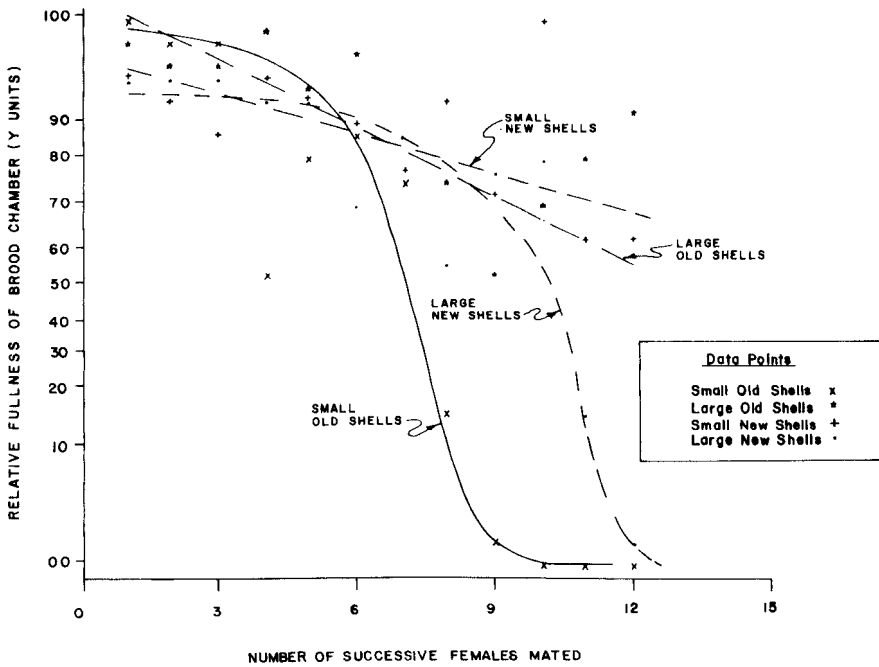


FIGURE 2.—Mating ability of male king crabs expressed as relative fullness of brood chamber of mated females.

regression line for large old-shell males for relative fullness of brood chamber is quite steep (-0.616) and nearly approaches the slope for large new-shell males (-0.677); however, there are no points in the vicinity of zero to indicate that mating ability for large old-shell males drops off suddenly after a certain number of matings. Furthermore, the other measurement variable indicates that the mating ability of large old-shell crabs does not decline at a significant rate when exposed to a maximum of 13 females.

DISCUSSION

This study indicates that all classes of males tested possessed considerable ability to mate repeatedly at the approximate rate of one female every 5 days. Mating ability of small old-shell and large new-shell male king crabs decreases markedly after approximately the seventh to ninth mating. The decline for large old-shells and small new-shells is not as noticeable.

Although the analysis of covariance for this experiment does not indicate significant differences in mating ability attributable to size, one should be hesitant in saying categorically that size is not a relevant factor. By examining the individual slopes in the graphs, it is evident that certain combinations of age and size have a marked effect on mating ability and one must realize that when a given factor is examined, the other factor is averaged out.

The knowledge obtained as a result of this investigation represents just a beginning in the understanding of the mating of king crabs. To what extent these findings are applicable to mating in nature remain uncertain. The effects of holding experimental crabs in undersea pens must be understood before realizing full application of the data to practical management of the fishery.

Holding males in pens could adversely affect mating ability of some classes, particularly later matings after prolonged captivity, while simultaneously enhancing ability of others by forcing partners into constant close association with one another. Larger females used later in the experiment may also have affected results.

Even though size does not appear to be a significant factor in mating ability as far as the number of repeated matings is concerned, and

even though small males appear to be capable breeders, it remains a possibility that in some instances in nature small males may not serve adequately as brood stock. Measurements of 6,804 king crabs captured by divers as mating pairs, 1963-1971, reveal that small young females are the first to mate each season followed three months later by large old females (Powell, Rothschild, and Buss, 1972). Further, males mating in nature with "pubescent" females (i.e., those mating for the first time and therefore the smallest found) are older and larger, averaging 42 mm more than females, with grasping observed as early as January 9 (Powell, Shafford, and Jones, 1972).

Apparently male size and male-female ratios are not the only factors affecting mating in nature. The presence in recent years of high incidence of adult females without eggs and with partial clutches within certain locations of the Kodiak fishery seem to be fishery-related because they occur only in areas of intense fishing (Powell, 1969⁷).

Adult female king crabs form mating congregations in shallow water from January through April and these congregations are intermittently distributed throughout the thousands of square miles of shallow habitat. For mating to be successful in each congregation, adequate numbers of capable males must be present during the relatively brief matable period following female ecdysis, otherwise delayed mating may adversely affect the success of ovulation and subsequent fertilization (Kurata, 1961; McMullen, 1969; and Wallace, Pertuit, and Hvatum, 1958).

The ratio of males to females necessary for complete mating success in nature appears dependent upon factors other than just numbers alone. The rate at which females molt and spatial distribution and size differences of adults inhabiting the location are also believed important. The greater the rate of female molting, the greater the number of males required. Male crabs select partners as early as 16 days prior to mating and continually grasp them until copulation occurs soon after female ecdysis (Powell, Rothschild, and Buss, 1972). Because of pre-mating "grasping" behavior, it is possible that females molt without male partners though a

⁷ Powell, Guy C. 1969. Some aspects of king crab biology. Proc. Am. Fish. Soc., West. Div. Meeting, Jackson Hole, WY, June 1969. (Processed)

favorable male-female ratio exists, because all males are either preoccupied grasping other females or resting between subsequent matings.

King crabs segregate to varying degrees according to size, sex, age, and time of year. Commercial fishing is concentrated in areas inhabited by large males with total effort varying according to factors such as accessibility. Thus cropping of males may be excessive in one area but not in another. Incidence of nonovigerous adult females is lowest in areas where sublegal sized males are abundant, but is often high in exploited areas with few adult males (unpublished, Alaska Dept. Fish & Game).

Size differences between partners, presence of competing males, and time of year also must be considered in evaluating the reproductive potential of mating populations.

It is conceivable that even with many young adult males present, a population of large old females may be inadequately serviced partly because the few surviving large males may, through aggressive behavior, keep smaller males away. To what extent competitive behavior exists is presently unknown but large old males commonly are found mating small young females in nature. Of the 14 matings in this experiment, where females were larger than males, 79 percent produced partial clutches.

Small males probably produce less reproductive material (sperm) than large males, and as a result, may be less capable of fertilizing the greater masses of eggs of large females.

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