FEEDING AND GROWTH OF THE RED KING CRAB *PARALITHODES CAMTSCHATICUS* UNDER LABORATORY CONDITIONS

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ABSTRACT

Feeding and growth in wet weight of the red king crab *Paralithodes camtschaticus* were studied under laboratory conditions for 4 months from September 1993 to January 1994. Crabs were divided into 3 groups: ovigerous females, juvenile females, and mature males. Food consumption ($g \cdot d^{-1}$) significantly increased with crab wet weight (W), while feeding rate (FR, $g \cdot kg^{-1} \cdot d^{-1}$), weight-standardized food consumption, decreased significantly with crab weight. The relationship of FR~W significantly differed between ovigerous females and juvenile females and males, but not between juvenile females and males, and can be expressed as FR = 70.9 – 0.017 W ($P < 0.001$) for ovigerous females, FR = 64.1 – 0.017 W ($P < 0.001$) for juvenile females and males. Crabs ceased feeding during molting, and feeding rates were significantly lower between 12 days before and 8 days after ecdysis than during the nonmolting period. Molted male crabs rapidly increased weight after molt. Their growth rate averaged 412.3 $g \cdot kg^{-1}$ ± 89.6 SD (wet weight) and decreased with crab weight. Among unmolted crabs, growth rates significantly differed between ovigerous females (66.6 $g \cdot kg^{-1}$ ± 19.4 SD), juvenile females (50.4 $g \cdot kg^{-1}$ ± 14.5 SD), and males (5.2 $g \cdot kg^{-1}$ ± 4.0 SD).

The red king crab *Paralithodes camtschaticus* (Tilesius) is a well-studied species that supports one of the most valuable fisheries in Alaska. Because red king crabs have slower growth and older age (≈7 years) of maturity than many other crab species, they are vulnerable to overfishing (Kruse, 1993). Most Alaskan stocks of red king crabs declined in the early 1980s; fishing and environmental factors may have contributed to these declines (e.g., Zheng *et al.*, 1995; Tyler and Kruse, 1996). New management alternatives, such as reduced- or slot-size limits and allowing the harvest of females, have been suggested for this species. Such management changes, however, require more knowledge of the biology of the red king crab to evaluate potential benefits (Kruse, 1993). Feeding, molting, and growth of the red king crab have attracted many investigations, but most have been field studies where feeding rates could not be measured.

Quantification of food consumption is essential to the investigation of metabolism and growth and can usually be obtained by rearing animals in the laboratory. Previous studies on the feeding rate of the red king crab have focused on juvenile crabs < 50-mm carapace length (Rice *et al.*, 1985; Molyneaux and Shirley, 1988). For adult crabs, food preference and diet, rather than feeding rate, have been emphasized (Marukawa, 1933; Bright,

1967; Feder and Paul, 1981; Jewett and Feder, 1982). Matsuura and Takeshita (1976) measured feeding rates of adult red king crabs, but, since data were collected from only one male and one female, and experimental methods were not described, more information on the food consumption of the red king crab and its relationship to sex and size is needed.

In crustaceans, changes in food consumption with the molt cycle affects catchability by baited traps (Miller, 1990). In other decapod species, feeding rate decreases to zero when the animal approaches ecdysis and recovers after ecdysis (Chittleborough, 1975; Lipcius and Herrnkind, 1982; O'Halloran and O'Dor, 1988). The relationship between feeding and molt cycle for the red king crab is unknown.

Growth of the red king crab has been extensively studied both by laboratory rearing (Gray, 1963; Weber, 1967; Matsuura and Takeshita, 1976; Shirley *et al.*, 1989; Matsuura and Takeshita, 1989) and mark and recapture of field-caught crabs (Bright *et al.*, University of Southern California, unpublished; Powell, Alaska Department of Fish and Game, unpublished; Bright, 1967). Since the exoskeleton of a crab does not grow continuously, but increases in size only at molt, previous studies used the change in carapace size as a growth index (McCaughran and Powell, 1977). Weight changes are rarely con-

sidered as a growth index. When juvenile crabs were kept at relatively uniform conditions for an extended period, weight after ecdysis yielded a clearer index of growth than did linear measurements of carapace size (Bright *et al.,* University of Southern California, unpublished). Under controlled laboratory conditions, weight change is the preferred index of growth, especially during the intermolt period, when carapace size does not change. However, only juvenile red king crabs have been used in the few studies where weight data were recorded (Bright *et al.,* University of Southern California, unpublished; Weber, 1967; Gharrett, 1986; Molyneaux and Shirley, 1988).

The purpose of our study was to investigate the effects of sex, size, and molt cycle on food consumption, feeding rate, and growth in wet weight and size of red king crabs held in the laboratory. This study provides information on feeding and increase in weight of adult red king crabs, and data on juveniles allow comparison with previously published studies.

MATERIALS AND METHODS

Red king crabs were collected in August 1993 with baited commercial and sport king crab pots at depths of approximately 60 m in Barlow Cove (58°22′N, 134°53′W), in southeast Alaska, approximately 35 km northwest of the laboratory in Juneau. Crabs were transported to the laboratory immediately and kept in tanks with flowing sea water from a 30-m deep intake. At the start of the experiment, carapace lengths (CL, the straight line distance from the posterior margin of the right eye orbit to the medial-posterior margin of the carapace) of all crabs were measured to the nearest millimeter, and live weights were measured to the nearest 0.1 g. When a crab was weighed, a towel was placed on the pan bottom and the crab was covered with another towel. Crabs with missing legs were not used. Crabs were marked with a numbered disk tag around the base of the third walking leg. One hundred and thirty-five crabs were divided into 3 groups of 45 crabs each: ovigerous females (females with eggs), juvenile females (females without eggs), and males. Most (over 90%) juvenile females became primiparous just after the experiment terminated, because they mated and extruded eggs in the following spring. All males were functionally mature, since all successfully mated and induced egg extrusion by females in spring immediately after the experiment. The range (mm) and mean (mm) ± SD of CL were 88–125 and 112 ± 8 for ovigerous females, 70–105 and 87 ± 9 for juvenile females, and 78–125 and 100 ± 12 for males.

Fifteen crabs from each group were selected by randomized block design for feeding and growth experiments. These crabs were kept in individual compartments covered with green fiberglass which provided a dim light condition in the compartment. Each compartment had a volume of approximately 43.5 l of sea water, exchanged

at a rate of 1.05 l·min⁻¹. Food consumption was measured by placing weighed, cut squid (*Loligo opalescens* Berry) into each crab container and weighing the uneaten remainder 24 h later. The food was blotted dry with paper towels before weighing. Control food was soaked for 24 h in a tank without crabs to determine wet weight changes due to immersion, and consumption was corrected accordingly. Food consumption was measured every 3 days (e.g., fed on day 1, uneaten food removed on day 2, no food on day 3, fed again on day 4) for 3 months. Food consumption (FC in $g·d^{-1}$) per crab was the amount of food eaten within 24 h, and feeding rate (FR in $g·kg^{-1}·d^{-1}$) was the proportion of body weight of food consumed per crab, i.e., FR = FC/W, where W is crab weight in kilograms at the beginning of the experiment.

The remaining 30 crabs from each group were used to study growth only. These crabs were also fed every 3 days, but their food was not weighed. Each of these crabs occupied a similar amount of water with a similar water exchange rate as crabs in the feeding experiment. Live weight and CL were measured at the beginning and end of the experiment. Weight gain (W_g in g) was the net weight increase during the 4 months and the growth rate (GR in $g·kg^{-1}$) was obtained by GR = W_g/W. Here, we define growth rate as relative weight change, although both true tissue growth and water intake during molting may contribute to weight change.

The experiments were conducted during September 1993 to January 1994. Natural water temperature ranged from 5.4–9.4°C and salinity was constantly 32 ppt. ANOVA and regression methods were used to analyze different experimental indexes and are noted in the results. Statistical power was calculated for nonsignificant results (Cohen, 1988).

RESULTS

Food Consumption and Feeding Rate during Nonmolting Period

Crabs began feeding immediately after food was placed in the tank. Mean of food consumption (FC) varied from 49.3–69.0 $g·d^{-1}$ for ovigerous females, 20.3–42.7 $g·d^{-1}$ for juvenile females, and 38.4–63.3 $g·d^{-1}$ for males. During the three-month feeding experiment, mean FC ($g·d^{-1}$) and standard deviations were 57.7 ± 6.17 for ovigerous females, 30.3 ± 7.31 for juvenile females, and 48.4 ± 8.53 for males. When FC was standardized by crab weight to feeding rate (FR), FR differed significantly among ovigerous females, juvenile females, and males (ANOVA, $P < 0.001$). Female crabs had a significantly higher feeding rate than males (Scheffe's test, $P = 0.004$ for ovigerous females and males, and $P < 0.001$ for juvenile females and males). There was no difference, however, between juvenile females and ovigerous females ($P = 0.099$). Mean FRs and standard deviations were 51.3 ± 12.9 $g·kg^{-1}·d^{-1}$ for ovigerous females, 54.0 ± 16.8 $g·kg^{-1}·d^{-1}$ for juve-
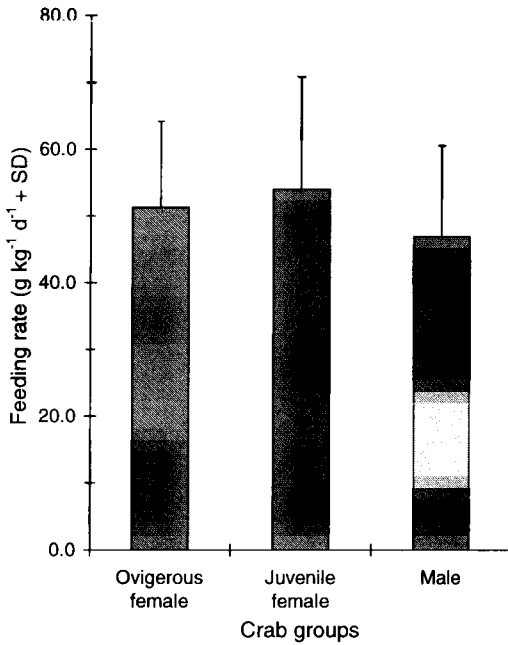
Fig. 1. Mean feeding rate of the red king crab *Paralithodes camtschaticus*. The feeding rate is standardized as grams of wet squid weight consumed per kilogram live weight of crab in 24 h.
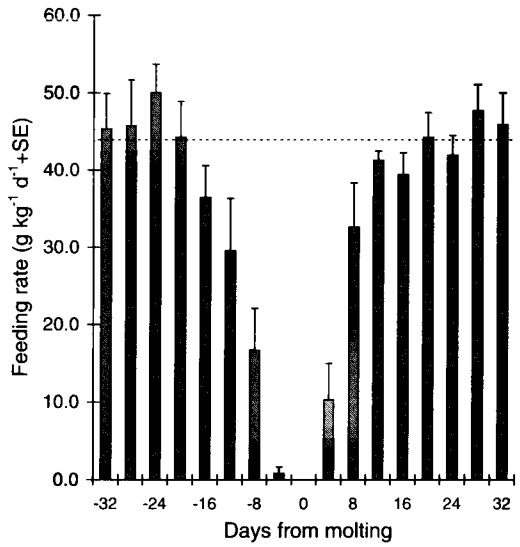

Fig. 2. Feeding rate of the male red king crab *Paralithodes camtschaticus* during the molting period, considered here to be 32 days before and after ecdysis. The dashed line indicates the mean feeding rate of these molted crabs during the nonmolting period.

nile females, and 46.9 ± 13.7 g·kg^{-1}·d^{-1} for males (Fig. 1).

Food Consumption and Feeding Rate during Molting Period

Eleven male crabs molted during the feeding experiment. They had a mean feeding rate of 43.8 g·kg^{-1}·d^{-1} (± 13.5 SD, $N = 59$) during the nonmolting period. Since feeding rate changed with molting activity, we conservatively estimated the mean feeding rate during the nonmolting period by excluding the data 32 days before and after ecdysis. Crabs decreased food consumption as they approached ecdysis, stopped feeding during ecdysis, and resumed normal feeding rates after ecdysis (Fig. 2). The feeding rates from

12 days before ecdysis to 8 days after ecdysis were significantly lower ($P < 0.05$) than feeding rates during the nonmolting period (Table 1).

Changes in feeding rate before and after ecdysis appear to be asymmetric. Feeding rate began to decrease a longer period before ecdysis, whereas crabs resumed normal feeding in a shorter time after ecdysis. For example, 18.2% of the crab stopped feeding at day −12, while all crabs resumed feeding at day +12 ("−" and "+" denote before and after ecdysis, respectively); 88.9% of the crab stopped feeding at day −4, while only 42.9% did not feed at day +4 (Table 1). Mean feeding rate at day +4 was 9.5 g·kg^{-1}·d^{-1} higher than at day −4 (ANOVA, $P = 0.028$), and it was 15.9 g·kg^{-1}·d^{-1} higher at day +8 than at day −8 ($P = 0.06$, statistical power = 0.516 at $\alpha = 0.05$).

Table 1. Feeding rate of male red king crabs that molted during the feeding experiment. Days prior to ecdysis are represented by a minus sign (−), whereas days after ecdysis are shown by a plus sign (+). % = percentage of crabs that did not feed. FR = mean feeding rate from a total of 11 crabs. The P values were calculated by one-way ANOVA to analyze differences from the mean feeding rate (43.8 g·kg^{-1}·d^{-1}) during the nonmolting period.

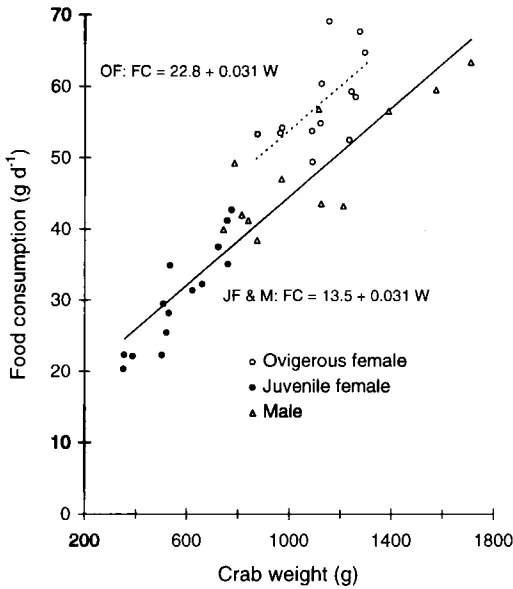| Days	−20	−16	−12	−8	−4	+0	+4	+8	+12	+16	+20
%	0.0	0.0	18.2	33.3	88.9	100.0	42.9	11.1	0.0	0.0	0.0
FR	44.3	36.5	29.5	16.7	0.83	0	10.3	32.6	41.2	39.4	44.3
SD	14.7	13.7	22.5	16.2	2.5	0	12.4	17.1	3.9	8.5	10.1
P	0.247	0.108	0.006	<0.001	<0.001	<0.001	<0.001	0.030	0.641	0.136	0.815

Fig. 3. Relationships between food consumption (grams wet food weight consumed in 24 h per crab) and live weight of the red king crab *Paralithodes camtschaticus.*

Fig. 4. Relationships between feeding rate and crab weight in *Paralithodes camtschaticus.* Feeding rates of ovigerous females were significantly higher than for juvenile females and males.

Feeding rates at day +12 and +16 were also higher than at day −12 and −16, respectively, but these differences were not significant ($P > 0.10$, statistical power = 0.364 and 0.054, respectively, when $\alpha = 0.05$).

Whether compensatory food consumption (an increase to compensate for the period of decreased feeding) occurred shortly before and after ecdysis was not clear. For example, at day −24 the mean feeding rate was 50.0 $g \cdot kg^{-1} \cdot d^{-1}$ or 6.2 $g \cdot kg^{-1} \cdot d^{-1}$ (14.1%) higher than the mean feeding rate in the nonmolting period (Fig. 2). However, the null hypothesis of no difference could not be rejected (ANOVA, $P = 0.194$, statistical power = 0.264 at $\alpha = 0.05$). Also, at day +28, the mean feeding rate was 3.8 $g \cdot kg^{-1} \cdot d^{-1}$ (8.7%) higher than that for the nonmolting period, but low statistical power prevents definitive conclusions ($P = 0.883$, statistical power = 0.053 at $\alpha = 0.05$).

Effect of Crab Size and Sex on Food Consumption and Feeding Rate

Daily food consumption increased with crab weight. The relationship between food consumption and live weight differed among the crab groups (ANCOVA, $P < 0.001$). Further analysis with Scheffe's test indicated that s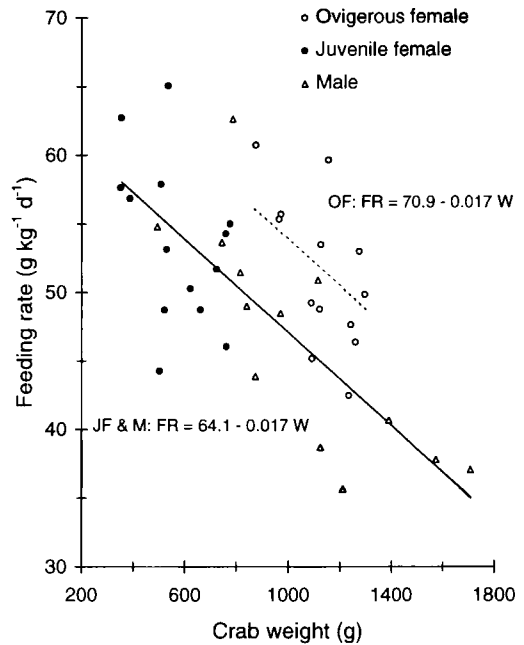ignificant differences existed between ovigerous females and juvenile females ($P < 0.001$) and ovigerous females and males ($P < 0.001$), but not between juvenile females and males ($P = 0.491$). On this basis, juvenile females and males were considered as one group. Linear regression of FC versus W was FC = 32.1 + 0.031 W − 9.3 Gp ($r = 0.942$, $P < 0.001$), where crab group Gp = 1 for ovigerous females and Gp = 2 for the juvenile females and males (Fig. 3). On the average, ovigerous females consumed 9.3 g more food daily than juvenile females or males of the same weight.

Feeding rate declined with increasing crab weight (Fig. 4). The regression of FR versus W had the same slope for all three crab groups (ANCOVA, $P = 0.873$). There were no detectable differences in regression intercepts between juvenile females and males (Scheffe's test, $P = 0.764$), but intercepts differed significantly between ovigerous females and juvenile females ($P = 0.021$) and ovigerous females and males ($P = 0.012$). The relationship can be expressed as: FR = 77.7 − 0.017 W − 6.8 Gp ($r = 0.727$, $P < 0.001$), where group Gp = 1 for ovigerous females, Gp = 2 for juvenile females and males. For

Table 2. Percentage of weight gain during the 4 month experiments with *Paralithodes camtschaticus*.

	Molted male	Unmolted male	Ovigerous female	Juvenile female
Mean	41.2	0.52	6.7	5.0
Minimum	30.4	0.1	2.9	1.9
Maximum	59.2	1.0	10.4	7.9
SD	8.96	0.40	1.9	1.45
N	20	6	35	37

crabs with the same weight, ovigerous females had a feeding rate of 6.8 $g \cdot kg^{-1} \cdot d^{-1}$ higher than juvenile females and males.

Weight Changes and Growth Rate by Size, Sex, and Molt Condition

Data from all crabs in the feeding and growth experiments were combined. All crabs gained weight over the four months of laboratory rearing. No ovigerous females and only four juvenile females molted during the experiment. Because of the limited sample size, data on molted juvenile females were not analyzed further. Since most male crabs (82%) molted during this period, male crabs were divided into two groups for analysis: molted males and unmolted males. Significant differences existed among the four groups of crabs (ovigerous females, juvenile females, molted males, and unmolted males). In addition, the relationships between weight gain (W_g) and initial weight (W) differed among groups: (1) ovigerous females: W_g = 15.1 + 0.051 W (r = 0.691, P < 0.001); (2) juvenile females: W_g = 0.2 + 0.051 W (r = 0.691, P < 0.001); (3) molted males: W_g = 141.4 + 0.212 W (r = 0.802, P < 0.001); and (4) unmolted males: W_g = 3.9 (±2.45 SD).

Male crabs gained the most weight after molting. On the average, their weight increased 41.2% (±15.9% SD). Unmolted male crabs gained on the average 3.9 g. This was unrelated to initial weight (regression analysis, P = 0.332). On the other hand, weight gain increased with initial female crab size, and ovigerous females gained more weight than juvenile females (ANCOVA, P = 0.018), although the mean difference was only 1.7% (Table 2).

When weight change was analyzed as a growth rate (GR in $g \cdot kg^{-1}$), significant differences existed among the four crab groups. We used multiple regression methods to examine the effect of weight and feeding rate on growth rate. Growth rate tended to increase
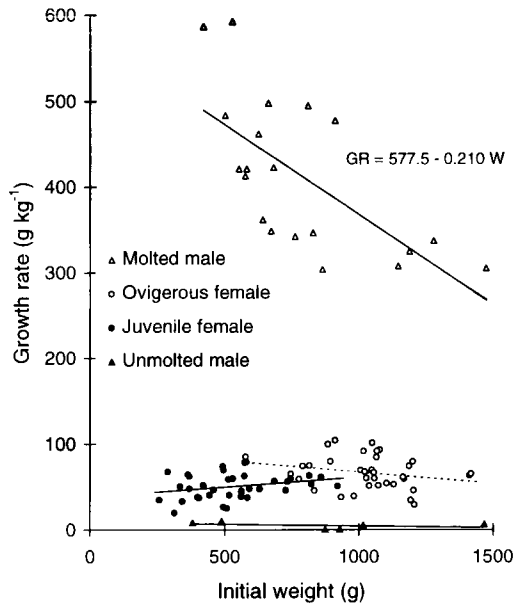

Fig. 5. Relationships between growth rate and initial crab weight in *Paralithodes camtschaticus*. Growth rate is expressed as grams of weight gained during 4 months per kilogram of initial weight.

with feeding rate for all crabs except juvenile females and decreased with weight for molted males. Since, in many cases, the effects were insignificant, the results were reduced to: (1) Ovigerous females: GR = −83.0 + 2.8 FR (r = 0.802, P = 0.001); (2) Juvenile females: GR = 50.5 (SD = 14.50, N = 37); (3) Molted males: GR = 577.5 − 0.210 W (r = 0.667, P = 0.001); and (4) Unmolted males: GR = 5.2 (SD = 3.96, N = 6).

The effect of weight on growth rate was significant only for molted males (Fig. 5), whereas the effect of feeding rate on growth rate was significant only for ovigerous females (Fig. 6). Our inability to detect other effects may be due to lower statistical power. For example, the power to detect the effect of weight on the growth rate of ovigerous females was 0.33. Despite the appearance of a relationship for molted males, the power to detect the effect of feeding rate was only 0.25 (GR = 159.4 + 2.6 FR, r = 0.381, P = 0.247, if α = 0.05, two-tailed test) due to high variance (Fig. 6). Mean growth rates ($g \cdot kg^{-1}$) and standard deviations were 412.3 ± 89.60 for molted males, 5.2 ± 3.96 for unmolted males, 66.6 ± 19.35 for ovigerous females, and 50.4 ± 14.50 for juvenile females.
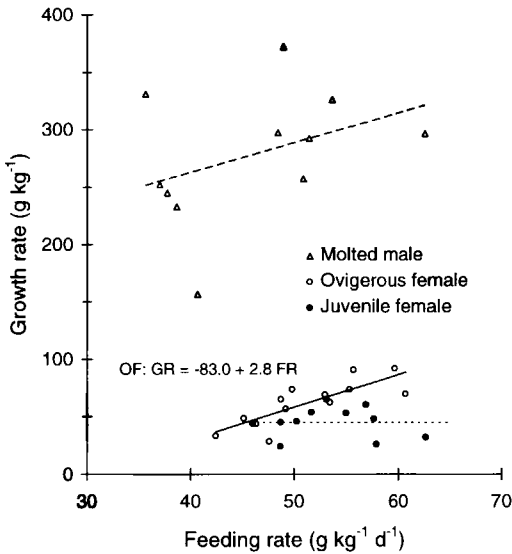
Fig. 6. Relationships between growth rate and feeding rate in *Paralithodes camtschaticus*. The regression was significant for ovigerous females, but not for molted males and juvenile females.

Fig. 7. Growth increment (increase in carapace length) of molted male red king crabs, *Paralithodes camtschaticus*. The slope of the relationship is not significant ($P = 0.926$, $r = 0.018$) and the mean increase was 10.9 mm ± 2.4 SD after one molt.

Growth Increment and Carapace Size

Carapace length of males increased 10.9 mm (mean ± 2.4 mm SD, $N = 28$) after one molt, and growth increment (GI in mm) did not vary with premolt carapace length (CL_1) over the sizes used in our experiment (from 75.7 to 119.1 mm CL, $P = 0.926$, Fig. 7). As a result, the growth increment as a percentage of CL decreased with size as $GI\% = 23.1 - 0.12\ CL_1$ ($P = 0.01$, $r = 0.481$). The relationship between CL_1 and carapace length after molt (CL_2) was $CL_2 = 10.5 + 1.004\ CL_1$ ($r = 0.979$, $P < 0.001$, $N = 28$).

DISCUSSION

Food Consumption and Feeding Rate in the Red King Crab

Literature on the feeding rate of the red king crab to compare to our study is scant. The only published data on feeding rates of adult red king crabs were collected from one male (124.3-mm CL) and one female (101.1-mm CL) crab (Matsuura and Takeshita, 1976). These two crabs were provided with varied diets and had an average food consumption of 12.9 g·d⁻¹ and 7.8 g·d⁻¹, respectively. The lack of information on feeding schedule and food intake measurements from the study by Matsuura and Takeshita, coupled to the wider size range of crabs that
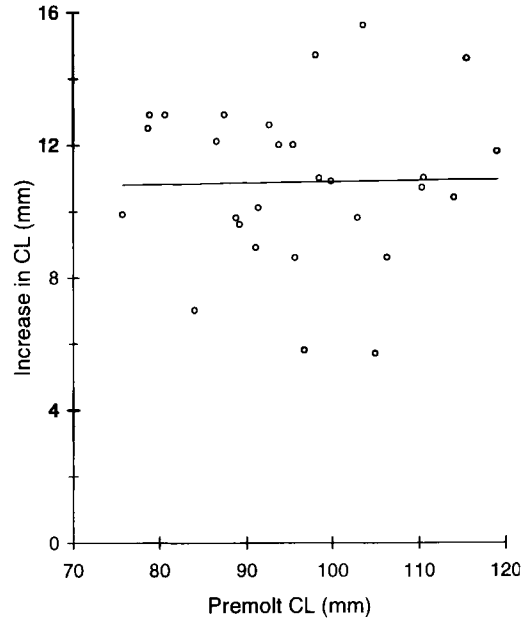
we studied, makes it difficult to compare results. In another study based on the examination of stomach contents, Tarverdieva (1978) estimated that the daily rations of red king crabs equaled 0.31% of the body mass of the crab. Because of totally different study methods, this low feeding rate cannot be compared with our results. Hawkes *et al.* (1987) reported mean food consumption for blue king crab (*Paralithodes platypus* Brandt) of 76–125 mm CL to be 44 ± 14 (SD) g·d⁻¹. This rate is comparable to the congeneric red king crab in our study.

Two studies have demonstrated large differences in feeding rates of small juvenile red king crabs. Gharrett (1986) reported that juvenile red king crabs of 20–40 mm CL in a control experiment had a feeding rate of approximately 9.6 mg dry food per gram of wet crab per day, which equals about 55.8 g·kg⁻¹·d⁻¹ wet food. Rice *et al.* (1985) found juvenile red king crabs of 30–40 mm CL had a feeding rate of 12 g·kg⁻¹·d⁻¹ at 10°C and 32 g·kg⁻¹·d⁻¹ at 20°C. Our results are intermediate between these two rates. However, since feeding rate varies with crab size and temperature, direct comparisons of these stud-

ies with ours are not appropriate. The largest crabs studied by Gharrett (1986) and Rice *et al.* (1985) were smaller than crabs included in our study. Since food consumption and feeding rate are related to crab size, direct comparisons between their feeding rates and ours should be made with caution.

Effects of Molt Activity on Crab Feeding Rates

That feeding rate varies with the molt cycle of the red king crab is consistent with findings in other crustaceans. O'Halloran and O'Dor (1988) observed that the snow crab *Chionoecetes opilio* (Fabricius) stopped feeding 3–6 weeks before ecdysis and resumed feeding 3–4 weeks after ecdysis. Molt stage affected feeding rates of the spiny lobster *Panulirus argus* (Latreille) (see Lipcius and Herrnkind, 1982). Feeding rate declined about 10 days before ecdysis and recovered slowly to a maximum about 8 days after ecdysis. Feeding of the rock lobster *Panulirus longipes* (A. Milne Edwards) ceased 2–6 days before the molt, resumed within 2 days of molting, and increased rapidly to a peak on the fourth or fifth day; thereafter, the daily food intake followed a downward, albeit fluctuating, trend (Chittleborough, 1975). These three species (rock lobster, spiny lobster, and snow crab) consumed more food or ate more quickly shortly after ecdysis compared to before ecdysis. In our study, the red king crab completely stopped feeding during ecdysis and fed at lower rate before and after ecdysis. The lack of apparent compensatory feeding before and after ecdysis by the red king crab is not unexpected. In an experiment in which the Tanner crab *Chionoecetes bairdi* Rathbun and the Dungeness crab *Cancer magister* Dana were deprived of food for 30, 60, and 90 days, compensatory feeding did not occur (Paul *et al.*, 1994).

Weight Change as a Growth Index: Effect of Sex and Reproductive Stages

The patterns of weight change depend on the initial weight of the crab and whether the crab has molted. The rapid increase in weight during molting results from water uptake, whereas weight gain during intermolt period results from growth of somatic tissue and gonad (Weber, 1967; Chittleborough, 1975; Molyneaux and Shirley, 1988). Weight changes in our study (Table 2) and their negative rela-

tionship with initial weight are comparable to observations in other studies. Weber (1967) noted juvenile red king crabs < 50-mm CL gained an average of 10% weight during intermolt. In a four-month observation on cage-reared juvenile red king crabs (sex unreported), Bright *et al.* (University of Southern California, unpublished) observed that the weight gain was approximately 2.7% for crabs with initial mean weight of 940 g. Juvenile red king crabs that weighed 18–55 g (29.3–42.3-mm CL) gained 13–47 g (48.6–85.5%) in weight after one molt (Weber, 1967). In a mark-recapture study, Powell (1960) reported that male red king crabs weighing from 1.40–10.10 kg (120–224 mm CL) increased 0.86–3.06 kg (equal to 286.9–428.6 $g \cdot kg^{-1}$ or 30.3–61.4%) after one molt.

During the intermolt period, unmolted female red king crabs (both ovigerous females and juvenile females) had a higher growth rate than unmolted males, whereas ovigerous females (multiparous in our study) gained more weight than juvenile females. Several factors may have contributed to these differences, including size increase with molt, somatic and gonad growth, feeding rate, and energy distribution. After maturity, the size of female crabs increases more slowly with each molt than in males (Marukawa, 1933; Bright, 1967; Weber, 1967). During the intermolt period, somatic growth of male crabs is largely offset by the loss of water taken up at the previous molt; therefore, weight gain is less significant. While female crabs increase less in size with molting, somatic growth may surpass the water replacement. In addition, gonad growth in females contributes to total weight. Ovigerous females had a higher feeding rate (Fig. 3), and feeding rate had a positive relation with growth rate (Fig. 6). Paul and Fuji (1989) reported that male Tanner crabs allocated most (about 60%) of assimilated energy to respiration, but less (30%) to somatic energy storage. Primiparous female Tanner crabs allocated 11% of their energy to the first egg clutch, whereas the clutches of multiparous females contained about twice as much energy as the egg clutches of primiparous females. Newly extruded egg clutches of red king crabs had an average energy content of 256 kcal, whereas the postmolt whole body had 508 kcal energy (Paul and Paul, 1996). The number of eggs, clutch dry weight, and clutch energy content in female

red king crabs tended to increase with corresponding growth in carapace length (Paul and Paul, 1996). All these factors appear to complicate the growth pattern in red king crabs.

Management and Research Implications

Our results may be useful in considerations of new management strategies for the red king crab. For instance, our finding of declining growth rate (in weight) with increasing male size contributes to current analyses of fishery yields under alternative legal size limits. Since male red king crabs achieve larger sizes than those we studied, additional laboratory observations on the growth of large males are desirable. Likewise, data on growth rates for ovigerous females may bear on considerations of legalizing female harvests for yield optimization. Relationships between feeding and growth rates may be relevant to future attempts to link crab population dynamics to broader ecosystem changes. In a single-species model of population dynamics, Zheng *et al.* (1995) found evidence for a density-dependent stock-recruit relationship for the red king crab in Bristol Bay, Alaska. In Bristol Bay, currently depressed abundance of the red king crab was preceded by record high abundance in the late 1970s, a sharp decline in abundance in the early 1980s associated with high natural and fishing mortality, and a long period of poor recruitment as a result of the series of very high and very low spawning stocks (Zheng *et al.*, 1995). Density dependence may be caused by reduced reproductive output by females and reduced survival of young crabs to recruitment attributable to cannibalism, as was found for *Chionoecetes opilio* (see Lovrich and Sainte-Marie, 1997). We speculate that a coupled mortality-growth response could be involved and we recommend two feeding and growth studies to shed light on this aspect of population dynamics of the red king crab. First, we suggest a study on the effects of food limitation and crab density on cannibalism of young-of-the-year red king crabs. Second, we propose an investigation on the potential role of food limitation on growth and reproductive energetics and tradeoffs of mature female red king crabs.

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