Mating Pairs of Red King Crabs (*Paralithodes camtschaticus*) in the Kodiak Archipelago, Alaska, 1960-1984

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**Abstract**

Mating activity of red king crabs, *Paralithodes camtschaticus*, includes the grasping of females by males prior to and during copulation. We review and present extensive data from published and unpublished sources on grasping pairs of red king crabs collected from the Kodiak archipelago, Alaska. There were 3,651 grasping pairs of red king crabs captured from 22 locations along the eastern portion of the Kodiak archipelago. Pairs were captured from 1960 to 1984 with the majority (79%) captured during the 1966-1968 mating seasons. St. Paul Harbor was the most accessible location, received the most effort, and accounted for 41% of the pairs captured. Divers captured 99% of the grasping pairs, most in kelp beds with water depths $\leq 18$ m. Pairs were collected from January through May with most collected in April (63%) and May (32%). Pairs collected per dive minute tended to peak in April. The mean size of males (159 mm carapace length [CL]) was larger than the mean size of female crabs (126 mm CL), and males were larger than their female partners in 95% of the pairs. The mean carapace length of females in grasping pairs increased markedly over the mating season, whereas such a trend was less evident in males. Legal-sized males ($\geq 147$ mm CL) composed 75% of the males in pairs and only 4% of all males in pairs were $<130$ mm CL. Fifty-nine percent of the grasping males were anexuviants. These data suggest that the present size limit alone does not provide adequate protection to the reproductive potential of the stock and that 130 mm CL should be used as a lower size bound for identifying functionally mature males when developing fishery management measures for the Kodiak area red king crab fishery.
Introduction

Precopulatory grasping of females by male crabs is a behavior common to many crab species (Knudsen 1964) including red king crabs, *Paralithodes camtschaticus* (Powell and Nickerson 1965). Male red king crabs use their chelipeds to grasp the upper meropodite of a female's chelipeds prior to copulation (Marukawa 1933). The male faces the female and grasps her until she molts, then he regrasps her until mating is completed. The male passes spermatophores from his fifth pereiopods to the gonopores and coxae on the female's third pereiopods (Nyblade 1987). The eggs are fertilized during ovulation and attach to the female's pleopodal setae (McMullen 1967c). Females are usually mated within hours after molting (Powell and Nickerson 1965), but can mate up to 13 days after molting (McMullen 1969). Males generally must wait at least 10 days after ecdysis before mating (Powell et al. 1973). Unlike females, male red king crabs do not need to molt prior to mating (Powell and Nickerson 1965).

Alaska Department of Fish and Game (ADFG) biologists captured 3,651 grasping pairs of red king crabs from the Kodiak archipelago, Alaska, during 1960-1984. Portions of these data have been presented by Powell (unpubl. manuscript), Powell and Nickerson (1965), Gray and Powell (1966), McMullen (1967a,b), Kingsbury and Yoshihara (1970), Powell et al. (1973), and Blau (1986). Much of the grasping pairs data were previously presented only in an unpublished manuscript (G.C. Powell, B.J. Rothschild, and J. Buss).

Grasping pairs data for red king crabs from the Kodiak archipelago have been important in the assessment and development of fishery management practices for Alaskan king crabs. The Alaska red king crab fishery is prosecuted as a males-only fishery with a minimum size for legal retention. The size limits have been established on the basis of market considerations and the need to protect the reproductive potential of the stock. The minimum legal size for the Kodiak area red king crab fishery was initially established at 140 mm carapace width (CW) in 1940, increased to 165 mm CW in 1950, and increased again to the present size limit of 178 mm CW in 1963 (Donaldson and Donaldson 1992). The current legal size of 178 mm CW corresponds to a carapace length (CL; the measurement generally used by biologists to record size of king crabs) of 147 mm (Pengilly and Schmidt 1995). Eldridge (1975) noted that the males in breeding pairs collected during 1964-1971 were predominantly in old-shelled (anexuviant) condition and were larger than the commercial fishery’s legal-size limit. He assessed the possible effects of size limits and quotas in the males-only commercial fishery on the stock's reproductive potential. Schmidt and Pengilly (1990) examined the male and female size distribution in over 3,400 red king crab grasping pairs collected during 1964-1971 and described by G.C. Powell, B.J. Rothschild, and J. Buss (unpubl. manuscript). They interpreted those data as indicating males <130 mm CL played an insignificant role in mating in natural conditions. Based on that observation, Schmidt and Pengilly (1990) argued that 130 mm CL is a more appropriate
lower size bound for functionally mature red king crab males in the development of Kodiak area harvest strategies than are the smaller sizes of male physiological sexual maturity (Powell et al. 1973) or of males capable of mating in captivity (Paul and Paul 1990). Pengilly and Schmidt (1995) also extrapolated their estimated size at functional maturity for male red king crabs from the Kodiak area to other Alaskan king crab stocks to develop harvest strategies for Bristol Bay red king crabs, St. Matthew Island blue king crabs (*P. platypus*), and Pribilof Islands blue king crabs. The estimated size of males at functional maturity based on the Kodiak area grasping pair data remains an important component in the present harvest strategies for red king crabs in the Kodiak area and Bristol Bay, and blue king crabs off the Pribilof Islands and St. Matthew Island (Pengilly and Schmidt 1995, ADFG 2000a).

In this paper we summarize data from published and unpublished sources and analyze the following topics including size and shell-age composition by sex and season, location and timing of mating, and clutch conditions. These data provide information for red king crabs from the Kodiak area on habitat used by molting mature females and mating pairs, season of peak mating activity, trends in timing of mating activity related to size and reproductive history of females, and the size of mating males as compared to the minimum size limit for the commercial fishery.

**Methods**

All grasping pairs of red king crabs were assumed to be mating pairs. We examined data on 3,651 grasping pairs that were captured at 22 locations along the eastern portion of the Kodiak archipelago by ADFG biologists from 1960 to 1984 (Table 1, Fig. 1). The 22 locations, spanning a north-to-south distance of 160 km, lie between latitudes 56º50'N and 58º50'N and longitudes 151ºW and 155ºW. Three locations accounted for 74% (2,676) of the grasping pairs collected by divers: St. Paul Harbor (41%), Kitoi Bay (22%), and Middle Bay (11%). Most pairs were collected in April (63%) and May (32%). The majority of the pairs (61%) were captured during the 1966 and 1967 mating seasons.

Scuba divers captured 99% (3,603) of the grasping pairs in an opportunistic manner, without a formal sampling design. Typically, two divers worked together, trading between diving and dive-tendering responsibilities, during each collection trip. Dive collection trips were led by the senior author and assistant divers worked under the training and guidance of the senior author. Seventy-eight percent (2,843) of the diver-collected pairs were captured during 1966-1968. Less than 1% (45) of the pairs were captured in standard 400-mesh eastern otter trawls during ADFG surveys (Powell, unpubl. manuscript; Gray and Powell 1966; McMullen 1967a,b; Kingsbury and Yoshihara 1970; Blau 1986). Three of the grasping pairs were collected in pots (two during an ADFG survey and one during commercial fishing).
**Table 1. Number of red king crab mating pairs captured in the Kodiak archipelago, Alaska, 1960-1984, by location, year, and month.**

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\textsuperscript{a}All grasping pairs were captured by scuba divers unless otherwise footnoted.

\textsuperscript{b}Grasping pairs captured in king crab pots.

\textsuperscript{c}Grasping pairs captured in 400-mesh eastern otter trawls.

\textsuperscript{d}Place name is of local origin and not used by the U.S. Geological Survey or the National Oceanic and Atmospheric Administration.
Table 1. (Continued.) Number of red king crab mating pairs captured in the Kodiak archipelago, Alaska, 1960-1984, by location, year, and month.a

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*aAll grasping pairs were captured by scuba divers unless otherwise footnoted.
*bGrasping pairs captured in king crab pots.
*cGrasping pairs captured in 400-mesh eastern otter trawls.
*dPlace name is of local origin and not used by the U.S. Geological Survey or the National Oceanic and Atmospheric Administration.
Figure 1. Location and number of red king crab grasping pairs captured in the Kodiak archipelago, 1960-1984.
Divers transported grasping pairs to the surface by holding one rear leg (fourth pereiopod) of the male in a pair (Idyll 1971). During capture and transport to the surface by divers, most male crabs continued to grasp their female partners despite considerable disturbance. Males grasped their partner up to an hour while out of water for data recording. Grasping males caught in trawls continued to grasp their female partners despite the rough treatment of being caught in a trawl and shaken out on deck.

Data recorded from captured pairs included: location, date, and depth of capture; carapace lengths; carapace widths; estimated shell (exoskeleton) ages; legal status of males; and the status of female clutches (clean setae, presence of uneyed, eyed, or hatched embryos). Carapace length was measured in millimeters using Vernier calipers according to Wallace et al. (1949). Sublegal- or legal-size status was determined for males beginning in 1968 by measuring width outside the spines, and was based on the minimum legal size of 177.8 mm (7.0 inches) CW outside the spines (ADFG 2000a). For the males that did not have legal status recorded at collection, we assigned legal status prior to our analysis to those ≥ 147 mm CL, the carapace length that most closely corresponds to legal carapace width (Pengilly and Schmidt 1995). We limited our analysis of size and shell age attributes to the 3,618 grasping pairs with recorded carapace lengths.

There were 3,610 pairs with both carapace length and shell ages recorded. Shell age was estimated as the number of months since last molt based on shell condition and appearance according to Weber and Miyahara (1959). For our analyses, we classified females and males by estimated shell age and size. Females with estimated shell ages of 1 or 2 months were classified as “postmolt,” and those with estimated exoskeleton ages of 11 or 12 months were classified as “premolt.” We classified males into shell-age classes as follows: “new-shell” for 1-8 months old, “old-shell” for 9-16 months old, and “very-old-shell” for 17-36 months old. We also classified legal-sized males into two groups based on carapace length and shell-age class according to Peterson et al. (1986). New-shell legal males ≤164 mm CL were classified as “recruits” that were estimated to be in their first year of availability to commercial harvest. The remaining legal-sized males were classified as “postrecruits.”

Catch per unit effort (CPUE) was calculated as the number of grasping pairs collected for each dive (in minutes) and provided an index of relative density of grasping pairs in an area during a collecting period. We grouped effort and catch over semimonthly periods from March through May using data available from 1966-1968 diver logs to compute CPUE. Only data from locations and years in which CPUE could be computed for at least one semimonthly period in each of March, April, and May are presented and discussed here.
Results

**Habitat and Depth of Collected Grasping Pairs**

The 3,603 grasping pairs collected by divers were captured at 18 locations in bays (Fig. 1, Table 1) that had a wide variety of substrates, primarily rocky kelp-covered areas near shore. Most diving occurred in depths of 9-21 m and rarely as deep as 46 m. Grasping pairs were most commonly found in 5-15 m of water in kelp beds (*Agarum, Alaria, Costaria, Laminaria*, or *Nereocystis*) adjacent to deeper areas devoid of kelp. Water temperatures ranged from –0.5 to 4.5ºC.

Of the 45 grasping pairs caught in trawls, 14 were from Middle, Kalsin, Kaguyak, and Alitak bays, and 31 came from offshore banks, Marmot Flats, and Portlock Bank (Fig. 1, Table 1). Grasping pairs were caught during trawl surveys at depths of 18-50 m in the bays and 48-90 m on the offshore banks. One grasping pair was captured in a commercially fished pot at a depth of 62 m on Portlock Bank. Two other grasping pairs were captured in pots in Perenosa Bay, but no depth was recorded with their capture.

**Observations by Scuba Divers**

Divers commonly observed large aggregations of adult females on various substrates. Aggregated females were generally in one layer in numbers estimated at several thousand. Several aggregations in close proximity to one another totaled an estimated 10,000 crabs. Some adult males were common near the aggregations of females, but males were never seen aggregated or in large numbers during the mating season.

Exuviae on the bottom alerted divers to ongoing or recently completed molting in the area. Exuviae began deteriorating as soon as shed. The thin arthrodial membranes, in particular, attracted gastropods, shrimp, and urchins that feed on them. Some exoskeletons were consumed by anemones (Powell 1976). Chelae and dactyls were the last parts to deteriorate.

Clutch conditions were recorded on 466 postmolt females in grasping pairs. Ninety-nine percent of those females had not ovulated and were without embryos, whereas 1% had clutches of uneyed embryos. Spermatophore bands were present on the gonopores of 24% of the 461 postmolt females. By comparison, the embryos of 69% of the 2,948 premolt females examined in grasping pairs had hatched, and 31% had clutches with varying percentages of hatched and unhatched embryos. The incidence of unhatched embryos in the clutches of grasped premolt females decreased monthly from March through May. The clutches of 67% of 115 grasped premolt females collected in March contained unhatched embryos, as compared to 37% of the 2,053 collected in April and 13% of the 779 collected in May (chi-square = 220.73, d.f. = 2, *P* < 0.00001).

Three hundred and sixteen male crabs from grasping pairs were tagged and released, some still grasping their female partners during release. Eleven of the tagged males were recovered later in the same season grasping different females from when originally tagged. Intervals of freedom for those
11 ranged from 5 to 42 days, illustrating that males continue to mate with more than one female through the mating season.

**Seasonal Presence of Grasping Pairs and Seasonal Changes in Diver CPUE**

The percentage of pairs captured by month was <1% in January, 1% in February, 4% in March, 63% in April, and 31% in May (Table 1). January 9 and May 26 were the earliest and latest dates in any year that grasping pairs were captured. The disparity in number of grasping pairs by month may reflect the opportunistic sampling by scuba divers, seasonal changes in mating activities, and year-class strength. To quantify seasonal changes in mating activity we examined diver CPUE of grasping pairs over semi-monthly periods during March-May at the three locations for which such data were available.

CPUEs ranged from 0 to 1.188 pairs per dive minute (Table 2). All zero values occurred during March, the first half of April, or the last half of May. Highest CPUEs were during the last half of April with slightly lower values during the first half of May.

**Size and Shell-Age Composition of Females and Males**

Of 3,610 grasped females, 86% were premolt and 14% postmolt. Sizes of premolt and postmolt females were similar but variable. Premolt females ranged from 81 mm to 181 mm CL (mean = 125 mm CL), whereas postmolt females ranged from 96 mm to 166 mm CL (mean = 126 mm CL). Given the slight variation in size between premolt and postmolt categories, all females regardless of shell age were pooled in our subsequent analyses. Carapace length of 3,618 females ranged from 81 mm to 181 mm CL with a mean size of 125 mm CL (Fig. 2). Only 3% of the females in the grasping pairs were smaller than the estimated size at 50% maturity (SM50) for Kodiak area female red king crabs (102 mm CL; Pengilly et al. 2002).

The size of 3,618 grasping males ranged from 80 mm CL to 216 mm CL with a mean of 159 mm (Fig. 2). Only 4% of the males were smaller than the 130 mm CL size used to define male functional maturity in the harvest strategy for red king crabs in the Kodiak Management Area (Pengilly and Schmidt 1995). Seventy-four percent of the males were either recorded as legal-sized at their capture or later identified as legal-sized on the basis of carapace length. Of those legal-sized males, 52% were recruits and 48% were postrecruits. Old-shell and very-old-shell animals accounted for 54% and 5% of the 3,616 males for which shell age was recorded. Old-shell and very-old-shell males predominated in both the legal (61%) and sublegal (56%) size classes.

The size distribution of males differed markedly by shell age (Fig. 2). New-shell males had a nearly symmetric, unimodal size-frequency distribution (mean = 152 mm CL) and ranged from 80 mm to 190 mm CL. Old-shell males ranged from 85 mm to 216 mm CL (mean = 163 mm CL) and had a
Table 2. Minutes of scuba diving needed to capture grasping pairs of male and female red king crabs from Kitoi Bay, Afognak Island; and St. Paul Harbor and Kalsin Bay, Kodiak Island, 1966-1968.*

<table>
<thead>
<tr>
<th>Year</th>
<th>Location</th>
<th>March 1-15</th>
<th>March 16-31</th>
<th>April 1-15</th>
<th>April 16-30</th>
<th>May 1-15</th>
<th>May 16-31</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Minutes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1966</td>
<td>St. Paul Harbor</td>
<td>0</td>
<td>60</td>
<td>110</td>
<td>0</td>
<td>295</td>
<td>105</td>
</tr>
<tr>
<td></td>
<td>Pairs</td>
<td>—</td>
<td>0</td>
<td>0</td>
<td>—</td>
<td>256</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>CPUE$^b$</td>
<td>—</td>
<td>0.000</td>
<td>0.000</td>
<td>—</td>
<td>0.868</td>
<td>0.019</td>
</tr>
<tr>
<td>1967</td>
<td>Kitoi Bay</td>
<td>18</td>
<td>63</td>
<td>285</td>
<td>103</td>
<td>124</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Pairs</td>
<td>3</td>
<td>19</td>
<td>199</td>
<td>104</td>
<td>41</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>CPUE</td>
<td>0.167</td>
<td>0.302</td>
<td>0.698</td>
<td>1.010</td>
<td>0.331</td>
<td>—</td>
</tr>
<tr>
<td>1967</td>
<td>St. Paul Harbor</td>
<td>19</td>
<td>23</td>
<td>153</td>
<td>85</td>
<td>117</td>
<td>64</td>
</tr>
<tr>
<td></td>
<td>Pairs</td>
<td>0</td>
<td>0</td>
<td>54</td>
<td>101</td>
<td>101</td>
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<td>0.000</td>
<td>0.353</td>
<td>1.188</td>
<td>0.863</td>
<td>0.000</td>
</tr>
<tr>
<td>1968</td>
<td>Kitoi Bay</td>
<td>68</td>
<td>0</td>
<td>184</td>
<td>119</td>
<td>241</td>
<td>123</td>
</tr>
<tr>
<td></td>
<td>Pairs</td>
<td>4</td>
<td>—</td>
<td>67</td>
<td>13</td>
<td>11</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>CPUE</td>
<td>0.059</td>
<td>—</td>
<td>0.364</td>
<td>0.109</td>
<td>0.046</td>
<td>0.000</td>
</tr>
<tr>
<td>1968</td>
<td>St. Paul Harbor</td>
<td>0</td>
<td>105</td>
<td>223</td>
<td>258</td>
<td>157</td>
<td>117</td>
</tr>
<tr>
<td></td>
<td>Pairs</td>
<td>—</td>
<td>3</td>
<td>147</td>
<td>162</td>
<td>37</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>CPUE</td>
<td>—</td>
<td>0.029</td>
<td>0.659</td>
<td>0.628</td>
<td>0.236</td>
<td>0.000</td>
</tr>
<tr>
<td>1968</td>
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<td>0</td>
<td>132</td>
<td>0</td>
<td>67</td>
<td>51</td>
<td>268</td>
</tr>
<tr>
<td></td>
<td>Pairs</td>
<td>—</td>
<td>6</td>
<td>—</td>
<td>26</td>
<td>3</td>
<td>1</td>
</tr>
</tbody>
</table>

*Only data from years and locations in which diving for grasping pairs occurred during March, April, and May is included.

$^b$CPUE = number of grasping pairs collected per dive-minute for semimonthly period by year and location.
bimodal size-frequency distribution with peaks at 145 mm and 170 mm CL. Very-old-shell males had a highly skewed size-frequency distribution with the highest frequencies occurring at the largest sizes. Very-old-shell males tended to be larger than the new-shell or old-shell males and ranged from 130 mm to 203 mm CL (mean = 177 mm CL).

Size Relationships of Males and Females within Pairs
Male carapace length was larger than female carapace length in 95% of the grasping pairs. Males were larger than their female partners in 99.5% of the pairs involving very-old-shell males, as compared to 94.8% of the pairs involving new-shell males and old-shell males (chi-square = 8.74, d.f. = 2, $P < 0.013$). Carapace length had a weak but significant ($P < 0.0001$) positive correlation with the carapace length of grasped female in each shell-age class of males ($r = 0.25$ for new-shell males, $r = 0.24$ for old-shell males, and $r = 0.46$ for very-old-shell males) and for all males combined ($r = 0.29$). LOWESS smoothings (Chambers et al. 1983) of the data, however, indicate that the relationship of male to female carapace length within grasping pairs was not linear (Fig. 3). Male carapace length tended to increase with female carapace length with a steeper slope for females <125 mm CL than for females >130 mm CL. The size difference between males and females was not constant over the female size range and females 160-180 mm CL tended to approach the size of their grasping male (Fig. 3).
Monthly Changes in Size of Mating Females and Males

Pairs were grouped by date into semimonthly periods for investigating seasonal trends in size of females and males. Pooling data from all years and all locations revealed an increase in size of pairs with date (Fig. 4). This trend also existed for males but was less pronounced. Females collected during January and February tended to be close to or less than the female SM50 estimated for Kodiak area red king crabs (102 mm CL). Females collected during March through May were generally larger than the female SM50.

Three samples were available for investigating trends in size of mating males and females over the period March through May 15 within the same location and year: Kitoi Bay in 1967, St. Paul Harbor in 1968, and St. Paul Harbor in 1969. Females were larger in later sampling periods in each of the three samples, and carapace length varied significantly by semimonthly period ($P < 0.05$) in each case (Table 3). Females in grasping pairs collected during May 1-15 were larger than those collected during April 1-15 by 14 mm or more in each sample. Results of post hoc pairwise comparisons of mean female carapace length using the Bonferroni pairwise
Table 3. Mean carapace length (mm) of male and female red king crabs in grasping pairs by semimonthly sampling period, March-May 15, collected from Kitoi Bay, Afognak Island in 1967 and St. Paul Harbor, Kodiak Island in 1968 and 1969.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>Females</td>
<td>Males</td>
</tr>
<tr>
<td>March 1-15</td>
<td>3</td>
<td>115.7</td>
<td>173.0</td>
</tr>
<tr>
<td>March 16-31</td>
<td>19</td>
<td>129.2</td>
<td>181.0</td>
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<tr>
<td>April 1-15</td>
<td>199</td>
<td>129.1</td>
<td>178.0</td>
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<td>April 16-30</td>
<td>104</td>
<td>134.9</td>
<td>176.1</td>
</tr>
<tr>
<td>May 1-15</td>
<td>41</td>
<td>143.4</td>
<td>175.9</td>
</tr>
<tr>
<td>F</td>
<td>21.568</td>
<td>0.797</td>
<td>88.546</td>
</tr>
<tr>
<td>d.f.</td>
<td>4, 361</td>
<td>4, 361</td>
<td>3, 345</td>
</tr>
<tr>
<td>P</td>
<td>&lt;0.0001</td>
<td>0.528</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

*N* is the number of grasping pairs collected per sampling period; and *F*, d.f., and *P* are for the results of analysis of variance of carapace length.

Figure 4. Box plots of size distributions by semimonthly periods of female and male red king crabs in 3,618 grasping pairs collected from the Kodiak archipelago during 1963-1984.
procedure at a significance level of $P = 0.05$ (results not shown here) were consistent with a trend of increasing size.

Male size varied significantly ($P < 0.05$) over time during March-May only for the 1968 St. Paul Harbor sample (Table 3). Differences in mean carapace length of males among semimonthly sampling periods in that case was $<6$ mm, and only the comparison between the mean carapace lengths for April 1-15 and May 1-15 were significant ($P < 0.05$) in the post hoc Bonferroni pairwise tests. Although variation in carapace length of males over time was not statistically significant for the 1969 St. Paul Harbor sample, the males collected during March had a smaller average carapace length than those collected during April and May. The males collected from Kitoi Bay during 1967, however, showed no consistent trend in carapace length over time. Shell-age composition of mating males also varied over time within the three samples. Males in the 1967 Kitoi Bay sample were exclusively old-shelled or very-old-shelled in all periods except for May 1-15, in which two of 33 males were new-shelled. Although new-shell males were predominant in the grasping pairs collected in St. Paul Harbor during March-May of both 1968 (332 of 349) and 1969 (38 of 58), old-shell males predominated in the pairs collected during March of each year and all 10 grasping males collected during March 1969 were in old-shell condition.

Forty-nine grasping pairs were collected during January-February from St. Paul Harbor or Middle Bay during the 1970s (39 from 1971 and 1972). Shell age and carapace length were recorded for males and females in 46 of those pairs. Females collected during January-February were all in premolt condition, ranged from 81 mm to 130 mm CL, and averaged 98 mm CL. Only one female exceeded 113 mm CL, and 30 of 46 females were smaller than the estimated size at 50% maturity (102 mm CL) for Kodiak area females. In contrast, of the 3,602 mating females captured during March-May, only 92 were premolt and $<103$ mm CL. Forty-three of the mating females captured during January-February had their clutch condition recorded. Of those, 84% (36) had only silky setae on their pleopods (indicative of first mating) and the remainder had clutches of hatching embryos. Of the 3,422 mating females collected during March-May that had clutch condition recorded, only 13% had only silky setae indicative of first mating.

Males collected during January-February tended to be smaller than those collected later (Fig. 4). The 46 males averaged 140 mm CL and ranged in size from 85 mm to 177 mm CL; only one male was smaller than 112 mm CL. Sixty-five percent of the males were sublegal-sized and 24% were smaller than the size of functional male maturity used in the Kodiak area harvest strategy (130 mm CL; Pengilly and Schmidt 1995). Old- and very-old-shelled crabs accounted for 78% of the 46 males.

**Discussion**

Male red king crabs from the Kodiak area and Bristol Bay become physiologically mature at a younger age and smaller size than females (Powell
et al. 1973, Paul et al. 1991). The size at 50% maturity for Kodiak area female red king crabs is 102 mm CL (Pengilly et al. 2002), whereas male red king crabs from the Gulf of Alaska can mate under controlled conditions at 80-100 mm CL (Powell et al. 1973, Paul and Paul 1990). Nonetheless, nearly all males in the grasping pairs examined in our study were larger than their female partners and were larger than lower-size bounds of mating males. The greater size of males in grasping pairs is at least partly attributable to the divergence in growth rates of male and female crabs at the onset of maturity at 5 years of age (McCaughran and Powell 1977); female growth rates decrease markedly after maturity resulting in mature males being larger at similar ages. However, the size-frequency from grasping pairs captured during January-February indicates that at least small pubescent females tend to be grasped by larger older males. The average growth per molt of males in the Kodiak area is <20 mm CL (McCaughran and Powell 1977, Schmidt and Pengilly 1990) and males in the January-February pairs averaged 42 mm CL larger than females and were predominantly in old-shell or very-old-shell condition. Hence, few females collected during January-February were grasped by males from their own cohort, and most were grasped by males that were at least 2 years older than themselves.

Powell et al. (1973) captured king crabs in December 1970-March 1971 in Middle Bay and found that most males were 63-100 mm CL, whereas grasping pairs were composed of males ≥123 mm CL. They suggested that the absence of small, physiologically mature males in the grasping pairs under natural conditions was due to the crabs’ inability to compete with larger males and that small males may mate in the absence of large males or in the presence of a surplus of pubescent females. Later work by Paul and Paul (1990, 1997), however, revealed that matings by males 80-89 mm CL may not always result in successful fertilization of clutches and that the ability to fertilize clutches in successive matings increases with the size of males.

The role of female size in determining the size of the grasping male remains unresolved. Red king crab males 80-110 mm CL can mate when paired with larger females under controlled conditions (Powell et al. 1973). However, the larger size of males could confer advantages when they are grasping females under natural conditions. Those advantages may include better ability to retain the grasp on a resistant female, protect a newly molted female from predators (e.g., Pacific cod, Gadus macrocephalus; Blau 1986), and lift and carry away the female when disturbed. The data from grasping pairs show a weak positive correlation between size of males and females within pairs for females <130 mm CL, suggesting some effect of female size on the size of the grasping male.

Variable recruitment and abundance of older cohorts during the period of data collection may also be responsible for the large size, and predominance of old-shell and very-old-shell males. Most grasping pairs were collected during 1966-1968. Harvests in the red king crab commer-
cial fishery in the Kodiak area peaked at an all time high in 1966 and declined in subsequent years due to poor recruitment (ADFG 2000b). Hence, these data may largely reflect a period during which mature males were dominated by the aging remnant of large cohorts that supported growth of the commercial fishery up to its 1966 peak. Males in the small sample of grasping pairs collected during January-February of the early 1970s were on average 19 mm CL smaller than males in the total data set. That may be due to a smaller population size distribution for males during the early 1970s or a tendency of smaller males to mate with pubescent females during the early portion of the mating season. Unfortunately, red king crabs in the Kodiak area were not surveyed annually prior to 1972 to provide information on the population size and shell-age distribution for the periods during which most of the grasping pair data were collected. However, the size distribution of females in the grasping pair data agrees closely with the size distribution of all mature females captured during the Kodiak area pot surveys conducted during 1972-1986 (Pengilly et al. 2002). Hence, the size distribution of the females in the grasping pair data is apparently characteristic of mature female red king crabs in the Kodiak area over the long term.

A progressive increase in the mean size of females caught in grasping pairs through the January-May mating season was clearly evident, indicating females tend to release their larvae and mate later in the mating season with increasing age. Unlike females grasped later in the season, females grasped earliest in the season were predominately pubescent. Although the grasping males showed only a slight trend of increasing size through the mating season, the shell age of grasping males decreased through the mating season. That trend in shell age of males may reflect only the molt timing of males that participated in mating throughout the season. That trend may also reflect the advantage in mating that anexuviant males have over any molting males early in the mating season. Males that are not molting would clearly have an advantage in grasping females over those that are in the process of molting and that advantage extends into the minimum 10 days after ecdysis during which males are incapable of mating (Powell et al. 1973).

Red king crabs migrate to shallow water for mating during April and May in Japan (Marukawa 1933), Russia (Vinogradov 1945), and Alaska (Jewett and Powell 1981). In the data from the Kodiak Island area, grasping pairs occurred from January through May, but the peak of mating activity, indicated by diver CPUE, occurred during April. The observations by divers reported here suggest that hatching of embryos closely coincides with the onset of mating activity of multiparous females. Thirty-one percent of all grasped females that were collected in premolt condition carried clutches of hatching embryos, with that percentage declining from 66% of those collected during March, to 37% during April and 13% during May. We suggest that the March-May period with an April peak for mating activity of multiparous females confers survival advantages to the larvae
released prior to mating. Some diatoms are an important energy source for first-feeding king crab larvae, and hatching concurrently with the spring phytoplankton bloom may be an important factor affecting their survival (Paul et al. 1989). We have no data on the timing of phytoplankton bloom relative to the data on hatching and mating collected during this study. However, in a study conducted in Auke Bay, Alaska, April was the month during which the primary spring phytoplankton bloom occurred (Ziemann et al. 1990) and the peak abundance of red king crab first zoal stage always followed the peak in chlorophyll (Shirley and Shirley 1990).

Large aggregations of unpaired females were also observed by divers while they were collecting grasping pairs. Powell et al. (1973) described the formation of female aggregations in shallow waters off Kodiak Island during April-May, with aggregation formation of primiparous females preceding that of multiparous females. Seasonal aggregations of primiparous and multiparous female red king crabs and their movement to shallow waters during March-May have also been described from Auke Bay, Alaska (Stone et al. 1992, 1993). Mature males were not noted to form aggregations during the mating season, although they were deeper and less available to divers, whereas the aggregations of females would comprise several thousand animals. Possible benefits of adult female congregations during mating may be to emit pheromones in mass to guide adult males to them. In blue crabs, *Callinectes sapidus*, “pubertal” females release a pheromone that triggers courtship display by males (Gleeson 1987) and in the American lobster, *Homarus americanus*, females emit pheromones at or around the time of ecdysis (Cowan 1991).

The depth zone most important for red king crab reproduction is unknown. In this study grasping pairs were caught from 5 m to 90 m. Although we cannot affix a percentage of grasping pairs to different depths, we infer that a higher proportion of mating occurs at depths <20 m than in deeper waters because king crabs annually migrate from deep to shallower water in January-May to reproduce in kelp-fringed areas, before moving deeper again. Kodiak Island has a coastline of 4,000 km (Kodiak Island Borough 1988), and kelp covers much of the lower rocky intertidal and subtidal areas. Nearshore (<30 m) subtidal areas of the remaining islands in the archipelago substantially add to available king crab mating habitat.

Both from this study and others (Haynes 1974, Armstrong et al. 1986), red king crab larvae are known to hatch nearshore. Hatching of larvae in nearshore waters may improve the viability of the young crabs settling there. Red king crab glaucothoe are known to settle to substrates <30 m deep in Cook Inlet and the Kodiak area (Sundberg and Clausen 1979, Blau et al. 1992), but they are seldom found in deeper waters. Age 0-3-year-old red king crabs were found in water depths <50 m along the north side of the Alaska Peninsula and in Bristol Bay (McMurray et al. 1986). Sasakawa (1970) stated that red king crab larvae released 24 km offshore from the west coast of the Kamchatka Peninsula added little to the success of small crabs in that area. Nonetheless, the presence of grasping pairs in deeper
waters on offshore banks in the Kodiak area indicates that larvae released offshore may still be transported to suitable habitat prior to settling.

The data on red king crab grasping pairs presented here have impacted management of king crab fisheries in Alaska. Coupled with laboratory experiments indicating increased mating success with size (Paul and Paul 1990), these data were used in development of the current harvest strategies that aim to protect stock reproductive potential by limiting the harvest rate on “functionally mature” and legal-sized males (Pengilly and Schmidt 1995, ADFG 2000a). The current 178 mm CW legal size limit (which corresponds with 147 mm CL) for Kodiak area red king crabs was believed to allow males to mate for 3 years prior to entering the commercial fishery (Donaldson and Donaldson 1992). These data, in which few of the grasping males were <130 mm CL and most were legal-sized, led fisheries managers to reevaluate the protection afforded by current size limits (sublegal males ≥130 mm CL in the Kodiak area are generally only one molt from legal size). Based on these data, 130 mm CL currently defines the lower size bound of functionally mature male red king crabs for management purposes in the Kodiak area; lower size bounds for defining functional maturity that are above the size of physiological maturity have similarly been established for management of other king crab stocks in Alaska (Pengilly and Schmidt 1995).

Acknowledgments

Special thanks to B.J. Rothschild and J. Buss, coauthors of the 1972 manuscript which was the main source of data for this report. Noteworthy too were the efforts of all divers, tenders, and crab survey participants who help gather or enter the red king crab grasping pairs data. This is contribution PP-213 of the Alaska Department of Fish and Game, Commercial Fisheries Division, Juneau.

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Acoustical Behavior in King Crab (*Paralithodes camtschaticus*)

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Abstract
Aquarium observations on crab acoustical activity demonstrated that several crab species produced intensive acoustic signals during feeding as well as while they endured unfavorable environmental conditions.

Feeding sounds of their own species, as well as an imitation of these sounds emitted by a transducer, increased movements of the king crab (*Paralithodes camtschaticus*). Some king crabs directly approached the sound source. Other sounds, including feeding sounds of different crab species, did not provoke discernable king crab reactions.

Numerous aquarium experiments on the king crab’s reactions to emission of various natural king crab feeding sounds and their imitations have allowed determination of signal parameters for attracting king crab. Precise duplication of signals resulted in the development of an acoustic crab lure (ACL). Fishing experiments proved that the ACL attracts king crab.

Introduction
The king crab is the most valuable fishery resource in the Okhotsk Sea. They are caught either in small conical traps with a base diameter of 1.3-1.5 m and a height 0.8-1.0 m or in large square pots measuring ca. 2.8 m × 2.8 m × 1.0 m. These traps are passive fishing gear and require bait to attract crab to them. At present, various fishes are used for bait but these lose their attractiveness with time and work efficiently only during the first 18 hours. This provides quite good catches when crab concentration is high. When concentration is low, a supplementary stimulus might result in higher catches. The most efficient stimuli, such as smell, visibility or sound, would be capable of reception over relatively long distances. Sound propagates quickly through water over long distances and is easily generated. Acoustical signals are hence practical for aquatic organism behavior management. Observations of Black Sea crabs showed that feed-
ing crabs produced sound as a series of pulses, and some crabs moved
toward the feeding crab and sometimes approached (Protasov and
Romanenko 1962).

In this study, the properties of king crab feeding noises and the be-
havioral response of king crabs to both natural and synthesized sounds
were investigated. Our objective was to create an acoustic crab lure (ACL)
which could increase a trap's efficiency in catching large males and also
serve conservation goals by avoiding capture of females and undersized
males in traps.

**Materials and Methods**

King crabs with carapace widths ranging from 5 to 24 cm were held com-
munally (10-12 males and 0-2 females, or 5-8 males and 0-1 females) in a
wooden tank measuring about 3 × 2 × 1 m or 2.0 × 1.2 × 0.8 m, respec-
tively. Water was changed once in each 12-24 hour trial period. Water tem-
perature was controlled within the interval of 2.0-5.0ºC. Crabs were fed
with fresh-frozen fish every two days.

**Sound Studies**

King crab sounds were recorded in both wooden tanks and a commercial
aquarium. Underwater acoustic signals were recorded by a piezoceramic
hydrophone (spherule with diameter 50 mm) and a tape recorder (Report-
L 4000, Uher) or video-recorder (NV-S7E, Panasonic). The sensitivity of
hydrophone with tape recorder or video-recorder allowed instruments to
register signals in frequency range from 0.1 kHz to 20 kHz with dynamic
range 56 or 90 dB, when the signal sound pressure in the point of hydro-
phone reception was higher than 0.5 or 0.2 Pa, respectively.

Recorded acoustic signals were analyzed with the help of channel os-
cillograph (MPO-2), a model 2034, self-writing, spectrum analyzer (filter
1617A, graphic recorder 2313, Bruil and Kjar) and the program-apparatus
complex “Biooptima” created by Sergey Andrgievsky (St. Petersburg, Russia).

Analysis included the following signal data: oscillogram (amplitude-
time), spectrogram (amplitude-frequency) including summary and instan-
taneous spectra, dynamic spectrogram or sonogram (amplitude-
frequency-time), and sonogram numeric data.

**Reaction Studies**

The effect of acoustic stimuli on the behavior of king crabs was studied in
eight experiments. Seven experiments were conducted in wooden aquari-
ums with dimensions 3 × 2 × 1 m. The eighth experiment was conducted in
a wooden aquarium with dimensions 2 × 1.2 × 0.8 m.

Acoustic signals were emitted in the aquarium by a transducer cre-
ated at VNIRO using a tape recorder (Report-L 4000, Uher) audio amplifier
with max output level 10 V, and special electrical generators created in
VNIRO. Also, octave, band-pass filters were used. The transducer sensitivity is 0.3 Pa per volt at 1 meter, in the frequency range from 1 to 20 kHz.

Positive reactions of king crabs were evaluated by a system of 0 to 1 marks (0 mark = no reaction, 0.5 mark = moving toward a transducer, 1 mark = approach a transducer). All reaction marks of each crab reaction were summarized during the emitting of acoustic signals.

Three one-factor experiments consisting of 75, 15, and 10 replications were carried out to study king crab behavior in response to recorded natural feeding sounds of king crab, hairy crab (*Erimacrus isenbeckii*), and Black Sea shore crab (*Carcinus maenas*). Then five multi-factorial experiments were done: four were carried out by means of Latin square designs (Fisher 1935), and the final one by means of the Box-Wilson method.

The fourth experiment with a rectangles plan of 4 × 8 was carried out to study king crab behavior in response to eight feeding king crab sounds (the factor “biosignal”), and to reveal biosignals attracting king crabs most precisely. The “intensive” factor had four gradations from 1.5 to 0.05 V and from 0 to –30 dB. The third and fourth nonsearched factors were “time” and “date,” also with four gradations.

The fifth experiment with square plan of 6 × 6 in common with a magic square of 6 × 6 was carried out to study king crab behavior in response to six feeding king crab sounds (third factor, “biosignal”) emitted using five band-pass filters, which were 1/3 octave with the center frequencies 0.5, 1, 2, 4, 8 kHz, and band-pass filter with the range of 0.5-20 kHz. The first factor was “frequency” and the second factor was “intensive.” All three searching factors had six gradations. Time drift was removed by means of the magic square by sum of six elements of tiers and columns.

The sixth and seventh experiments were carried out to study king crab behavior in response to various imitations of feeding king crabs and to define structure and parameters of attracting king crab most precisely.

The eighth experiment was carried out to search for optimum parameters of attracting large king crab males most precisely.

**Fishing Experiments**

Fishing experiments were carried out using a large acoustic crab lure (ACL-l) installed above a trap and a smaller ACL (ACL-s) installed within a large square pot measuring about 2.8 m × 2.8 m × 1.0 m. The small acoustic crab lure (ACL-s) produces high frequency acoustic signals (pressure 5-10 Pa at 1.0 m) and has an effective attractive radius of 100 m. The ACL-l produces high frequency sound pressure (about 100 Pa at 1.0 m) and has an effective radius of about 1,000 m.

During the introductory period and trial exploitation of 70 ACL-l, six harvesting vessels operated in one area of western Kamchatka, of which three were equipped with acoustic lures. The first three vessels (trial) and the second three vessels (control) set 332, 349, 344, and 392, 403, 379 trap series (respectively) in regions of the largest concentrations of crab.
Results

Crab Sounds
Sounds produced by crabs during feeding represent a series of species specific, complicated pulses and have a wide-continuous frequency spectrum from 0.1 to 20 kHz. For example, feeding sounds of Black Sea shore crabs (*Carcinus maenas*) have pulses with frequency about 5 kHz with its envelope like an exponential pulse.

Feeding sounds of hairy crabs (*Erimacrus isenbeckii*) consist of pulses with a rectangular envelope and chaotic amplitude and frequency modulations.

King Crab Sounds
King crab feeding sounds consist of pulses with an envelope likened to exponential pulse, with additional chaotic amplitude modulation (frequency 0.6-1.5 kHz, coefficient of modulation 20-100%), and frequency modulations. The frequency spectrum of king crab feeding sounds is continuous or a band in the range of 0.1-18 kHz. The duration of feeding acoustic signals, which consist of 1-40 (sometimes more) pulses, varies widely from 0.03 to 3.00 s. Pulse length varies from 2 to 30 ms. The sonogram and oscillogram of a typical king crab feeding sound are shown in Fig. 1.

The duration of the signal consisting of 16 pulses is 315 ms. Frequency spectrum of 16 pulses is continuous or band in the ranges from 1 kHz to 0.5-15 kHz.

Discomfort sounds of king crabs were recorded three times in 50 minutes when fresh water and air were shut off. The first discomfort sounds were recorded by chance. Discomfort sounds of king crab are perceived by human ears as a “crack” with a frequency range of 0.1-12 kHz, with pulse duration of 1-10 ms. Duration of both types of signals usually consist of 3-30 pulses, up to 3 s. Intervals between pulses are 3 to 100 ms. The sonogram and oscillogram of a typical king crab discomfort sound are shown in Fig. 2.

King Crab Behavior
In the aquariums, the presence of food usually increased king crab motor activity. Crabs made non-directed, chaotic movements that resembled “Brownian movement.” These random movements resulted in finding food only after 0.5 to 2.0 hours. This kind of behavior indicated that king crabs were using organs for the sense of smell or chemoreception which detected the presence of food particles in the aquarium, but not the direction toward the source of corresponding stimuli. From time to time different crabs approached the feeding crab and produced characteristic intensive sounds. These crabs approached directly, very often in a straight line. Analogous behavior was observed while feeding sounds and their imitation were emitted by the transducer and tape-recorder or special generators.
Figure 1. Sonogram and oscillogram of the king crab feeding signal. The duration of the signal consists of 16 pulses in 315 ms.

Figure 2. King crab signal produced when oxygen concentration in water decreased. The duration of this signal consists of 20 pulses in 140 ms.
**King Crab Reactions to Natural Crab Sound Emission**

The results of three one-factor experiments showed that king crabs approached the transducer in 47 out of 75 experiences. However, Black Sea shore crab and hairy crab feeding sounds did not provoke discernable king crab reactions.

The fourth experiment, in which king crab natural feeding sounds were emitted by the transducer, revealed six feeding crab sounds to use in the next experiment. For the fifth experiment, it was necessary to exclude two feeding king crab sounds, damaged while emitting, and change the experiment plan from $6 \times 6$ to $4 \times 6$. The experiment results are shown in Table 1. These results proved that only gradations of the factor “frequency” were significant, and the signal with the second gradation frequency attracts king crab most precisely (Tolstoganova 1983).

The sixth and seventh experiments carried out to study king crab behavior in response to various imitations of feeding king crab defined structure and parameters of impulse signal imitating feeding king crab sound. The study of crab reaction to acoustical signals created using special generators has shown that crabs may react to some of these signals more often than they do to their own feeding sounds (in the marking system from 0 to 12 marks, during 5 minutes) (Tolstoganova 1983). Using the results of these experiments, the acoustic crab lure (ACL) has been made.

**Fishing Experiments**

During the introductory period and trial exploitation of 70 ACL-l, six harvesting vessels operated in the area of western Kamchatka, three of which were equipped with acoustic lures. Catches of the first three vessels (trial) and the second three vessels (control) were 7.461, 7.629, 8.072, and 7.499, 7.881, 7046 tons, respectively. The average catch per gear set in the first three vessels (trial) was $2.26 \pm 0.30$ tons, i.e., 18% higher than in the three control vessels with food bait only. The average catch per gear set in the three control vessels was $1.943 \pm 0.42$ tons.

**Discussion**

Observations on king crab behavior have shown that king crabs possess not only the ability to hear sounds, but also to determine the direction of the sound source. Research on king crab reactions to natural and synthetic acoustical signals demonstrated that crabs react to synthetic signals more often and more clearly than to their own feeding sounds both in aquarium and open-sea conditions, likely because during recording aquarium reverberation and ambient noise are present.

Synthetic and natural sounds were discovered by trial and error, while in search of acoustical signals that appeared to cause large male king crab to move toward the sound source. Some of these sounds were not attractive to small males and females.
Table 1. **King crab behavior in response to six king crab feeding sounds**

<table>
<thead>
<tr>
<th>Biosignal</th>
<th>0.25</th>
<th>0.5</th>
<th>1.0</th>
<th>2.0</th>
<th>4.0</th>
<th>8.0</th>
<th>Sum</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>0.5</td>
<td>2</td>
<td>6</td>
<td>3</td>
<td>4</td>
<td>16.5</td>
<td>2.8</td>
</tr>
<tr>
<td>2</td>
<td>1.0</td>
<td>6.0</td>
<td>1.0</td>
<td>3.0</td>
<td>0</td>
<td>0</td>
<td>11</td>
<td>1.8</td>
</tr>
<tr>
<td>9</td>
<td>3.0</td>
<td>4.0</td>
<td>2.0</td>
<td>0.5</td>
<td>1</td>
<td>0</td>
<td>10.5</td>
<td>1.8</td>
</tr>
<tr>
<td>10</td>
<td>1.0</td>
<td>1.0</td>
<td>3.0</td>
<td>0</td>
<td>0.5</td>
<td>0</td>
<td>5.5</td>
<td>0.9</td>
</tr>
<tr>
<td>Sum</td>
<td>6.0</td>
<td>11.5</td>
<td>8</td>
<td>9.5</td>
<td>4.5</td>
<td>4</td>
<td>43.5</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>1.5</td>
<td>2.9</td>
<td>2.0</td>
<td>2.4</td>
<td>1.1</td>
<td>1.0</td>
<td>1.8</td>
<td></td>
</tr>
</tbody>
</table>

**Frequency midband (kHz)**

<table>
<thead>
<tr>
<th></th>
<th>0.5</th>
<th>1.0</th>
<th>2.0</th>
<th>4.0</th>
<th>8.0</th>
<th>0.5-20</th>
</tr>
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<tr>
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<td>10</td>
<td>10</td>
<td>2.5</td>
<td>2.5</td>
</tr>
<tr>
<td>Mean</td>
<td>0.8</td>
<td>3.9</td>
<td>2.5</td>
<td>2.5</td>
<td>0.6</td>
<td>0.6</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Factors</th>
<th>Degrees of freedom</th>
<th>Sum of squares</th>
<th>Mean square</th>
<th>Fisher degree</th>
<th>Handbook value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biosignal</td>
<td>3</td>
<td>11.0</td>
<td>3.7</td>
<td>2.1</td>
<td>3.7</td>
</tr>
<tr>
<td>Intensive</td>
<td>5</td>
<td>10.9</td>
<td>2.2</td>
<td>1.2</td>
<td>3.3</td>
</tr>
<tr>
<td>Frequency</td>
<td>5</td>
<td>36.6</td>
<td>7.3</td>
<td>4.1</td>
<td>3.3</td>
</tr>
<tr>
<td>Remainder</td>
<td>10</td>
<td>17.5</td>
<td>1.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>23</td>
<td>76.0</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Numerous single and multiple factor aquarium experiments on king crab searching reaction to king crab feeding sounds, as well as synthetic signals, allowed determination of the structure and optimal parameters of signals that attracted commercial-size male king crab. These experiments resulted in construction of an acoustical crab lure ACL. Now we are legalizing a patent based on these optimal parameters.

Discomfort sounds of king crabs were recorded three times in 50 minutes when the fresh water and air were shut off. Perhaps the crabs produced discomfort sounds because the oxygen content decreased.

Unlike crab feeding sounds that were systematically studied over several years, the sounds of crab discomfort were recorded only by chance. Hair crab (*Erimacrus isenbeckii*) emitted sounds of discomfort when placed in an aquarium that was contaminated with oil.

Fishes also produce sounds of discomfort. The low acoustic activity of beluga sturgeon (*Huso huso*) juveniles increased while they were feeding on toxic or semitoxic food. During this time juveniles produced a series of pulses and short whistles. The number of acoustic signals was correlated with the condition of the toxic food and the amount of toxic food consumed before. In addition, juveniles fed with toxic and semitoxic food produced similar acoustic signals when the oxygen content decreased from 7.8 mg to 5.3 mg per L (Tolstoganova 2000).

Possibly, detailed studies of acoustic activity could be used to monitor the health of various aquatic organisms and hence remotely monitor and possibly even control certain environmental conditions.

**Acknowledgments**

I am very grateful for help and assistance from the crew and all the staff of fishing vessels on which my studies were conducted. Especially I would like to thank the captain of factory vessel *Vastly Poutintcev*, Mr. V.N. Gridnev, and Mr. A.F Nikolaytchouk for help, kind advice, and cooperation during sea experiments.

**References**


Preliminary Notes on the Reproductive Condition of Mature Female Snow Crabs (*Chionoecetes opilio*) from Disko Bay and Sisimiut, West Greenland

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**Abstract**

In the first week of June 1998-2000, female snow crabs were collected from exploited populations in Disko Bay and the area around Sisimiut, to study the reproductive condition of mature females. Analyses of ovaries and broods were performed on the females. Eggs hatched mainly in April and May and the fecundity was positively correlated with carapace width at both locations. Based on the development of ovaries and brood, females seem to have a 2-year reproductive cycle in the colder area around Sisimiut and a 1-year reproductive cycle in Disko Bay where bottom temperature is warmer.

**Introduction**

The snow crab, *Chionoecetes opilio*, has recently become commercially exploited in Greenland. The fishery developed in 1996 and landings reached 11,000 t in 2000. The fishery is distributed (Fig. 1) from Paamiut in the south (61ºN) to Uummannaq in the north (71ºN). Until 1998, mainly an inshore fishery prosecuted snow crab, but in the past 2 years an offshore fishery has developed. Until 2000, the fishery was little regulated. Only males > 90 mm in carapace length are harvested, while females are protected.

Biological research and monitoring were started in 1996. Since 1997 an annual trap survey has been conducted in Disko Bay and inshore areas near Sisimiut, on the west coast of Greenland. Owing to the recent development of the fishery and lack of research on snow crab, knowledge of this stock and its biology are poor.
Figure 1. Greenland.
Based on the existing knowledge of snow crab biology in eastern Canada, it is clear that gaining a better understanding of the female reproductive cycle is very important for fishery management (Comeau et al. 1999). Both sexes are functionally mature after their terminal molt, which can occur over a wide range of sizes (e.g., Conan and Comeau 1986, Sainte-Marie and Hazel 1992, Sainte-Marie et al. 1995). Mature females include primipara, which are first-time spawners, and multipara which are repeat spawners (Sainte-Marie 1993). Multiparous females can be distinguished from primiparous females by their older carapace and the presence on their legs of scars inflicted by males during previous matings (Sainte-Marie and Carrière 1995).

In eastern Canada, Mallet et al. (1993) showed that eggs were brooded for 2 years in the Gulf of St. Lawrence. Sainte-Marie (1993) observed that maturation of the brood and ovaries took 24 or 27 months for multiparous and primiparous females, respectively, in Baie Sainte-Marguerite; Comeau et al. (1999) noted an egg incubation period of 2 years for multiparous females in Bonne Bay. The common conclusion was that the females from those areas have a 2-year reproductive cycle. Moriyasu and Lanteigne (1998) pointed out that females also have a 2-year reproductive cycle in the southern Gulf of St. Lawrence owing to the low temperature. In Japan, laboratory studies by Kon (1974) determined that the embryonic development lasted 1 year at temperatures greater than 4.5ºC.

The main objective of this study was to obtain preliminary information on egg stage, brood and ovary development, and fecundity from mature females collected in Disko Bay and around Sisimiut. I sought possible evidence of differences in the reproductive cycle between the two areas, based on the assumption that their different temperature regimes would influence ovary development and egg incubation. This study will also provide knowledge on the period of hatching and spawning in the fishing areas in Greenland.

**Materials and Methods**

**Study Area and Sampling Procedure**

Female snow crabs were collected in Disko Bay (68º40’N to 69º25’N, 51º15’W to 53ºW) (Fig. 2) and in three fjords: Itilleq, Qeqertalik, and Kangerluarsuuk near Sisimiut (66º30’N, 53º30’W) (Fig. 3). Snow crabs were captured in traps with a mesh size of 21 mm from randomly selected locations in the study area, at depths of 200-400 m. Bottom temperature was recorded by a Seamon mini-recorder (made by Hugrún, Iceland), which was secured to the traps and programmed to record every 15 minutes. Samplings were conducted in the first week of June in 1998, 1999, and 2000. Primiparous and multiparous females were sorted onboard, carapace width (CW) was measured with a vernier caliper to the nearest 0.01 mm, and shell and brood condition were determined according to the criteria given by Sainte-
Figure 2. Study area in Disko Bay. Samples were taken during the trap survey in June from 1998 to 2000.
Figure 3. Study area of Sisimiut. Samples were taken in the fjords Itilleq, Kangerluarssuk, and Qeqertalik, during the trap survey conducted in June from 1998 to 2000.
Marie (1993). Unfortunately, analysis of data subsequently showed that primiparous and multiparous females were not all properly classified. Therefore the two types were not distinguished in analyses.

**Subsampling of Females and Laboratory Processing**

Subsamples of both primi- and multiparous females were taken each year for analysis in the laboratory. Following the sampling procedure described by Mallet et al. (1993), three to five females were selected in each available 5 mm size class. Females were fixed in 4% seawater-diluted formalin. In the laboratory, the egg clutch, ovaries, and a subsample of 30 eggs from each female were weighed to the nearest $10^{-5}$ g.

**Data Analysis**

Fecundity was determined by dividing the weight of the whole clutch by the weight of individual eggs for each female. Descriptive statistics, correlation, and linear regression (Sokal and Rohlf 1981, Fowler et al. 1998) were used to describe variables and relationships among them.

**Results**

**Weather and Temperature Conditions**

In 1998, ice covered both areas during winter and it broke up in the beginning of May in Disko Bay and in the fjords near Sisimiut. Owing to the mild winters in 1999 and 2000, the ice cover in Disko Bay was very thin and the ice broke up in late April. The temperature measurements in Disko Bay and in the fjords near Sisimiut are given in Table 1. The temperature in Disko Bay was higher than in the fjords near Sisimiut, where shallow sills prevent offshore, deep warm water from entering the fjords.

**Annual Changes in Color of Brood in Mature Females of Disko Bay and Sisimiut**

In Disko Bay, a total of 1,105 mature females, ranging from 49 to 89 mm CW, were sampled in the first week of June from 1998 to 2000. The proportion of mature females carrying bright orange eggs without eyespots was 98% in 1998-1999 and 96% in 2000. Less than 1% of mature females carried broods with dark orange eggs having eyespots and only 4 mature females were observed with dark brown eggs. No females with empty eggshells were observed.

Near Sisimiut, a total of 6,404 mature females, ranging from 46 to 95 mm CW, were sampled from 1998 to 2000. In 1998 and 1999, 99% of mature females carried bright orange eggs without eyespots while the remainder carried dark orange eggs with eyespots or dark brown eggs. In 2000, 79% of the mature females carried bright orange eggs without eyespots and 16% carried dark orange eggs with eyespots. Three percent of females carried dark brown eggs, 4% had empty eggshells, and 1% had no brood.
Clutch and Ovary Weight in Subsamples

A subsample of 475 mature females from Disko Bay and Sisimiut was examined to determine the weight of the clutch and ovaries. All females were carrying bright orange eggs without eyespots, except three females collected from Disko Bay in 2000, which had dark brown eggs. Clutch weight was positively correlated with carapace width for the mature females in Disko Bay and Sisimiut (raw data in Fig. 4; data transformed to their natural logarithm in Fig. 5).

Considering females from the Sisimiut area, scatterplots of ovary weight on female carapace width showed two clouds of points, which were also evident in data from June 2000 (Fig. 5). The two clouds of points were quite parallel and differed only in elevation. The upper cloud represents females with orange ovaries while the lower cloud represents females with beige ovaries. Proportions of females with orange and beige ovaries were respectively 40% and 60% in 1998, 63% and 37% in 1999, and 33% and 67% in 2000. A one-tailed $t$-test revealed that orange ovaries were significantly heavier ($P < 0.05$) than beige ovaries for females collected in Sisimiut. The equation of the regression line for females with orange ovaries was:

$$\ln(\text{ovary weight}) = 3.9552 \ln(\text{CW}) - 15.3009$$

$$(r^2 = 0.679, F = 54.79, P < 0.05),$$

while for females with beige ovaries it was:

$$\ln(\text{ovary weight}) = 2.7932 \ln(\text{CW}) - 11.3454$$

$$(r^2 = 0.841, F = 164.26, P < 0.05).$$

Females in Disko Bay had beige ovaries, excepting the three females with dark brown eggs, which had orange ovaries. A one-tailed $t$-test showed that mean ovary weight for females with beige ovaries was the same in Disko Bay and in fiords near Sisimiut ($P > 0.05$).

Number of Eggs per Clutch in Mature Females

Females from Disko Bay that were examined for fecundity probably carried recently extruded eggs, because their ovaries were very small. Three females

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Table 1. Bottom temperature (ºC) in Disko Bay and Sisimiut in June 1998-2000.

<table>
<thead>
<tr>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Disko Bay</td>
<td>3.1</td>
<td>2.6</td>
<td>4.1</td>
<td>3.3</td>
<td>2.5</td>
<td>3.9</td>
<td>2.7</td>
<td>1.9</td>
<td>3.7</td>
</tr>
<tr>
<td>Sisimiut</td>
<td>0.8</td>
<td>0.6</td>
<td>1.9</td>
<td>1.1</td>
<td>0.5</td>
<td>2.1</td>
<td>0.4</td>
<td>-0.8</td>
<td>1.7</td>
</tr>
</tbody>
</table>
with dark brown eggs were excluded from the analyses of fecundity. However, females from Sisimiut probably carried either recently extruded or older eggs, based on the difference in ovary development. Fecundity was positively correlated with carapace width (Fig. 6) and the equations

\[ y = 0.7244 \, CW^{2.6712} \quad (r^2 = 0.619) \] and \[ y = 0.5395 \, CW^{2.7295} \quad (r^2 = 0.678) \]
described the relationships between number of eggs and carapace width for Disko Bay and Sisimiut, respectively. From Table 2 it appears that the average number of eggs carried by the females was different between Disko Bay and Sisimiut in 1998 and 1999. In general, the mean number of eggs, for females of similar mean carapace width, was greater for females in Disko Bay than in Sisimiut.
Discussion

Egg stages

Since clutches with bright orange eggs predominated in Disko Bay and in Sisimiut in June, and only a small number of clutches had dark brown eggs, it is likely that females may hatch their eggs in early June or before. Observations from the fjord Eqaluit Paarliit in Greenland showed the same composition of brood stages in June and the hatching period was determined to occur between April and May 2000 (Burmeister, unpubl. data). Therefore it is reasonable to assume that mature females from Disko Bay and Sisimiut might hatch their eggs in the same period. Mallet et al. (1993) showed that egg hatching for multiparous females occurs in June in the southern Gulf of St. Lawrence, while Sainte-Marie (1993) showed it occurred from April to June in the northern Gulf of St. Lawrence. However, the time of hatching may vary inter-annually. Unpublished data from

Figure 5. Weights of ovaries vs. carapace width for mature females from Disko Bay and Sisimiut, June 1998-2000.
Greenland show that females with dark brown eggs (i.e., soon to hatch) were dominant in Kangaatsiaq (68°N) in June 1996.

**Ovaries and Clutch**

The development of ovaries based on color and weight was different between Disko Bay and Sisimiut. In Disko Bay, females with beige ovaries and bright orange eggs predominated. Based on the stage and color of the ovaries and eggs during the period 1998-2000, I infer that: (1) mature females in Disko Bay spawn during May and June, and (2) maturation of ovaries lasts approximately 12 months. Therefore snow crab females from Disko Bay seem to have a 1-year reproductive cycle.

In Sisimiut, females could be separated into two groups based on ovary weight and color. Two clouds of points in scatterplots of weight of ovaries against carapace width were apparent in 1998 and were even more evident in 2000. The upper cloud represents females with orange eggs without eyespots and orange ovaries and the lower cloud represents females with beige ovaries and bright orange eggs without eyespots. On the assumption that females hatch their eggs from April to May, females represented in the upper cloud probably spawned their eggs about 1 year before the time of sampling, while females in the lower cloud probably spawned their eggs only a few weeks before I collected my samples. If this interpretation is correct, then maturation of ovaries and brood of mature females might take at least 2 years. This conclusion is consistent with more detailed studies from Canada. In Baie Sainte-Marguerite, it was estimated that maturation of brood and ovaries lasted 27 months in primiparous females and 24 months in multiparous females (Sainte-Marie 1993). Comeau et al. (1999) demonstrated a 2-year incubation period for eggs of multiparous females. Mallet et al. (1993) suggested that maturation lasts 2 years.
based on histology of female gonads in habitats with temperature from –1 to 1ºC. Moriyasu and Lanteigne (1998) also showed that the duration of embryo development is 2 years at low temperature and suggested that the reproductive cycle could be annual if females remained in deep warmer waters with temperature ranging from 1.3 to 6.3ºC.

In 1999, there was no distinct separation in development stages of ovaries for mature females from Sisimiut. Bottom temperature was also warmer than average that year (Table 1). Perhaps females are able to shift between a 2- and 1-year cycle when the bottom temperature increases. If this is the case, then differences in temperature between my study sites may provide some indication of the temperature threshold at which the shift occurs. Females in Disko Bay seem to have a 1-year reproductive cycle at 1.9 to 4.1ºC, while females from Sisimiut seem to have a 2-year reproductive cycle at temperatures ranging between –0.8 and 2.1ºC.

Females from Disko Bay carried more eggs than similarly sized females from Sisimiut. In Disko Bay, the number of eggs ranged from 25,000 to 120,000, as seen also in females from Bonne Bay, Canada (Comeau et al. 1999). In Sisimiut, the number of eggs was generally lower than those from Disko Bay. The difference in fecundity could be due, for example, to differential egg mortality resulting from the difference in the rate of egg development between the two study sites, or to different mixtures of primiparous and multiparous females.

### Conclusion

The results of this preliminary study cannot provide a definitive interpretation of the reproductive biology of snow crab in Disko Bay and Sisimiut. However, they do give a preliminary idea of some biological parameters and therefore contribute to a better understanding of the population of snow crab in Greenland waters. Further work will be conducted to address the issue of primiparous and multiparous females carefully, to gain a better understanding of the fecundity variations among sites. Furthermore, studies with different focuses, such as an estimate of the abundance of females with a 1-year or 2-year reproductive cycle, seasonal movement of

| Year | Disko Bay | | Sisimiut |
|------|-----------|-----------------|-----------|-----------------|
|      | N | Mean | Mean CW | S.D. | N | Mean | Mean CW | S.D. |
| 1998 | 51 | 66,689 | 72 mm | 22,833 | 54 | 45,089 | 72 mm | 34,047 |
| 1999 | 63 | 73,203 | 72 mm | 31,772 | 71 | 50,429 | 71 mm | 34,012 |
| 2000 | 135 | 65,725 | 70 mm | 28,344 | 101 | 53,936 | 66 mm | 24,007 |
ovigerous females in relation to depth and water temperature, and the
effect of male exploitation on mating and egg production will be con-
ducted to develop a better understanding of the reproductive strategies
of the snow crab and the impact of harvesting in Greenland.

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