GROWTH OF JUVENILE RED KING CRABS, Paralithodes camtschaticus, THROUGH SEQUENTIAL MOLTS IN THE LABORATORY

Bradley G. Stevens *
Living Marine Resources Cooperative Science Center, University of Maryland Eastern Shore, Princess Anne, MD 21853, USA

ABSTRACT

Studies of crustacean growth, including king crabs, have typically used modal analysis rather than growth of individual crabs. I studied the individual growth of several hundred juvenile red king crabs (initial size 14-35 mm carapace length, CL) that were captured from a pod in Kodiak, Alaska, in July and August 2000, and retained in the laboratory for up to 14 months. During that period, 295 crabs molted at least once, including a subset of 52 that molted twice, and a subset of 9 that molted three times. Mean molt increment (MI) was 5.5 mm, and did not differ significantly between the three molts. MI increased significantly with premolt size for molt 1, and proportional growth rate at molt 1 was greater than that of molts 2 or 3. The first molt occurred earlier (August-October) and at warmer temperatures among smaller crabs than among larger crabs, which molted in January-February at colder temperatures. Post-molt CL for first molts was a simple ratio: Post-molt CL = 1.25 · (Pre-molt CL) (R² = 0.9587, df = 291). Growth during the second molt was less than during the first molt, possibly reflecting a limitation imposed by the holding conditions. This is the first study to record growth information for individual juvenile red king crabs in the size range of 15-50 mm CL, through sequential molts, and results can be used to fill a gap in current growth models.

KEY WORDS: Anomura, Decapoda, growth, molting, Paralithodes camtschaticus, red king crab

INTRODUCTION

Crustacean growth can be separated into two components: intermolt period (IP), the time interval between molts for an individual organism, and molt increment (MI), the absolute increase in size at molting for an individual that is usually measured as length, width, or weight (Hartnoll, 1982). Most studies of crustacean growth have been made by following the change in means of size frequency modes of aggregated data through time (Weber, 1967; Stevens, 1990; Hosssain and Ohtomi, 2010). Such studies can provide relative rates of growth for population components (sex, reproductive, or maturity stage) but cannot provide IP or MI for individuals. In many cases, growth information cannot be obtained from analysis of size-frequency modes because of great variability in growth rates and subsequent overlap of modes (Loher et al., 2001). Fewer studies have followed individual animals through a molt, and of those, fewer still have been carried out long enough to include multiple sequential molts of individual animals. Most of the these studies involve tagging and recapture of wild animals (Powell, 1967; Corgos et al., 2007), in which case the number of recaptured animals is small, and multiple molts can only be inferred. Laboratory studies allow observation of repeated molts in individuals, but are necessarily limited to the study of small or juvenile king crabs due to the size of adults and the length of time between molts (one year or more).

The red king crab Paralithodes camtschaticus (Tilesius, 1815) in the eastern Bering Sea (EBS) has traditionally supported one of the most lucrative fisheries in the United States. Landings peaked at 84,000 mt in 1980, with a value of $169 million, then plummeted to 1362 t in 1982. The fishery was closed in 1983, then reopened in 1984; recent (2009) landings were 9080 mt worth $100 million [see http://www.adfg.alaska.gov/static/fishing/PDFs/commercial/09shellfish_value.pdf]. The National Marine Fisheries Service conducts annual stock assessment surveys of red king crab abundance (RKC), which are then used in a length-based model to reduce annual measurement errors; resulting data are used to determine annual recruitment, mortality, spawning stock biomass and total allowable catch (NPFMC, 2009). Inherent in this process is the need to understand growth rates, in order to estimate size at age and age at sexual maturity. Growth rates of adult RKC have been relatively well studied, because of the ease with which they can be tagged and recaptured (Weber and Miyahara, 1962; Powell, 1967). However, studies on growth of juvenile RKC are sparse, both geographically and temporally. As a result, models of juvenile red king crab growth are based on a number of assumptions, or are specific to a particular time and place.

Early studies of red king crab growth were carried out by different authors in different locations with greatly varying results. Since crabs are difficult to find during their first 1-2 years of life, estimates made for the size of 3 yo RKC range from 17 mm in the EBS (INPFC, 1959), 22 mm in the Sea of Okhotsk (Vinogradov, 1968), 60 mm at Unalaska, AK (Weber, 1967), and 61 mm in Kodiak, AK (Powell, 1967);
the latter author studied growth of larger crabs by mark-recapture. Kurata (1961, 1962) demonstrated that growth of RKC was a function of temperature acting primarily on intermolt period, and Nakanishi (1987) concluded that degree-days for a given instar were constant within the range of temperature tolerance. Subsequently, temperature-based growth models were developed for RKC which predicted that 3 yo crabs would be approximately 65 mm in Kodiak, but only half that in the EBS (Stevens, 1990; Stevens and Munk, 1990). A modeling study using seasonalized Gompertz growth models concluded that 3 yo crabs would be 66 mm in Unalaska, but only 47 mm in Bristol Bay, AK (Loher et al., 2001). Most previous studies were conducted by collections of wild crabs and measurement of size frequency modes in aggregate; few studies have monitored growth of individual RKC, or small crabs in their first few years of life, and those that did used small numbers of crabs. Matsuura and Takeshita (1976) monitored the growth of five crabs in the laboratory over a period of four years and recorded from 2-4 molts for each crab, but the smallest was 76 mm. Mortenson (1995) studied collective growth of hatchery raised crabs for the first six months, to a size of 6 mm carapace length (CL), by measuring only 10 crabs per sampling period. Growth of juvenile females >70 mm CL has also been studied in the laboratory (Zhou et al., 1998).

Small king crabs are difficult to find and collect during their first year of life due to the cryptic nature of their habitats, so few growth studies have targeted them. After hatching, king crabs pass through four zoeal stages, then a transitional (postlarval) glaucothoe stage before metamorphosis to the first stage crab (Sato and Tanaka, 1949). Glaucothoe settle preferentially into structurally complex habitats (Stevens and Kittaka, 1998; Stevens, 2003); during their first year of life, king crabs are extremely cryptic, remaining embedded in a variety of complex substrata including mussels, bryozoans, polychaete colonies, and their associated fouling communities (Sundberg and Clausen, 1977; McMurray et al., 1986; Stevens and MacIntosh, 1991). At the age of one year and approximately 15 mm CL they begin to emerge, and are first seen "hitch-hiking" on the sea star *Evasterias troschelii* (Dew, 1990). At a size of about 25 mm they begin to form pods containing hundreds of crabs of both sexes (Powell and Nickerson, 1965; Dew, 1990). Although pods are difficult to find due to their scarcity, once found, they provide access to large numbers of juveniles.

In late summer of 2000, juvenile crabs were collected from a single pod in the vicinity of Womens Bay, Kodiak, AK. This afforded the opportunity to observe and track molting and growth of individual crabs in the laboratory over the subsequent year. This report offers the first study on individual growth of red king crabs in the size range of 15-50 mm CL over sequential molts.

**METHODS AND MATERIALS**

A group of 88 juvenile red king crabs were captured from a single pod of crabs in Womens Bay, Kodiak, Alaska, by scuba diving on 26 July 2000; another group of 332 were captured from the same location (and probably the same pod) on 29 August 2000. All crabs were collected from the same aggregation, and were therefore assumed to be all of the same year class. Previous studies (Powell, 1967; Stevens, 1990; Stevens and Munk, 1990) indicate that crabs of this size were probably from the 1999 year class, and were therefore 1.5 years old. All crabs were taken to the Kodiak Fisheries Research Laboratory, where they were held in a communal tank (2.1 \times 0.61 \times 0.56 m) with flow-through seawater at ambient temperature, and a gravel bottom. All crabs were measured to the nearest 0.01 mm from the right orbit to the rear margin of the carapace, and marked by gluing individually numbered plastic tags to the carapace. Measurements taken prior to molting were termed premolt CL (PreCL), and those taken after molting were termed postmolt CL (PostCL). Crabs were fed twice weekly with small pieces of chopped squid. The crab tank was checked daily, and any crabs that showed a marked swelling of the abdomen were removed and placed in separate chambers within compartmentalized plastic boxes, approximately 14 \times 10 \times 15 cm with flow-through seawater until they molted. Recently molted crabs were remeasured between 3 and 7 days after molting. All tanks were covered with green translucent lexan (ambient light level was approximately 5 lux), and water temperatures were recorded with an electronic data logger in the tank. The study was continued for 14 months; crabs that died (either from cannibalism or other factors) or that did not molt during that interval are not included in this study.

In order to visualize instar modes, the combined length frequencies of all crabs prior to molting were analyzed using the Normsep procedure contained in the FiSAT II analytical package, producing an estimated mean, SD, and proportion of crabs in each mode (United Nations FAO-ICLARM). Absolute growth of crabs was expressed as molt increment (MI = PostCL − PreCL) in mm and as proportional growth rate (GR = MI ÷ PreCL). To analyze MI of individual crabs, postmolt CL was regressed against premolt CL separately for each molting group (first, second, or third). Analysis of covariance (ANOVA) was used to determine if the regression equations differed between crabs collected in July or August, and between first and second molts. Mean MI and proportional growth rate (GR) for first, second, and third molts were also compared by ANOVA. Mean MI and growth rate were compared between first and second molts for individual crabs with a paired t-test. All statistics were computed using the R statistical environment [see http://www.r-project.org/; http://www.fao.org/fishery/topic/16072/en].

**RESULTS**

Temperature in the laboratory tanks during the period of the study (26 July, 2000 through 31 October, 2001) ranged from 4.5 to 12.6°C (mean 8.2 ± 2.5°C). During that period, 295 crabs molted at least once, including a subset of 52 that molted twice, which included another subset of 9 crabs that molted three times. The mean pre-molt size for all 420 crabs (including non-molters and those that died later) was 24.9 ± 4.3 mm CL. At least three (and possibly four) different instars were present, with modes (and numbers) at approximately 15, 21, 26, and 31 mm CL (Table 1, Fig. 1). First molts occurred primarily during the period of September-October 2000, and January-February 2001,
Table 1. Mean and SD of modes, and number and proportion of total red king crabs in each mode prior to their first molt in the laboratory, as computed by FiSAT/NormSep.

<table>
<thead>
<tr>
<th>Mode</th>
<th>Mean</th>
<th>SD</th>
<th>No.</th>
<th>Proportion (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>14.83</td>
<td>0.883</td>
<td>7</td>
<td>1.6</td>
</tr>
<tr>
<td>2</td>
<td>20.89</td>
<td>2.637</td>
<td>191</td>
<td>45.6</td>
</tr>
<tr>
<td>3</td>
<td>26.08</td>
<td>1.357</td>
<td>109</td>
<td>25.9</td>
</tr>
<tr>
<td>4</td>
<td>30.75</td>
<td>1.619</td>
<td>113</td>
<td>26.9</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>420</td>
<td></td>
</tr>
</tbody>
</table>

and second and third molts occurred primarily during June-July 2001 (Fig. 2). Smaller crabs molted earlier than larger crabs. Among first molts, crabs that molted in July-August had a mean pre-molt CL of 18.9 ± 2.2 mm; those that molted in September-November averaged 24.2 ± 3.0 mm, and those that molted in January-March 2001 averaged 28.7 ± 3.0 mm (Fig. 3). Although these means do not match exactly the modes identified by NormSep, they suggest that three different instars molted sequentially at different times.

Analysis of covariance for first molts demonstrated that the regression lines for crabs collected in July or August had similar slopes, and intercepts that were not significantly different from 0 (Table 2). The combined regression equation indicates that CL increased by 25% regardless of size:

\[
\text{Post-molt CL} = 1.248 \cdot (\text{Pre-molt CL})
\]

\[
(R^2 = 0.9587, df = 291).
\]

The ANCOVA for first and second molts demonstrated that the regression lines had different slopes and intercepts (Fig. 4, Table 3). Third molts (n = 9) were not analyzed due to the small sample size. Regression equations were:

First molt: \[
\text{Post-molt CL} = 1.242 \cdot (\text{Pre-molt CL})
\]

Second molt: \[
\text{Post-molt CL} = 5.869 + (1.242 - 0.237) \cdot (\text{Pre-molt CL}).
\]

Differences in the third decimal of slopes in the above equations result from the order in which data were analyzed. Mean molt increment was 5.5 mm CL and did not vary between molt numbers (\(F = 0.227, P = 0.634; \text{Table 4}\)). However, growth rate differed significantly between molt numbers (\(F = 83.591, P < 2.2e-16\)). Mean growth rate was 0.218, 0.155, and 0.142 for first, second, and third molts, respectively. A multiple comparison test (with Bonferroni correction) showed that growth rate for first molts differed significantly from that for second and third molts (\(P < 0.001\)), but the latter two did not differ (\(P = 0.95\)).
the first molt, MI increased significantly with premolt size (Fig. 5A, F = 218.4, P < 0.0001), but growth rate did not (Fig. 5B; F = 0.252, P = 0.6159; Table 5). For the second molt, MI was not related to premolt size (Fig. 6A), but GR decreased significantly with premolt size (Fig. 6B; F(1.42) = 6.277, P = 0.0258; Table 5).

Molt increments for first molts decreased significantly with temperature on the day of molt, (F(2,291) = 169.65, P < 0.0001; Table 5). However, molting dates were bimodally clumped around a period of high temperatures in August-October, and a period of lower temperatures during January-February. Rather than being the result of temperature, these differences are more likely to be the result of the timing of molting (early vs. late) and the size of crabs that molted on those dates.

For 52 crabs that molted twice, the mean molt increment (MI) for molt 1 (6.9 mm) was significantly greater than MI for molt 2 (5.4 mm) (paired t-test, t = 4.142, P < 0.0001, df = 98), and mean growth (GR) rate for molt 1 (0.240) was significantly greater than that for molt 2 (0.154) (paired t-test, t = 8.412, P < 0.0001, df = 98). Among the 9 crabs that molted 3 times MI did not differ between molts 2 (6.9 mm) and 3 (5.8 mm) (paired t-test, t = 1.340, P < 0.187, df = 12), but mean GR for molt 2 (0.142) was significantly less than that for molt 3 (0.202) (paired t-test, t = -3.083, P < 0.010, df = 11). Within individual crabs, there was no significant relationship for MI between molts 1 and 2 (R² = 0.033, P = 0.196, df = 1, 50), or between molts 2 and 3 (R² = 0.141, P = 0.320, df = 1, 7) (Fig. 7A), i.e., crabs grew the same absolute amount during all molts. For GR, a significant negative relationship existed between molts 1 and 2 (R² = 0.145, P = 0.005, df = 1, 50), but not between molts 2 and 3 (R² = 0.016, P = 0.745, df = 1, 7) (Fig. 7B). Thus, crabs that exhibited above average proportional growth rates during the first molt exhibited below average proportional growth rates during the second molt, and vice versa. Intermolt period (IP) increased significantly with CL for molt 2 (R² = 0.130, P = 0.014, df = 44) but not for molt 3 (R² = 0.020, P = 0.786, df = 4) (Fig. 8).

**DISCUSSION**

This is the first study to follow the growth of individual juvenile RKC through multiple molts. Although the initial size range was narrow (14-35 mm), and the study only covered one year of their life, it afforded a unique opportunity to observe various phenomena during that interval. The results clearly demonstrate a number of features about growth of juvenile RKC: 1) juvenile RKC continue to molt and grow throughout the winter at ambient temperatures in Kodiak, AK; 2) among a group of same-age crabs, smaller crabs (or those belonging to smaller instars) molted earlier in the year than larger crabs; 3) molt increment did not vary over the size range studied (but growth rate did because of different pre-molt sizes); and 4) growth rates for individual crabs were not consistently high or low, but were compensatory; crabs that grew at a higher than average rate during the first molt grew at a lower than average rate during the second molt, and vice versa.

Unlike crabs in Bristol Bay, AK, or Unalaska, AK, that stop growing during the winter, juvenile RKC in

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Table 2. Results of ANCOVA for post-molt CL on pre-molt CL for first molts of red king crabs by collection date (July vs. August). Intercept and Premolt (i.e. slope) were determined from 41 crabs collected in July, “August” and “PreMolt:August” are adjustments to the intercept and slope, respectively, after including 254 crabs collected in August. Only the July Premolt (i.e. slope) is significant. Adjusted R² value is 0.9587 (df = 291).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Coefficient</th>
<th>SE</th>
<th>t-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.2208</td>
<td>1.5481</td>
<td>0.143</td>
<td>0.8867</td>
</tr>
<tr>
<td>PreMolt</td>
<td>1.2484</td>
<td>0.0815</td>
<td>15.323</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>August</td>
<td>-2.9932</td>
<td>1.6248</td>
<td>-1.842</td>
<td>0.0665</td>
</tr>
<tr>
<td>PreMolt:August</td>
<td>0.0716</td>
<td>0.0836</td>
<td>0.856</td>
<td>0.3926</td>
</tr>
</tbody>
</table>

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Table 3. Results of ANCOVA for post-molt CL on pre-molt CL and molt number of red king crabs (first or second molt only). Intercept and Premolt (i.e. slope) were determined from first molts of 295 crabs. “Second” and “PreMolt:Second” are adjustments to the intercept and slope, respectively, after including second molts of 52 crabs. The first molt intercept is not significant. Adjusted R² value is 0.9589 (df = 343).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Coefficient</th>
<th>SE</th>
<th>t-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-0.6155</td>
<td>0.4624</td>
<td>1.331</td>
<td>0.1840</td>
</tr>
<tr>
<td>PreMolt</td>
<td>1.2425</td>
<td>0.0183</td>
<td>67.857</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Second</td>
<td>5.6869</td>
<td>1.5695</td>
<td>3.739</td>
<td>0.0002</td>
</tr>
<tr>
<td>PreMolt:Second</td>
<td>-0.2370</td>
<td>0.0455</td>
<td>-5.208</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

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Table 4. Mean and SD of molt increments (MI) and growth rates (GR) for red king crabs molting 1, 2, or 3 times in the laboratory. ANOVA F and P values for comparisons among MI and GR are listed at bottom of table. Superscript letters indicate mean values that were similar (Bonferroni test, α = 0.05).

<table>
<thead>
<tr>
<th>Molt No.</th>
<th>No.</th>
<th>MI</th>
<th>SD</th>
<th>GR</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>295</td>
<td>5.42a</td>
<td>1.59</td>
<td>0.2175b</td>
<td>0.0475</td>
</tr>
<tr>
<td>2</td>
<td>52</td>
<td>5.45a</td>
<td>1.95</td>
<td>0.1547c</td>
<td>0.0568</td>
</tr>
<tr>
<td>3</td>
<td>9</td>
<td>5.76a</td>
<td>1.07</td>
<td>0.1419c</td>
<td>0.0236</td>
</tr>
</tbody>
</table>

ANOVA F: 0.227, P = 83.5911
ANOVA P: 0.634, df = <2.2e-16

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Fig. 4. Post-molt carapace length (CL) vs. pre-molt CL of juvenile red king by molt number. First molt (circles, solid line), second (triangles, dashed line), or third (crosses, dotted line).
Fig. 5. Growth of red king crabs during their first molt in the laboratory. A, Molt increment vs. premolt size; B, Growth rate vs. premolt size. See Table 5 for regression equations.

Kodiak, AK, continue to molt throughout the winter, as previously documented by Powell and Nickerson (1965), Dew (1990), and Stevens and Munk (1990). Donaldson et al. (1992) also reported that young-of-the-year king crabs grew consistently through the winter in artificial collectors in the

field. Relatively consistent year-round growth is probably due to the moderate temperature range occurring in Kodiak waters. In contrast, water temperatures in Bristol Bay, AK, often go below 0°C, the lower limit for growth of RKC (Kurata, 1961, 1962), and crabs living in that environment

Table 5. Regression parameters for growth of red king crabs. MI, molt increment; CL, carapace length; GR, growth rate; DegC, degrees Celsius; MI1, MI2, and MI3 imply first, second, or third molt increments, respectively. Intercept and slopes are only given when significant.

<table>
<thead>
<tr>
<th>Molt group</th>
<th>n</th>
<th>Comparison</th>
<th>R²</th>
<th>P-value</th>
<th>Intercept</th>
<th>Slope</th>
</tr>
</thead>
<tbody>
<tr>
<td>First</td>
<td>295</td>
<td>MI × CL</td>
<td>0.427</td>
<td>&lt;0.0001</td>
<td>−0.6155</td>
<td>0.2425</td>
</tr>
<tr>
<td>First</td>
<td>295</td>
<td>GR × CL</td>
<td>0.0009</td>
<td>0.6159</td>
<td></td>
<td></td>
</tr>
<tr>
<td>First</td>
<td>295</td>
<td>MI × DegC</td>
<td>0.368</td>
<td>&lt;0.0001</td>
<td>8.5184</td>
<td>−0.3706</td>
</tr>
<tr>
<td>Second</td>
<td>52</td>
<td>MI × CL</td>
<td>0.0002</td>
<td>0.9292</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Second</td>
<td>52</td>
<td>GR × CL</td>
<td>0.0955</td>
<td>0.0258</td>
<td>0.2936</td>
<td>−0.0039</td>
</tr>
<tr>
<td>Second</td>
<td>52</td>
<td>MI2 × MI1</td>
<td>0.033</td>
<td>0.1961</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Second</td>
<td>52</td>
<td>GR2 × GR1</td>
<td>0.1452</td>
<td>0.0053</td>
<td>0.2683</td>
<td>−0.4735</td>
</tr>
<tr>
<td>Third</td>
<td>9</td>
<td>MI3 × MI2</td>
<td>0.1408</td>
<td>0.3197</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Third</td>
<td>9</td>
<td>GR3 × GR2</td>
<td>0.0161</td>
<td>0.745</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Second and third</td>
<td>62</td>
<td>IP × CL</td>
<td>0.130</td>
<td>0.138</td>
<td>57.9</td>
<td>2.11</td>
</tr>
</tbody>
</table>
do not grow during the winter (Stevens, 1990; Loher et al., 2001). As a result, a seasonalized Gompertz growth model accurately predicts growth of crabs in Bristol Bay, but not that of crabs in Kodiak (Loher et al., 2001).

That smaller crabs (or instars) molted earlier in the laboratory could be due to either differential growth rates or multiple settlement cohorts. If the larger crabs were faster growing, they may have just molted prior to capture, whereas smaller crabs might be slower-growing and may not have molted since late in the previous spring or winter. Alternatively, larger crabs may represent those that hatched earlier in the previous year (January-February 1999) and settled in early summer, whereas smaller crabs may have hatched later (March-April) and settled in late summer. Female king crabs may be classified as primiparous (hatching their first clutch), or multiparous (hatching later clutches), and the latter group may be further subdivided into first time multiparous (M-1, or second clutch), second multiparous (M-2 or third clutch), etc., groups (Stevens and Swiney, 2007). Primiparous red king crabs mate and fertilize their eggs up to 58 days earlier in the year than multiparous crabs, and have longer development times, averaging 365 days for primiparous and 328 days for M-1 crabs, respectively (Stevens and Swiney, 2007). Primiparous RKC also hatch their larvae earlier in the year than multiparous crabs; mean hatching dates for female crabs in the laboratory in 2001 and 2003 were 5 and 21 February, respectively, but these were based on small samples of 12 crabs, and hatching dates for wild crabs extend well into April (Stevens and Swiney, 2007). As a result, multiple cohorts of larvae may hatch over an extended period of time from January through April, leading to multiple cohorts of settling juveniles as well. This is supported by studies conducted using sausage-shaped artificial collectors (SACs), that demonstrated two pulses of settlement in mid-June and mid-July, 1991 (Blau and Byersdorfer, 1994). Earlier hatching could allow some crabs to become one or two instars ahead of their hatching-year cohorts by age 1.5. Whether due to variable growth or multiple hatching cohorts, at least 3 instars were present in the SACs by December, 1991 (Donaldson et al., 1992). A third possibility is that there may be inherent differences in growth rates or offspring quality between primiparous and multiparous parents, but evidence for this is lacking. Dew (1990) captured and measured individual crabs from two pods located in October 1988 and November 1987, respectively, and determined that each consisted of three modes or instars, with mean sizes of 25.3, 33.3, and 39.6 mm CL. Of the four modes of premolt crabs identified in this study, modes 3 and 4 (Table 1), with mean sizes of 26.1 and 30.8, were similar in size to the two smallest modes measured by Dew (1990). The difference in modal size is probably due to the fact that my samples were collected two months earlier in the year (July and August). Nonetheless, my data are consistent with the conclusion that all crabs were sequential instars of the same 1999 year class, making them approximately 16 ± 2 months post-hatch age.

Molt increments were similar between the three molting groups, but the size range covered (15-50 mm) was relatively narrow, and perhaps greater variability would have been
observed over a longer period of time. The constant MI of 5 mm, however, is essentially equal to the difference in CL between the three initial instars prior to molting. Proportional growth was 22%, 15%, and 12% for first, second, and third molts in the laboratory; this decrease is computationally due to the fact that MI was constant, but premolt size increased. However, this decline in growth could be a laboratory artifact due to inadequate diet or constraints caused by the holding chambers. Powell (1965) measured individual growth of 24 king crabs captured from a pod in Kodiak in 1961 containing crabs in the same size range (25-49 mm, mode 37 mm) as the crabs in this study; mean MI was 7.0 mm, and growth rate was 21.1%, essentially identical to that of the first molt in this study. This rate is similar to that of older (4-5 yo) juvenile and pre-pubescent female crabs that had been recently collected from the wild; they grew at a rate of about 18%, whereas growth rates of primiparous and multiparous females were 6.7% and 3.6%, respectively (Stevens and Swiney, 2008). Takeuchi (1960) held small RKC that were captured from fishing vessels near Port Moller, Alaska, in an aquarium aboard ship until they molted; the average growth rate for 31 crabs from 9 to 16.6 mm pre-molt CL was 18.1%. Thus, juvenile crabs should continue to grow at rates of 18-22% until reaching sexual maturity. Growth rates during the first two molts in the laboratory were compensatory, i.e. juvenile RKC that grew at a high rate (0.25-0.30) during their first molt in captivity grew at a lower rate (0.05-0.20) during their second molt, whereas those that grew at low rates (<0.20) did not vary much between molts. A constant rate of growth over sequential molts would appear as points along a diagonal line with a slope of 1, but the lines in Fig. 7 have slopes ranging from near 0 to −0.5. Although growth rate for molt 1 was independent of crab size (Fig. 6), growth rate during molt 2 was low for crabs >35 mm (Fig. 7).

The lower growth rates observed for subsequent molts in this study suggest that the holding conditions may have limited growth of larger crabs regardless of prior growth rate, and could possibly be a laboratory artifact. Such artifacts could arise from a number of sources that might include water quality, agonistic interactions in the communal holding tank, diet, and size of the holding chambers. Filtered sea water in the holding tanks was the same temperature as ambient seawater, and maintained at a high flow-through rate to eliminate any waste buildup, thus eliminating source #1. The 125 crabs that did not molt either died or were eaten by their cohorts; in most cases it was not possible to determine the cause of death because they just disappeared from the communal tank. Cannibalism among juvenile red king crabs has been documented by a number of authors (Broderson et al., 1989; Rounds et al., 1989; Stevens and Swiney, 2005). Rounds et al. (1989) demonstrated that increased crab density (from 3 to 11 crabs per tank) was associated with an increase in cannibalism but no change in growth rates. Furthermore, those crabs that survived (to molt a second time) probably did so because they ate their tank mates, which should increase their growth rate, but that was not evident. Thus there is no evidence to support source #2. Red king crabs normally eat a variety of wild foods including echinoderms, crustaceans, mollusks, and algae (Pearson, 1983; Dew, 1990). Diet can influence both growth and survival; juvenile RKC that were fed on shrimp tails exhibited greater cannibalism rates and lower growth rates than those fed whole mussels (Broderson et al., 1989). Therefore, it is possible that a strict diet of squid could produce lower than normal growth, due to lack of other essential nutrients; if so, such a reduction should increase over time. Among first molts, there is a strong positive correlation between molting date and molt increment (R² = 0.375, P < 0.0001), probably due to larger crabs molting later in the year. However, among similar sized crabs, i.e., those with premolt CL between 30 and 36 mm, MI was significantly greater for molt 1 (7.57 ± 1.41 mm CL, n = 41) than for molt 2 (6.26 ± 2.12 mm CL, n = 21; t-test, P < 0.05). Thus, this study provides equivocal evidence for a diet effect. The fourth possibility is that the size of the holding chambers limited growth of larger crabs, i.e., those that were molting for the second or third time. This effect is confounded with both size and time, however, so is not possible to isolate. In summary, reduced growth of larger crabs was most likely due to a combination of factors including diet and chamber size.

The results of this study can have utility for management purposes, if treated cautiously. Molt increments and growth rates for first molters are probably representative of growth rates for wild crabs, and therefore accurate enough for modeling purposes. Those for the second molt may be conservative, perhaps reflecting a laboratory effect. Other studies of RKC growth addressed the earliest instars or the first years of life via modal analysis (Weber, 1967; Stevens, 1990; Stevens and Munk, 1990; Donaldson et al., 1992), and a few have addressed individual growth of older crabs (Powell, 1967; Shirley et al., 1990; Stevens and Swiney, 2008). If placed in context, the present data can be used to fill a gap in the existing information about growth of 1-2 yo crabs, and incorporated into a more comprehensive growth model for red king crabs.

ACKNOWLEDGEMENTS

I thank P. Cumminskey for helping to collect the crabs by SCUBA, and S. Persselin and K. Swiney for helping to measure and tag crabs.

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**RECEIVED:** 15 June 2011.  
**ACCEPTED:** 20 September 2011.