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Growth of Female Red King Crabs *Paralithodes camtshaticus* from Kodiak, Alaska, during Pubertal, Primiparous, and Multiparous Molts

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ABSTRACT: Growth models for red king crabs *Paralithodes camtschaticus* typically apply increments based strictly on size and sex, but growth of female red king crabs depends on their specific life history stage and previous reproductive history. Over a period of 5 years, we held female red king crabs in the laboratory for periods up to 4 years, during which we recorded growth for 77 crabs that molted at least once, and some that molted 2 or 3 times, for a total of 121 different molting events. Molts (and data) were classified as being pubertal (i.e., the molt to maturity), primiparous, or multiparous. During their pubertal molt, female red king crabs grew an average of 18.2%, primiparous crabs grew an average of 6.7% and multiparous crabs grew an average of 3.6%. Relationships between premolt and postmolt size differed significantly between molting types. As a result, female crabs of a given size would have different molt increments depending on their reproductive history. Length of captivity did not affect the molt increment at a specific life history stage, i.e. during the primiparous molt; molt increments for females that molted within 6 months of capture were similar to those that molted after an additional year in captivity. Molt increments for multiparous crabs were essentially identical to those reported previously for tagged females. Models of red king crab growth, recruitment, and reproductive output could be significantly improved by considering both the size of female crabs and their reproductive history.

INTRODUCTION

Management of red king crab (RKC) *Paralithodes camtschaticus* fisheries requires an understanding of growth rates and frequencies. Development of models for growth of individual crabs (McCaughran and Powell 1977), or population abundance (Zheng et al. 1995; Zheng et al. 1996) requires estimates of various parameters including growth increments (in mm), relative growth, or probability of molting at given sizes. The utility and predictive ability of such models, or estimates of recruitment and stock-recruitment relationships derived from them (e.g., Zheng and Kruse 2000; Zheng and Kruse 2003) depend on accurate parameterization of the models. Growth models of the types described above typically use growth per molt increments that are relative to the size of crabs, but do not consider reproductive history, which may have an important influence on growth of female crabs.

Growth of juvenile king crabs has been studied by a number of authors, some of whom held crabs in captivity while they molted (e.g., Marukawa 1933; Kurata 1962; Weber 1967), or studied growth of wild cohorts (Stevens 1990; Stevens and Munk 1990). Those studies showed no difference in growth rates or molt increments between juvenile male and female crabs. Growth of adult males has also been studied—most commonly by recovery of individuals that were tagged and released into the ocean (Weber and Miyahara 1962; Powell 1967); others held crabs in tanks in the laboratory or aboard ship during molting (Mihara 1936; Takeuchi 1960; Matsuura and Takeshita 1976; Paul and Paul 1995).

Compared to the amount of data for juveniles and male crabs, there is relatively little growth data for adult female RKC. One reason females have not been studied well is that commercial fishing vessels are not allowed to retain them, so recovery of tagged crabs is impractical. For females, studying growth of captive crabs is more practical, but some studies indicate that growth of male crabs held in cages for extended periods may be less than that of wild molters (Powell 1967). However, female crabs just prior to molting can be easily distinguished and held for shorter periods. Powell (1967) provided growth data for 73 tagged female RKC that molted at liberty and

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were recovered a year after release. Gray (1963) held 140 mature female RKC from 105 to 160 mm in large (10 m^2) tanks and recorded decreasing molt increments with size, but measured crabs only to the nearest mm. Shirley (1990) studied molting of 25 adult female king crabs at different temperatures. Of these three studies, Powell (1967) is the most useful and the most often cited. However, none of these authors determined or reported the reproductive history of the female crabs, and none reported molt increments for females during their pubertal molt.

Female crabs may be described as juvenile (with immature ovaries), prepubescent (ripening ovary), pubescent (with mature ovaries just prior to the molt to maturity), primiparous (carrying their first clutch of eggs), or multiparous (carrying their second or later clutch of eggs; Alunno-Bruscia and Sainte-Marie 1998). The latter category can be further broken down into M-1 (second clutch or first multiparous year), M-2, M-3, etc (Stevens and Swiney 2007). The first 3 categories are difficult to distinguish in the field without examining the ovary, and the latter 3 are virtually impossible to distinguish, thus they have not typically been used to characterize the condition of wild female RKC. However, for the purposes of modeling population growth, it is important to distinguish these categories of female reproductive status, and to apply growth parameters that are appropriate to the type of molt.

Over a period of 5 years, we have held female RKC in captivity for a variety of research projects. During that time, we recorded molting data for numerous female crabs, many of which molted more than once in the laboratory. In this study, we review and analyze those data in order to answer 3 specific questions:

1. What is the mean growth increment, and premolt-postmolt relationship for female crabs undergoing their pubertal, first post-pubertal (primiparous), or second post-pubertal (multiparous) molt? Hypotheses to be tested include:
   - H_{01}: No difference between molt increment or relative growth due to molt type;
   - H_{a1}: Molt increment and relative growth decrease with age and molt type.
2. Does length of captivity affect molt increment, i.e., is there a difference in growth increment at the primiparous molt (or equivalent size), between crabs undergoing their first or second molt in the laboratory? Hypothesis to be tested is:
   - H_{02}: No difference between molt increment or relative growth due to length of captivity or previous number of molts in the laboratory;
   - H_{a2}: Molt increment and relative growth decrease with length of captivity.
3. How do growth data for laboratory-held crabs compare to data from wild-tagged crabs, as published by Powell (1967)?
   - H_{03}: No difference between growth of captive or wild crabs;
   - H_{a3}: Growth of captive crabs is less than that of wild crabs.

METHODS

Female king crabs were captured by scuba divers from Womens Bay, Kodiak, Alaska, without known bias at various times from 2000 to 2004. Reproductive condition was recorded, and for those that were ovigerous, color and condition of embryos (eyed, uneyed), and relative size of clutch (on a 6-point scale) were recorded. Crabs were held in 2500 L tanks with flow-through seawater at ambient temperatures and fed twice weekly with squid *Loligo* spp. or herring *Clupea harengus*. Each crab was tagged with a numbered tag on a cable-tie around one walking leg. Dates of molting, mating and death were recorded, and premolt and postmolt carapace length (CL) was measured to the nearest 0.1 mm for most crabs—from the right orbit to the midpoint of the rear margin of the carapace. Temperature of incoming seawater was recorded at 2 hr intervals by electronic data loggers. Average daily temperatures during molting ranged from 3.6 ºC to 5.5 ºC over the years studied (Stevens and Swiney 2007). Exact dates of molting are not of concern in this study, and are reported elsewhere for many of these same crabs (Stevens and Swiney 2007).

Captured female RKC were categorized into 4 different groups based on their reproductive stage when captured, and the timing of molting in the laboratory (Table 1). Group 1 included 29 crabs that were pubescent when captured, and underwent their first molt in the laboratory—their pubertal molt—within 0-104 days (mean ± SD = 56 ± 28) of capture. This group also included 2 juvenile crabs that molted in captivity to the pubescent stage. Group 2 consisted of 17 crabs from Group 1 (pubertal molters) that molted a second time in the laboratory as known primiparous crabs after an additional 12 months of captivity (mean 442 ± 37 days after capture). Group 3 included 44 females that were ovigerous when captured, and all experienced their first molt in the laboratory within 21 to 152 days (mean 91 ± 38) of capture, but whose reproductive history was unknown. These were divided into two subgroups: Group 3a included 31 crabs < 124 mm CL (the same size range as Group 1 crabs after their pubertal molt), that were tentatively categorized as primiparous; although we could not be absolutely cer-

Table 1. Descriptions of reproductive history, molt sequence, and molt type for female red king crabs in Groups 1–5. Crabs in Groups 1–4 were collected from Womens Bay in 2000–2004; those in Group 5 were wild-tagged by Powell (1967) and recovered after one year at liberty.

Group	Maturity at capture	Molt Sequence	Molt type	Number
1	Immature	First	Juvenile or Pubertal	31
2	Immature (subset of 1)	Second	Primiparous	17
3a	Mature	First	Primiparous?	31
3b	Mature	First	Multiparous?	13
4	Mature (subset of 2+3)	Second or third	Multiparous	31
5	Unknown (ovigerous)	Wild	Unknown	73

tain about the reproductive status of each crab in this group, this conclusion was supported by their similar size and growth patterns (see results) with enough certainty to test Hyphothesis 2 as defined. Group 3b included 13 crabs from 125 to 146 mm CL and probably contained a mix of primiparous and multiparous crabs. The cutoff of 124 mm was selected because it occurred at a break in the size frequencies; variations of that value from 122 to 128 mm included or excluded 2 or 3 additional crabs, but gave essentially identical results. Group 4 includes a subset (27 crabs) of group 3 that molted a second time (first multiparous, or M-1) in the laboratory; 4 crabs that molted a third time (M-2) were also included because the sample was too small for individual analysis. In order to compare growth in the laboratory to growth of wild crabs in the ocean, 73 adult female RKC that were tagged by Powell (1967) in 1955 in Marmot Bay were included as group 5. Their reproductive status when tagged was reported only as "mature" (presumably ovigerous), but they were not classified as primiparous or multiparous; all were recovered after one year of liberty and had molted only once in that time interval.

Premolt CL, postmolt CL, growth increment in mm, and relative growth (as % of premolt CL) were compared between all groups by single factor analysis of variance (ANOVA); multiple comparisons were conducted using Tukey's Honestly Significant Difference (HSD) test. This analysis tested both hypotheses H_{01} and H_{03} simultaneously. Data for pre- and post-molt CL met the assumptions of homoscedasticity (Shapiro-Wilk statistic, $P > 0.05$), but growth increment and relative growth did not, so growth increments were transformed using $Log_{10}(x+1)$, and relative growth was transformed using the arcsine transformation (Zar 1984). Relative growth was still heteroscedastic, but ANOVA is robust to minor departures from normality. In order to determine whether length of captivity affected growth, molt increment and relative growth were compared between subgroups 2 and 3a. Crabs in these two groups were of similar size (see results), and experienced their primiparous molt as either their second or first molt in the laboratory, respectively. Because this is a specific life-history stage or milestone, it can be compared between the groups without being influenced by size or reproductive history, which would confound any comparison using subsequent molts of the same crabs. For this purpose, a one-tailed *t*-test was used to test hypothesis H_{02}, i.e., that increment 2 = increment 3a, with the alternative hypothesis H_{a2}, i.e., that 2 > 3a. To determine if size-specific growth rates differed among groups, postmolt CL and growth increment were regressed on premolt CL and the resulting relationships were compared between groups by analysis of covariance (ANCOVA), with premolt CL as covariate. All statistics were conducted using SYSTAT 11 (SYSTAT 2004).

RESULTS

A total of 121 molting events were recorded for 77 different female crabs (Table 1) held in the laboratory. Mean premolt CL of crabs differed significantly among the 6 groups ($F_{(5,190)} = 87.620$, $P < 0.0001$), however, post-hoc comparisons showed that groups 2 and 3a were similar, group 3b was similar to both 4 and 5, but the latter two groups were not similar to each other (HSD test; Table 2). Postmolt CL also differed significantly among groups ($F_{(5,190)} = 59.215$, $P < 0.0001$); similarities among groups followed the same pattern as for premolt CL.

The mean of log-transformed growth increments differed significantly among the 5 groups of crabs ($F_{(5,190)} = 43.46$, $P < 0.0001$), so H_{01} was rejected. Group 1 crabs experienced their pubertal molt as the first molt in the laboratory, after which they extruded their first clutch of embryos. Growth of group 1 crabs (16.3 ± 1.8 mm) was significantly greater than for all other groups; mean growth increment and SD for the 2 juvenile crabs were identical to that for Group 1 (Table 2). Mean growth increments for groups 2 and 3a were identical (7.5 ± 1.9 mm), and similar to that of group 3b (6.3 ± 1.7 mm). Mean growth increment for groups 4 (4.9 mm) and 5 (4.3 mm) were similar,

Table 2. Descriptive statistics for female red king crabs in Groups 1–5. Letters indicate groups that were not significantly different (within columns) by Tukey's HSD test. Means are also shown for the combinations of similar groups 2+3a and 3b+4+5.

		Premolt		Postmolt		Growth		% Growth	
Group	N	CL	SD	CL	SD	(mm)	SD	%	SD
1	31	90.7	10.4	106.9	10.2	16.3	1.8	18.2%	3.3%
2	17	110.6[a]	5.8	118.1[a]	4.7	7.5[a]	2.1	6.9%[a]	2.2%
3a	31	113.6[a]	7.3	121.1[a]	6.8	7.5[a]	1.7	6.7%[a]	1.8%
3b	13	132.9[bc]	5.4	139.2[bc]	6.1	6.3[ab]	1.7	4.7%[ab]	1.3%
4	31	128.5[b]	9.9	133.4[b]	9.9	4.9[bc]	1.8	3.8%[bc]	1.4%
5	73	138.5[c]	15.1	142.8[c]	14.0	4.3[c]	2.6	3.3%[c]	2.1%
2+3a	48	112.5	6.9	120.1	6.3	7.5	1.9	6.7%	1.9%
3b+4+5	117	135.2	13.7	139.9	12.9	4.7	2.4	3.6%	1.9%

but significantly less than the other groups. Groups 3b and 4 were similar; the latter 3 groups averaged 4.7 ± 2.4 mm. The ANOVA for relative growth was also significant ($F_{(5,190)}$=115.41, P < 0.0001); post-hoc comparisons showed that Group 1 had the largest proportional increment (18.2 ± 3.3%), groups 2 and 3b exhibited similar but significantly less growth (with a combined mean of 6.7 ± 1.9%), and groups 3b, 4, and 5 showed the same pattern of similarity as seen for growth increment, averaging 3.6 ± 1.9%.

Crabs in groups 2 and 3a were identical in premolt size range, molt increment ($t_{(one\text{-}tailed,\ 0.05)}$ = 0.027, P = 0.489), and relative growth ($t_{(one\text{-}tailed,\ 0.05)}$ = 0.348, P = 0.365). Consequently, both groups were considered to be primiparous crabs that experienced their first post-pubertal molt as either their first (group 3a) or second (group 2) molt in the laboratory. Therefore H_{02} was accepted and H_{a2} was rejected; the difference in holding time of an additional 12 months had no effect on growth increment for crabs of similar size and reproductive history.

The mean growth increments for groups 4 (known multiparous) and 5 (Powell's crabs) were not significantly different, with an overall mean of 4.5 ± 2.4 mm. Therefore, H_{03} was accepted and H_{a3} was rejected. One multiparous crab (127 mm CL) had a growth increment of 21 mm; this was considered to be an erroneous measurement or perhaps it followed a second (unrecorded) molt, so it was excluded from analysis. Another crab in group 3 had a growth increment of 0 mm; it was considered valid because this result (zero growth per molt) is consistent with measurements of wild tagged crabs (Powell 1967).

Group 3b probably consisted of both primiparous and multiparous crabs; they exhibited growth increments similar to that of primiparous crabs, but relative growth similar to that of the multiparous crabs. Because of their intermediate and unknown status they were not used to test any of the stated hypotheses.

Postmolt CL (Figure 1) and growth increment (Figure 2) were significantly related to premolt CL. Preliminary ANCOVA indicated no interaction effects for either postmolt CL or growth increment, so regression lines were concluded to be parallel (equal slopes), and the final analysis included only group effects (i.e., elevations). For this analysis, groups 2 and 3a were combined as primiparous molters, and group 3b was omitted. Regression lines of postmolt CL on premolt CL for pubertal, primiparous, and multiparous molters were significantly different and both the groups and the covariate (premolt CL) had significant effects, indicating that mean postmolt CL (adjusted for premolt CL) was significantly different between groups. Premolt CL accounted for the greatest amount of variance ($F_{(3,178)}$=5306.09, P <0.0001), but the groups (i.e. intercepts) also differed significantly ($F_{(3,178)}$=65.59, P < 0.0001). The regression relationships (Table 3) for groups 1 (pubertal molters) and 2+3a (primiparous molters) were significantly different from all other groups (Table 4), but groups 4 (multiparous molters) and 5 (Powell's wild crabs) were similar to each other, so a combined regression equation was calculated. Growth increment is simply a scalar of postmolt CL (minus premolt CL) so the ANCOVA results and all intercepts were similar to those for postmolt CL, but groups ($F_{(3,178)}$ = 65.59, P < 0.0001) accounted for a larger portion of variance than premolt CL ($F_{(3,178)}$ = 31.34, P < 0.0001). Post-hoc comparisons among groups were identical with those for postmolt CL, however, the regression of growth increment on premolt CL was not significant for crabs in group 1 (Table 3), all of which molted over a relatively narrow size range.

DISCUSSION

Our growth data for female RKC during their pubertal molt are unique, and demonstrate that growth of female king crabs depends not only on their premolt

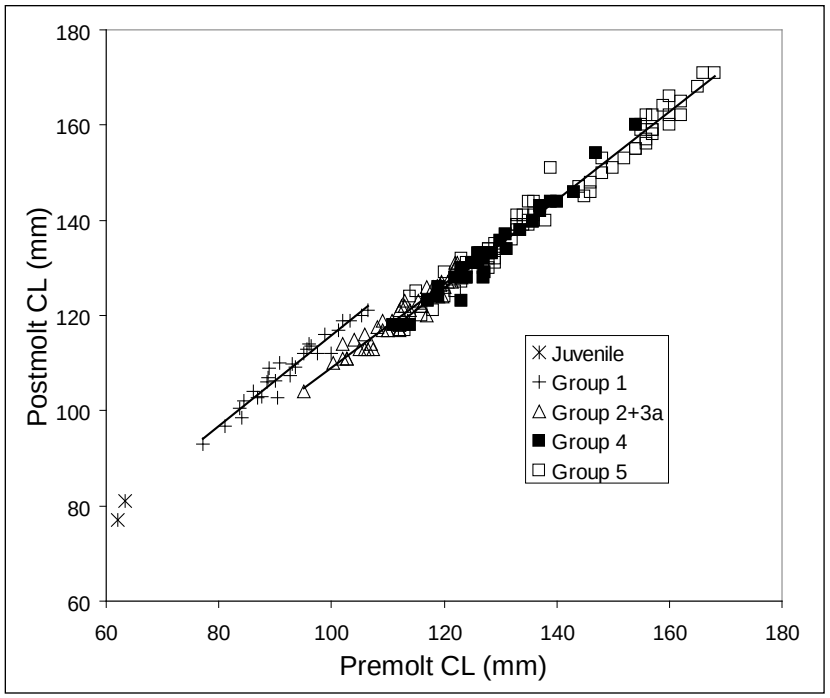


Figure 1. Regression of postmolt CL on premolt CL for female red king crabs that molted in the laboratory. Groups 1, 2+3a, and 4 represent pubertal, primiparous, and multiparous molters, respectively, whereas group 5 are data from Powell (1967); the latter two were combined for regression analysis. Two crabs that molted to another juvenile stage (far left) were excluded from the regression.

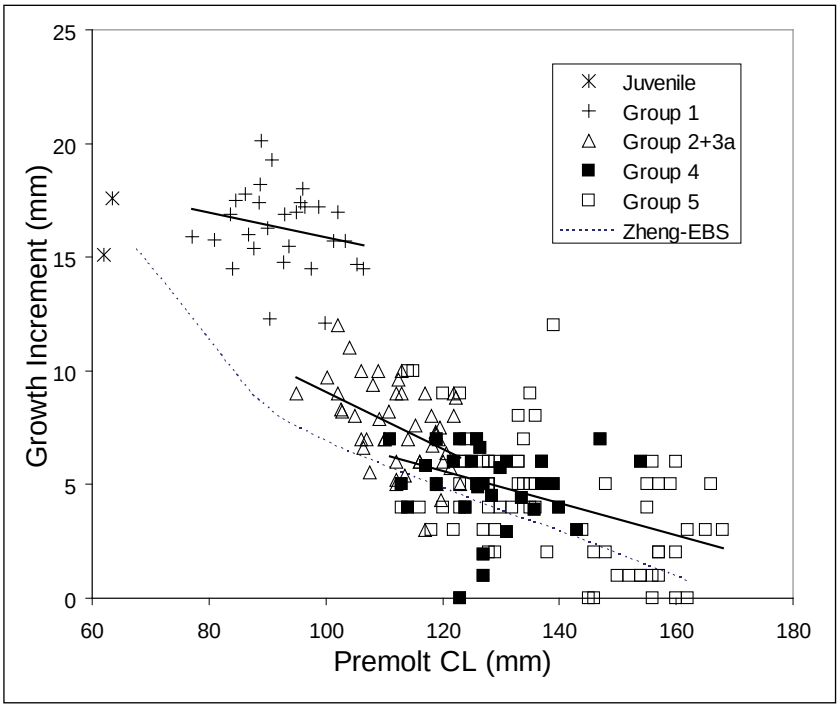


Figure 2. Regression of growth increment on premolt CL for female red king crabs that molted in the laboratory. Groups 1, 2+3a, and 4 represent pubertal, primiparous, and multiparous molters, respectively, whereas group 5 are data from Powell (1967); the latter two were combined for regression analysis. Two crabs that molted to another juvenile stage (far left) were excluded from the regression. Growth estimates used by Zheng and Kruse (2003) are also included for comparison.

Table 3. Regression parameters of postmolt CL (mm) and growth increment on premolt CL (mm) for female red king crabs in groups 1–4. Groups 2 and 3a were combined, as were groups 3b, 4, and 5. Data correspond to regression lines in Figures 1 and 2.

Group	Molt Type	α (Intercept)	B (slope)	n	r^2	*P*
Postmolt CL						
1	Pubertal	21.323	0.945	29	0.942	<0.001
2+3a	Primiparous	21.501	0.876	48	0.931	<0.001
4+5	Multiparous	14.099	0.929	104	0.974	<0.001
Growth Increment						
1	Pubertal	21.323	−0.055	29	0.051	0.238
2+3a	Primiparous	21.501	−0.124	48	0.214	0.001
4+5	Multiparous	14.099	−0.071	104	0.181	<0.001

Table 4. Analysis of covariance for female red king crabs: Comparisons of regression lines for postmolt CL (above diagonal) or growth increment (below diagonal) on premolt CL. All comparisons had 178 degrees of freedom and MSE equal to 4.009.

Group	1	2+3a	4	5
1		<0.001	<0.001	<0.001
2+3a	<0.001		<0.017	<0.041
4	<0.001	<0.017		<0.983
5	<0.001	<0.041	<0.983	

size, but also on their reproductive history. A female of 100 mm CL will increase by 18.2% during her pubertal molt, but will only increase by 6.7% if she is primiparous. Growth increments for juvenile male and female RKC ranging from 10 to 79 mm CL are similar (Weber 1967), with increments ranging from 21% to 25% (Powell 1967). Takeuchi (1960) reported that 300 juveniles (range 8 to 17 mm CL) grew an average of 18% per molt. Growth of female RKC during their pubertal molt (16.3 mm or 18.2%) was similar to that of similarly-sized male crabs (Powell 1967) and females undergoing additional juvenile molts. Powell (1967) reported that relative growth of 4 juvenile female crabs (range 80 to 100 mm CL) was 14.9%, whereas growth of 21 males ranging from 86 to 99 mm CL was 18%. The pubertal molt of female RKC, therefore, can be considered equivalent to an additional juvenile or male molt for crabs within that size range. Apparently, production of a ripe ovary during the prepubescent phase does not detract from subsequent growth during the pubertal molt.

Our data show that growth increments for female RKC decline after maturity, in agreement with Gray (1963). In contrast, growth of mature males tends to stabilize, although relative growth continues to decline; mean growth increment for 359 male crabs at liberty one year was 19.7 mm, and was similar over a range of 122 to 151 mm CL (Powell 1967). Mean growth increment reported by Paul and Paul (1995) for 64 mature male RKC (72 to 143 mm CL) from Cook Inlet was 10 ± 3.5 mm CL, i.e. smaller than that reported herein or by Powell (1967), and was not correlated with premolt size of crabs. The average growth increment for male RKC >110 mm in Bristol Bay was 16 mm (Weber and Miyahara 1962), whereas growth of 28 male RKC (premolt 75 to 120 mm CL) from Southeast Alaska that molted in captivity was only 11 mm (Zhou et al. 1998).

Growth during the primiparous molt is significantly less than during the pubertal molt, and growth during the first multiparous (M-1) molt is significantly less than during the primiparous molt. Growth during later multiparous molts (M-3, M-4) is small. To some degree these changes represent a general decline in growth with size, but size alone is not enough to predict the growth increment of female crabs accurately without information on reproductive status. Brooding females of *Cancer setosus* supply oxygen to embryos by flapping their abdomens and pleopods; oxygen consumption, and thus metabolic rates, of female crabs that were actively brooding late stage embryos were twice as high as those of non-brooding females (Baeza and Fernandez 2002; Fernandez et al 2002). Therefore, increased metabolic costs associated with brooding are probably responsible for reduced growth of primiparous and multiparous female crabs, when compared to growth of males, or during the pubertal molt.

Our data for growth of multiparous crabs (group 4) are not significantly different from those of Powell (1967) for 73 tagged female RKC (110 to 169 mm CL) that were at liberty for one year (i.e. one molt), suggesting that most of his crabs were also multiparous, and that length of captivity did not affect growth of our crabs. Powell (1967) did not differentiate between primiparous and multiparous females, and estimated the average annual molt increment over all sizes and years as 4.4 mm. Matsuura and Takeshita (1976) held 3 female RKC for several years during which they molted annually. One juvenile crab grew 15% during her pubertal molt. The average growth increase for her next 3 molts (as an adult) and that of 2 other crabs of

unknown reproductive history was 6.6%—similar to that for our primiparous crabs. The average increase during 4 multiparous molts by those same 3 crabs was 5.0% (Matsuura and Takeshita 1976).

In our study, length of captivity had no significant effect on growth increment, i.e. there was no difference in growth during the primiparous molt between female RKC that molted within 2 to 3 months of capture, and those that were held an additional year after their pubertal molt. Our conclusions contrast with those of Powell (1967), who observed reduced growth primarily with captive male crabs. The differences may be due to sex, size of crabs, or the fact that we compared growth during a specific life-history event, whereas other studies did not distinguish specific instars or life stages of crabs. Our results are consistent with those of Weber (1967) however, who compared growth of juvenile crabs that molted within 5 days of capture to those that molted later, and all crabs that molted in captivity to 12 crabs found molting in the ocean. He concluded that there was no difference in growth due to captivity. It could be argued that any captivity—whether 6 months or 12 months—caused a similar reduction in growth. However, the similarity between our data and that of other authors (Powell 1967; Matsuura and Takeshita 1976) argues against that conclusion.

Temperature also has an impact on growth rate of RKC, primarily by altering the length of the intermolt period rather than the molt increment (Kurata 1960; Kurata 1962; Stevens 1990; Stevens and Munk 1990). Shirley (1990) measured growth of 25 ovigerous female RKC with a mean size of 113 mm CW (not CL), that were held in the lab at 5 different temperatures (5 crabs per temperature). Although the actual increments are not comparable due to the different measurements used, mean growth increment at 3°C (11.9 ± 4.3 mm CW) was greater than that at 6°C (7.1 ± 1.9 mm CW), the two temperatures closest to those in our laboratory. However, Shirley (1990) did not distinguish whether crabs were primparous or multiparous, and the mixture of each type may have affected their average growth increment.

In contrast to RKC, mean growth increment for 101 female golden king crabs *Lithodes aequispinus*, ranging from 104 to 157 mm CL, held in captivity, was 6.6 mm, or 5.1% (Paul and Paul 2001), but this group of crabs included both primiparous and multiparous molters. Prepubescent female snow crabs *Chionoecetes opilio* grew 23.2% to 31.3%, but growth rate declined to 14.7% to 17.5% at their molt to maturity (Alunno-Bruscia and Sainte-Marie 1998). However, snow crabs differ significantly from king crabs because their pubertal molt is terminal, and they do not molt again as primiparous or multiparous crabs.

Growth models for RKC (e.g., McCaughran and Powell 1977) typically apply constant increments across a range of sizes, or use relative growth increments that are averages for a given size range. Models that are currently used for management of RKC populations incorporate a large number of parameters including size, growth increment, proportion molting, molting probability, and mortality (Zheng et al. 1995). Some of these parameters are poorly estimated due to a paucity of data; this lack of accuracy affects the precision of subsequent estimates of spawning biomass and egg production, which are directly related to the estimated size of crabs. Our data demonstrate, however, that growth of female crabs depends not only on size but also on reproductive history. The length-based population model for eastern Bering Sea RKC developed by Zheng et al. (1995) and subsequently used as the basis for stock rebuilding strategies (Zheng et al. 1997; Zheng et al. 1997), utilized an average growth increment for female RKC that was derived from Gray (1963), who sampled few crabs below 110 mm CL and only recorded measurements to the nearest mm. As a result of procedural and population differences, their model differs considerably from our data (see Figure 2); at premolt sizes above 110 mm their values are about 1 mm less than those for our combined groups 3 and 4 (multiparous) crabs, but growth increments for (pubertal) molters between 70 and 110 mm differ by up to 50%. Zheng et al. (1995) did not distinguish between the types of molts in their model, partially because those distinctions are not made during the National Marine Fisheries Service surveys from which their data originated. However, because such models typically start with estimates of recruits at sizes near that of maturity (e.g. 90 mm for female RKC), it should not be difficult to assign them to reproductive categories and model their growth using the appropriate relationships. Relationships calculated for Kodiak crabs may not be identical to those for the eastern Bering Sea population; mean size at 50% sexual maturity (SM_{50}), averaged over the years from 1975 to 1989, was 88.8 mm for eastern Bering Sea RKC (Otto et al. 1990), compared to a value of 112 mm for Kodiak RKC (Powell 1967). Relative growth may or may not differ. Incorporating growth data for crabs of specific life stages and reproductive history into future models should improve the accuracy of predicted values for growth, abundance, and fecundity.

LITERATURE CITED

Alunno-Bruscia, M., and B. Sainte-Marie. 1998. Abdomen allometry, ovary development, and growth of female snow crab, *Chionoecetes opilio* (Brachyura, Majidae) in the northwestern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences 55:459–477.

Baeza, J. A., and M. Fernandez. 2002. Active brood care in *Cancer setosus* (Crustacea:Decapoda): the relationship between female behaviour, embryo oxygen consumption and the cost of brooding. Functional Ecology 16(2):241–251.

Fernandez, M., L. M. Pardo and J. A. Baeza. 2002. Patterns of oxygen supply in embryo masses of brachyuran crabs throughout development: the effect of oxygen availability and chemical cues in determining female brooding behavior. Marine Ecology-Progress Series 245:181–190.

Gray, G. W., Jr. 1963. Growth of mature female king crab *Paralithodes camtschatica* (Tilesius). Alaska Department of Fish and Game, Informational Leaflet No. 26.

Kurata, H. 1960. Studies on the larvae and postlarvae of *Paralithodes camtschatica*. III. The influence of temperature and salinity on the survival and growth of the larvae. Bulletin of the Hokkaido Regional Fisheries Research Laboratory 21:9–14.

Kurata, H. 1962. Studies on the age and growth of crustacea. Bulletin of the Hokkaido Regional Fisheries Research Laboratory 24:1–15.

Marukawa, H. 1933. Biological and fishery research on the Japanese king crab *Paralithodes camtschatica* (Tilesius). Journal of the Imperial Fisheries Experimental Station 37:1–152.

Matsuura, S., and K. Takeshita. 1976. Molting and growth of the laboratory-reared king crab, *Paralithodes camtschatica* (Tilesius). Reports of the Fishery Research Laboratory, Kyushu University 3:1–14.

McCaughran, D. A., and G. C. Powell. 1977. Growth model for Alaska King Crab (*Paralithodes camtschatica*). Journal of the Fisheries Research Board of Canada 34:989–995.

Mihara, T. 1936. Observations on the time required for molting and on the growth of king crab (*Paralithodes camtschatica*). Ten day report of Hokkaido Fisheries Experimental Station 332:12–13.

Otto, R. S., R. A. MacIntosh and P. A. Cummiskey. 1990. Fecundity and other reproductive parameters of female red king crab (*Paralithodes camtschatica*) in Bristol Bay and Norton Sound, Alaska. Pages 65–90 *in* B. Melteff, editor. Proceedings of the International Symposium on king and Tanner crabs, November 28–30, 1989, Anchorage, Alaska, University of Alaska Sea Grant Program Rep. No. AK-90-SG-04.

Paul, A. J., and J. M. Paul. 1995. Changes in chela heights and carapace lengths in mature male red king crabs after molting in the laboratory. Alaska Fishery Research Bulletin 2(2):164–167.

Paul, A. J., and J. M. Paul. 2001. Changes in chela heights and carapace lengths in male and female golden king crabs *Lithodes aequispinus* after molting in the laboratory. Alaska Fishery Research Bulletin 6(2):70–77.

Powell, G. C. 1967. Growth of king crabs in the vicinity of Kodiak Island, Alaska. Alaska Department of Fish and Game, Kodiak. Informational Leaflet No. 92.

Shirley, T. C., S. M. Shirley and S. Korn. 1990. Incubation period, molting, and growth of female red king crabs: effects of temperature. Pages 51–64 *in* B. Melteff, editor. Proceedings of the international symposium on king and Tanner crabs, November 28–30, 1989, Anchorage. University of Alaska Sea Grant Program. Rep. No. AK-90-SG-04.

Stevens, B. G. 1990. Temperature-dependent growth of juvenile red king crab, *Paralithodes camtschatica*, and its effects on size-at-age and subsequent recruitment in the eastern Bering Sea. Canadian Journal of Fisheries and Aquatic Sciences 47(7):1307–1317.

Stevens, B. G., and J. E. Munk. 1990. A temperature-dependent growth model for juvenile red king crab, *Paralithodes camtschatica*, in Kodiak, AK. Pages 293–304 *in* B. Melteff, editor. Proceedings of the International King and Tanner Crab Symposium, November 28–30, 1989, Anchorage. University of Alaska Sea Grant Publications Rep. No. AK-90-SG-04.

Stevens, B. G., and K. M. Swiney. 2007. Hatch timing, incubation period, and reproductive cycle for primiparous and multiparous red king crab *Paralithodes camtschaticus* (Tilesius, 1815). Journal of Crustacean Biology 27(1):37–48.

SYSTAT. 2004. SYSTAT 11, SYSTAT Software Inc., Richmond, CA.

Takeuchi, I. 1960. Rearing experiment of juvenile king crab (*Paralithodes camtschatica*) in the eastern Bering Sea - Observations on molting and growth. Hokkaido Fishery Experimental Station Monthly Report 17(12):453–460.

Weber, D. D. 1967. Growth of the immature king crab *Paralithodes camtschatica* (Tilesius). Bulletin. International North Pacific Fisheries Commission 21:21–53.

Weber, D. D., and T. Miyahara. 1962. Growth of the adult male king crab *Paralithodes camtschatica* (Tilesius). Fishery Bulletin 200(62):53–75.

Zar, J. H. 1984. Biostatistical Analysis, 2nd Ed. Englewood Cliffs, NJ, Prentice-Hall.

Zheng, J., and G. H. Kruse. 2000. Recruitment patterns of Alaskan crabs in relation to decadal shifts in climate and physical oceanography. Ices Journal of Marine Science 57(2):438–451.

Zheng, J., and G. H. Kruse. 2003. Stock-recruitment relationships for three major Alaskan crab stocks. Fisheries Research 65(1–3):103–121.

Zheng, J., M. C. Murphy and G. H. Kruse. 1995. A length-based population model and stodk-recruitment relationships for red king crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 52(5):1229–1246.

Zheng, J., M. C. Murphy and G. H. Kruse. 1996. A catch-length analysis for crab populations. Fishery Bulletin 94(3):576–588.

Zheng, J., M. C. Murphy and G. H. Kruse. 1997. Alternative rebuilding strategies for the red king crab *Paralithodes camtschaticus* fishery in Bristol Bay, Alaska. Journal of Shellfish Research 16(1):205–217.

Zheng, J., M. C. Murphy and G. H. Kruse. 1997. Analysis of harvest strategies for red king crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 54(5):1121–1134.

Zhou, S., T. C. Shirley and G. H. Kruse. 1998. Feeding and growth of the red king crab *Paralithodes camtschaticus* under laboratory conditions. Journal of Crustacean Biology 18(2):337–345.

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