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in a Southeast Alaska Estuary**

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## Growth of Male Tanner Crabs *Chionoecetes bairdi* in a Southeast Alaska Estuary

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**ABSTRACT:** Growth of male Tanner crabs *Chionoecetes bairdi* from a glacial Southeast Alaska estuarine population was studied during 1999 and 2000. Premolt crabs were collected in situ by scuba divers and held in the laboratory until molting occurred ( $\leq 33$  d). An interannual difference in growth was not found, but growth was significantly greater (2.3% to 6.2%) than that observed for Kodiak Island area crabs during the 1970s. Current management of Tanner crabs throughout Alaska is based on growth estimated for Kodiak Island crabs in the 1970s. A significant change in allometric growth occurred at 96.5 mm carapace width. Growth was reduced for crabs held in the laboratory  $>13$  d, crabs missing three or more premolt limbs, and crabs missing two or more postmolt limbs. Crabs attained large-claw status over a wide size range (approximately 125.0 to 178.9 mm postmolt carapace width) and among large-clawed crabs a percent increase in chela height was not associated with a percent decrease in growth. Growth data indicated that the majority (53% to 70%) of Tanner crabs harvested in the Southeast Alaska commercial fishery during most years were newly recruited to the fishery.

### INTRODUCTION

The Tanner crab, *Chionoecetes bairdi* Rathbun, supports a large-scale commercial fishery from Southeast Alaska to the southeastern Bering Sea. In Alaska, Tanner crabs are managed separately in five geographical management areas (Donaldson and Donaldson 1992). The Southeast Alaska Tanner crab fishery is managed by setting a season length that would result in the harvest of 2 million pounds of crab if stock abundance and recruit class composition were the same as the historical average (Bishop et al. 2002). Recruit class composition is estimated from preseason surveys and dockside sampling and is based on carapace width (CW), exoskeleton condition (EC) as an indicator of time elapsed since last molt, and a growth rate estimated for Kodiak Island area crabs (Donaldson et al. 1981).

Only one study measured the growth of Tanner crabs held directly in situ (Donaldson et al. 1981), and results from that study have been liberally applied to the management of Tanner crab fisheries throughout Alaska. Additional information on adult growth has been collected in the laboratory during studies designed to investigate the reproductive potential of males in relation to maturity status (Paul and Paul

1995, 1996). Important fisheries for Tanner crabs occur throughout Alaska, yet little is known about the growth of this species. No growth information for Tanner crabs in Southeast Alaska has been collected despite the fact that it is the only management area in Alaska where a commercial fishery has occurred each fishing season since the 1970s (Bishop et al. 2002). Accurate information on the growth of Southeast Alaska Tanner crabs is therefore necessary for effective management of Southeast Alaska Tanner crab stocks.

Applying growth parameters derived for one geographical area to neighboring populations is a common practice in fisheries management when empirical data is lacking (Ulmestrand and Eggert 2001). Such practice has resulted in poor assessment of *Nephrops* stocks (ICES 1999) and miscalculations in red king crab *Paralithodes camtschaticus* stock-recruitment analyses in Bristol Bay, Alaska (Loher et al. 2001).

Growth of marine crustaceans is the product of the increment at each molt and the frequency of molting, and both are influenced by abiotic factors including temperature, salinity, and light (Kurata 1962). Intuitively, growth rates could vary considerably across the geographical range of a widely dispersed crustacean such as the Tanner crab. Somerton (1981) attributed much of the regional variability in size of adult fe-

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male *C. bairdi* and *C. opilio* in the eastern Bering Sea to variable bottom water temperature. Studies of juvenile Dungeness crabs *Cancer magister* indicate that growth rate is accelerated in estuaries and other nearshore bays where water temperatures are relatively high compared to more oceanic locations (Armstrong and Gunderson 1985; Stevens and Armstrong 1984). Biotic factors affecting growth rate in crustaceans include social interactions (Cobb and Tamm 1974, 1975), density-dependent factors (Tuck et al. 1997), and habitat quality (Chapman 1980). Furthermore, injury (i.e., limb loss) prior to ecdysis reduces the growth rate in some crustaceans (Sainte-Marie et al. 1995), but the effect of this factor on growth has not been examined in Tanner crabs.

Studies of crustacean growth are often limited to those in which animals are held for extended periods under controlled laboratory conditions. Late proecdysis and ecdysis is temporally quite brief in crustaceans, including Tanner crabs (Donaldson and Johnson 1988), so researchers are typically compelled to collect and pool animals in the laboratory until ecdysis occurs. In this study, however, ready access to a predictable source of crabs in premolt condition minimized holding time of crabs in the laboratory. This short holding time is important since laboratory conditions may affect both the molt increment and the duration of the intermolt period of crustaceans (Kurata 1962; Hartnoll 1982; Castro 1992).

The purpose of this study was to determine growth (the change in carapace width per molt) of adult male Tanner crabs from a population in Southeast Alaska and to determine if a change in growth rate occurs at a size associated with existing information about sexual maturity or other life history events. We compared the growth rates of crabs relative to their chelae growth and investigated the effect of laboratory holding time and limb loss on growth. We also compared growth equations derived in this study to existing data for Kodiak Island area crabs using statistical methods and selection criteria identical to those used by Donaldson et al. (1981) and provide an alternative method of joined regression lines to describe growth using selection criteria developed in this study.

## METHODS

### Study Area and Sampling

Scuba divers collected male Tanner crabs in situ at the head of Fritz Cove, Southeast Alaska. The study site and annual mass molting of Tanner crabs there

have previously been described (Stone 1999). Crabs were collected on six occasions between 22 March and 8 April 1999 and on seven occasions between 14 March and 6 April 2000. Collections spanned most of the observed molting period each year. All hard-shell male crabs found within the study area were collected and transported in running seawater to the Auke Bay Laboratory (5 km from the study site). Approximately 15% of the crabs collected were actively molting or exhibited premolt conditions as evidenced by swollen pericardial sacs. Profiles of water temperature and salinity were collected at least twice weekly (through 10 May 1999 and 1 May 2000) to a depth of 30 m at the central portion of the study area with a Seabird Electronics Seacat Profiler.

Crabs captured the same day were held communally (up to 12 per tank) in flow-through aquaria (0.8 m<sup>3</sup>) until molting occurred, at which time they were marked with numbered cinch tags around the third left pereopod and held communally with other newly molted crabs. Exoskeleton condition (EC), a subjective measure of exoskeleton age and approximate time since last molt, was recorded for each crab using the following criteria from Stone (1999): (1) soft, brick red, pliable exoskeleton indicative of a recent molt, (2) hard, clean exoskeleton with limited epifauna and scratches indicative of a molt within one year, and (3) hard, worn exoskeleton with epifauna, discoloration, and scratches indicating no molting within the past year. Old-shell crabs (EC > 2) were held communally and segregated from crabs expected to molt (EC ≤ 2), since we had previously observed old-shell crabs cannibalizing newly molted crabs in laboratory aquaria. Aquaria were maintained at ambient (25 m depth) temperature and salinity, and crabs were fed ad libitum a diet of chopped herring and squid twice weekly. Temperature and salinity were measured in laboratory aquaria at least twice weekly to ensure oceanographic conditions in the laboratory were similar to those at 25 m where most pre- and postmolt crabs were observed in situ.

Carapace width was measured as the straight-line distance across the widest part of the carapace excluding the spines (Jadamec et al. 1999). The legal minimum size is 140 mm CW including the spines and is equivalent to 138 mm CW excluding the spines. This latter measure is the standard biological measure and is used throughout this manuscript in reference to the legal minimum size. Chela height (CH) was measured at the widest section of the propodus excluding the spines (Jadamec et al. 1999). Both measurements were made with vernier calipers to the nearest 0.01 mm and rounded to the nearest 0.1 mm. Because Tanner crabs

are homochelous, height of both chelae was averaged if they differed by less than 1 mm. If CH differed by more than 1 mm, the larger CH was recorded to exclude regenerated or damaged chelae from analysis. Both measurements were made on exuvia (pre-molt measurements) and on the tagged crab a minimum of 14 days after molting (postmolt measurements). Measurements on exuvia may introduce some bias relative to measurements on live crabs, but the intent of this study was to replicate, as closely as possible, the measurements used by Donaldson et al. (1980). One person took all the measurements and an estimate of measurement error was calculated by measuring the CW and CH for seven crabs (mean CW range=70.21 to 156.89 mm) during five distant time intervals (e.g., 24 hrs). Measurement error, calculated as the standard error of the mean, ranged from 0.02 to 0.07 mm. Time held in the laboratory prior to molting was calculated as 0 d if the crab molted within 2 h, 1 d if the crab molted between 2 and 24 h, 2 d if molted between 24 and 48 h, and so on.

### Statistical Analyses

Growth data were modeled with the Hiatt model (Hiatt 1948), a linear regression of new carapace width (NCW) on initial carapace width (ICW):

$$y_i = \beta_0 + \beta_1 x_i + e_i, \quad i=1, 2, \dots, n, \quad (1)$$

where

$$\begin{aligned} y_i &= \text{NCW for crab } i, \\ x_i &= \text{ICW for crab } i, \\ \beta_0, \beta_1 &= \text{regression coefficients,} \\ e_i &= \text{random error for crab } i, \text{ iid } N(0, \sigma^2), \text{ and} \\ n &= \text{number of observations.} \end{aligned}$$

### Method of Donaldson et al. (1981)

Following Donaldson et al. (1981), two unjoined linear regression lines were fit to growth data: one for small crabs and one for large crabs. These two regression lines are hereafter referred to as line S (small) and line L (large). Donaldson et al. (1981) partitioned growth data into two sets at a cutoff value of ICW (Somerton 1980). Least-squares regression lines were sequentially fit to data sets as the cutoff value for ICW was incremented by 1 mm from smallest to largest ICW. The best-fitting lines yielded the lowest total residual sum of squares, and the point on the independent axis (ICW) at which one regression line ends and the other begins is called the “inflection” point (Donaldson et

al. 1981). This point presumably reflects a change in growth rate due to attainment of “maturity” (Donaldson et al. 1981). Fitted lines using this method are not constrained to join, however, potentially allowing the inflection point to take on two different values of NCW depending on which line is used. The growth model used by Donaldson et al. (1981) may be expressed as

$$y_i = \begin{cases} \beta_0 + \beta_1 x_i + e_i, & x_i \leq \hat{\alpha} \\ \beta_0^* + \beta_1^* x_i + e_i, & x_i > \hat{\alpha} \end{cases}, \quad (2)$$

where

$\hat{\alpha}$  = inflection point, and the other terms are defined in Equation (1).

Growth equations from Donaldson et al. (1981) were compared to growth equations estimated in this study using methods in Weisberg (1985). Specifically, we determined if estimated regression coefficients (slope and intercept) of lines S and L for Kodiak Island area crabs fell within 95% joint confidence regions of regression coefficients estimated in this study. Further, we determined if estimated slopes or growth rates from Donaldson et al. (1981) fell within 95% confidence intervals (CI) of slopes estimated in this study.

### New Method

In addition to fitting unjoined growth lines to small and large crabs, joined regression lines yielding the lowest total residual sum of squares were fit to growth data. Hudson (1966; Appendix 2) provides least-squares estimates of regression lines given the point at which the lines meet (called the join point). Growth data were partitioned into two sets at a cutoff value of ICW. Joined regression lines were sequentially fit to data sets, as the join point for ICW was incremented by 0.01 mm from smallest to largest ICW. The new growth model is the same as Equation (2) with the added linear constraint:

$$f_1(\hat{\alpha}; \hat{\beta}) = f_2(\hat{\alpha}; \hat{\beta}^*),$$

where

$$\begin{aligned} \hat{\alpha} &= \text{join point,} \\ \beta' &= (\beta_0, \beta_1) \\ \beta^{*'} &= (\beta_0^*, \beta_1^*) \\ \beta', \beta^{*'} &= \text{regression coefficients,} \\ f_1(\hat{\alpha}; \hat{\beta}) &= \hat{\beta}_0 + \hat{\beta}_1 \hat{\alpha}, \text{ and} \\ f_2(\hat{\alpha}; \hat{\beta}^*) &= \hat{\beta}_0^* + \hat{\beta}_1^* \hat{\alpha} \end{aligned}$$

If  $\hat{\alpha}$  equaled an observed ICW, then  $\hat{\alpha}$  was arbitrarily put in the second group. A 95% CI for the join point was computed using analytical methods developed in chemistry (Schwartz and Gelb 1984) with a corrected pooled variance term (Carter et al. 1991). Fitted regression lines S and L were compared to one line fit to the whole data (Neter and Wasserman 1977). Further, a 95% CI for the difference in estimated slopes of lines S and L was used to determine if slopes differed significantly (Neter and Wasserman 1977). Growth equations for small and large crabs were compared to growth equations of Donaldson et al. (1981) using the same methods described above. We examined whether estimated slopes or growth rates from Donaldson et al. (1981) fell within 95% CIs of slopes estimated in this study.

Since growth equations are used to predict NCW from newly observed ICW, 95% predictive intervals of a single prediction were computed (Weisberg 1985). A point prediction,  $\tilde{y}_*$ , of  $y_*$  (NCW associated with  $x_*$ ) is computed from a fitted regression equation:

$$\tilde{y}_* = \hat{\beta}_0 + \hat{\beta}_1 x_*$$

where

$$\hat{\beta}_0, \hat{\beta}_1 = \text{estimated coefficients and } x_* = \text{newly observed ICW.}$$

The 95% predictive interval for  $y_*$  given  $x_*$  is

$$\tilde{y}_* \pm t \left( \frac{0.05}{2}; \text{df} \right) \cdot \text{sepred}(\tilde{y}_* | x_*)$$

where

$t(\alpha; \text{df})$  is the  $\alpha \cdot 100$  percentile of the Student's  $t$ -distribution with  $\text{df}$  degrees of freedom and  $\text{sepred}(\tilde{y}_* | x_*) = \text{standard error of prediction at } x_*$ .

The standard error of prediction at  $x_*$  is defined as

$$\text{sepred}(\tilde{y}_* | x_*) = \hat{\sigma} \left[ 1 + \frac{1}{n} \frac{(x_* - \bar{x})^2}{SXX} \right]^{1/2},$$

where

$\hat{\sigma}$  = standard error of regression,  
 $n$  = number of observations,  
 $\bar{x}$  = mean ICW, and  
 $SXX = \sum (x_i - \bar{x})^2$ , corrected sum of squares for the  $x_i$ 's.

The predictive interval accounts for two sources of error in a prediction: error in estimating the regression coefficients and error in estimating the expectation of  $y_*$  using  $\tilde{y}_*$ . To assess the usefulness of predictive intervals in predicting NCW from newly observed ICW, we computed 95% predictive intervals for an independent dataset of 12 crabs collected at the study site in 1993. We determined if the 95% predictive intervals of NCW computed for these crabs covered the observed NCW.

### Limb Loss and Number of Days Held in the Laboratory

We investigated the effects of four variables on crab growth: number of limbs lost prior to ecdysis (Pre-LL), number of limbs lost during or immediately after ecdysis (Post-LL), number of days held in the laboratory prior to ecdysis (Day), and an interannual difference (Year). We fit a three-factor analysis of covariance (ANCOVA) model:

$$y_{ijkl} = \mu \dots + \alpha_i + \beta_j + \delta_k + \gamma_l (x_{ijkl} - \bar{x} \dots) + \gamma_2 (w_{ijkl} - \bar{w} \dots) + e_{ijkl},$$

$$i=1, 2, 3, 4; j=1, 2, 3; k=1, 2; l=1, \dots, n, \quad (3)$$

where

$y_{ijkl}$  = NCW,  
 $\mu \dots$  = general mean,  
 $\alpha_i$  =  $i$ -th level of factor Pre-LL,  
 $\beta_j$  =  $j$ -th level of factor Post-LL,  
 $\delta_k$  =  $k$ -th level of factor Year,  
 $\gamma_1, \gamma_2$  = regression coefficients for the relations between  $y$  and covariates  $x$  and  $w$ , respectively,  
 $x_{ijkl}$  = ICW,  
 $w_{ijkl}$  = Day,  
 $e_{ijkl}$  = random error, iid  $N(0, \sigma^2)$ , and  
 $n$  = number of observations.

Two-way interactions between all variables of the model (Equation 3) were also tested, using backward stepwise regression (S-Plus 2001). Four levels of Pre-LL were compared: Pre-LL=0, 1, 2 and Pre-LL  $\geq$  3. If the  $F$ -test for variation among levels was significant, growth of crabs with Pre-LL=0 was compared to growth of crabs with Pre-LL=1, Pre-LL=2, or Pre-LL  $\geq$  3, using Fisher's least significant difference test (Chew 1985). Crabs with Pre-LL  $\geq$  3 were combined in the analysis due to small sample sizes. Three levels

of Post-LL were compared: Post-LL=0, 1 and Post-LL  $\geq$  2. If the *F*-test for variation among levels was significant, growth of crabs with Post-LL=0 was compared to growth of crabs with Post-LL=1 or Post-LL  $\geq$  2, also using Fisher's least significant difference test (Chew 1985). Crabs with Post-LL  $\geq$  2 were combined in the analysis due to small sample sizes. The  $\alpha$ -level was 0.05.

### Carapace Width Versus Chela Height

We graphically compared the growth rates of crabs relative to their chelae growth. A discriminant function for separating large- and small-clawed crabs could not be fit to the measurements of carapace width (CW) and chela height (CH) since we could not definitively assign crabs a priori to either group.

## RESULTS

In total, 124 crabs molted in 1999 and 181 crabs molted in 2000. The ICW for molting crabs ranged from 67.4 to 146.0 mm and 57.1 to 144.9 mm, respectively, in 1999 and 2000. Crabs molted between 23 March and 1 May 1999 and between 14 March and 23 April 2000. Crabs that molted ( $n = 305$ ) were all EC  $\leq$  2 and none fed during the study. Conversely, old-shell crabs (EC  $>$  2) that fed throughout the study did not molt ( $n=12$ ). Mortality was low during the study (3.2%) and all deaths occurred during ecdysis.

Water temperature and salinity measured in laboratory aquaria and the in situ molting area on the same days during the study periods differed by less than 0.98°C and 0.44 practical salinity units (psu)

during both years. In situ water temperature ranged from 3.8°C to 4.5°C in 1999 and from 3.9°C to 4.9°C in 2000. In situ salinity ranged from 31.06 psu to 31.56 psu in 1999 and from 30.60 psu to 31.32 psu in 2000.

### Method of Donaldson et al. (1981)

We compared unjoined regression lines computed in this study to those computed by Donaldson et al. (1981). Following their criteria, growth analysis was limited to crabs that molted within seven days of collection and were missing three or fewer limbs prior to ecdysis. Growth data meeting these criteria ( $n=197$ ) were pooled from 1999 ( $n=66$ ) and 2000 ( $n=131$ ). Linear regression lines S and L, based on lowest total residual sum of squares, were fit to growth data, resulting in an inflection point of ICW = 103 mm (Table 1). Growth equations estimated by Donaldson et al. (1981) (Table 1) were significantly different than unjoined growth equations estimated in this study (lines S:  $F=264.6 \sim F_{2,112}$ ,  $P < 0.001$  and lines L:  $F=265.1 \sim F_{2,81}$ ,  $P < 0.001$ ). Further, slopes of growth equations estimated by Donaldson et al. (1981) were significantly less steep than slopes estimated in this study (S:  $F=1918.1 \sim F_{1,112}$ ,  $P < 0.001$  and L:  $F=3851.5 \sim F_{1,81}$ ,  $P < 0.001$ ).

### Limb Loss and Number of Days Held in the Laboratory

Before fitting joined growth equations for small and large crabs, we investigated effects on growth: limb loss prior to ecdysis (Pre-LL), limb loss during or immediately after ecdysis (Post-LL), length of holding

Table 1. Comparison of growth equations for small and large Tanner crabs, effective ranges of initial carapace width (ICW), and associated regression statistics. Inflection point for Donaldson et al.'s (1981) unjoined lines is 90 mm ICW; inflection point for unjoined lines in this study is 103 mm ICW; and the join point for joined lines in this study is 96.5 mm ICW. Some regression statistics were not available from Donaldson et al. (1981). NCW = new carapace width, S = small crabs, L = large crabs, SE = standard error.

Line	Growth equation	Range of ICW (mm)	SE $\hat{\beta}_0$ (Intercept)	SE $\hat{\beta}_1$ (Slope)	<i>n</i>	$\hat{\sigma}$	<i>R</i> <sup>2</sup>	<i>F</i>	<i>P</i> -value
<b>Unjoined lines (Donaldson et al. 1981)</b>									
S	$NCW=3.98+1.19 \cdot ICW$	[47.0,90.0]	-	-	128 <sup>a</sup>	-	-	-	-
L	$NCW=15.75+1.07 \cdot ICW$	[90.0,137.0]	-	-	204 <sup>a</sup>	-	-	-	-
<b>Unjoined lines (this study)</b>									
S	$NCW=-0.03+1.29 \cdot ICW$	[57.1,103.0]	1.55	0.018	114	2.03	0.98	5,266	< 0.001
L	$NCW=6.17+1.19 \cdot ICW$	[103.0,144.9]	3.26	0.026	83	2.22	0.96	2,083	< 0.001
<b>Joined lines (this study)</b>									
S	$NCW=0.003+1.28 \cdot ICW$	[57.1,96.5]	1.52	0.018	109	1.86	0.98	5,059	< 0.001
L	$NCW=16.20+1.11 \cdot ICW$	[96.5,144.9]	1.65	0.014	132	2.15	0.98	6,560	< 0.001

<sup>a</sup>Sample sizes are not explicitly given in Donaldson et al. (1981) but were determined from the data appendix of Donaldson et al. (1980).

time in the laboratory prior to ecdysis (Day), and an interannual difference (Year). Interannual difference in crab growth was not detected (ANCOVA,  $F=0.9 \sim F_{1,290}$ ,  $P=0.33$ ), and all two-way interactions were not significant. In a reduced growth model that excluded Year and two-way interactions, variables Pre-LL, Post-LL, and Day were significantly related to NCW (multiple  $R^2=99\%$ ). Growth for the different levels of Pre-LL was significantly different (ANCOVA,  $F=13.7 \sim F_{3,297}$ ,  $P<0.001$ ). Based on Fisher's least significant difference test, NCW was significantly smaller for crabs with Pre-LL=1 ( $n=78$ ) or 3 ( $n=11$ ), but not 2 ( $n=24$ ), compared to crabs with Pre-LL=0 (Figure 1A). However, based on the magnitude of the estimated coefficient (-0.7) for Pre-LL=1, the reduction in NCW is small and of doubtful biological significance. With the values of all other variables in the model held constant, one and three limbs missing prior to ecdysis compared to no limbs missing prior to ecdysis translated to a smaller NCW by 0.7 mm and 4.5 mm, respectively. Growth for the different levels of Post-LL was also significantly different (ANCOVA,  $F=3.5 \sim F_{2,297}$ ,  $P=0.03$ ). Based on Fisher's least significant difference test, NCW was significantly smaller for crabs with Post-LL  $\geq 2$  ( $n=8$ ) compared to crabs with Post-LL=0 (Figure 1B). Therefore, crabs with Pre-LL  $\geq 3$  or Post-LL  $\geq 2$  were excluded from growth analysis.

Using a reduced growth model with independent variables Pre-LL, Post-LL, Day, and ICW, growth decreased as a function of length of holding time in the laboratory prior to ecdysis (ANCOVA,  $F=8.5 \sim F_{1,297}$ ,  $P=0.004$ ) (Figure 2). With the values of all other variables in the model held constant, each day held in the laboratory prior to ecdysis translated to a smaller NCW by 0.06 mm. To determine the length of holding time in the laboratory prior to ecdysis that negligibly affects crab growth, NCW was sequentially regressed on variables ICW, Pre-LL, and Day, as Day was incremented by 1 from 0 to 33 d. Crabs with Pre-LL  $\geq 3$  or Post-LL  $\geq 2$  were excluded from this analysis. Crabs held in the laboratory 14 d or more prior to ecdysis showed significantly decreased growth (variable Day was significant) and were therefore excluded from further analysis.

## New Method

A subset of growth data using the criteria developed above (Pre-LL  $\leq 2$ , Post-LL  $\leq 1$ , and Day  $< 14$ ) was fit with joined lines and compared with Donaldson et al. (1981) growth data fitted with unjoined lines (Figure 3). This subset included 88 crabs from 1999 and 153 from 2000. The join point for the two growth equations

with lowest total residual sum of squares was estimated as ICW=96.5 mm (Table 1) (Figure 3). The 95% confidence interval for the join point was 91.1 to 102.0 mm. The estimated join point is shifted right of Donaldson et al.'s (1981) inflection point of 90 mm (Figure 3). Joined regression lines S and L fit better than a single

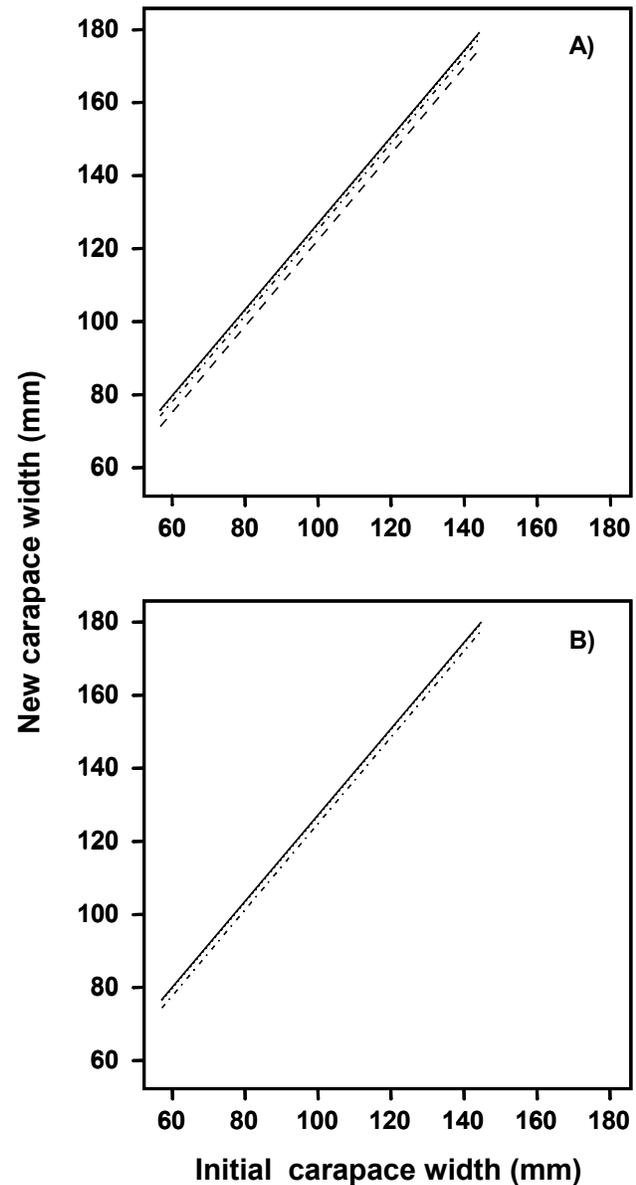


Figure 1. A) Fitted lines for Hiatt models (solid line, Pre-LL=0; dotted line, Pre-LL=1; mixed dashed-dotted line, Pre-LL=2; and dashed line, Pre-LL  $\geq 3$ ). Lines for Pre-LL=0 and Pre-LL=1 are nearly coincident. B) Fitted lines for Hiatt models (solid line, Post-LL=0; dotted line, Post-LL=1; and mixed dashed-dotted line, Post-LL  $\geq 2$ ). Lines for Post-LL=0 and Post-LL=1 are nearly coincident. Pre-LL=number of limbs lost prior to ecdysis; Post-LL=number of limbs lost during or immediately after ecdysis.

line fit to the whole data ( $F=25.8 \sim F_{2,237}^*$ ,  $P<0.001$ ). In addition, the 95% CI for the difference in slopes (0.17) for fitted lines S and L did not cover 0 (0.12, 0.21). Growth equations from Donaldson et al. (1981) were significantly different than joined growth equations fit in this study (lines S:  $F=234.3 \sim F_{2,107}^*$ ,  $P<0.001$  and lines L:  $F=477.8 \sim F_{2,130}^*$ ,  $P<0.001$ ). Further, slopes of growth equations estimated by Donaldson et al. (1981) were significantly less steep than slopes estimated in this study (lines S:  $F=1901.7 \sim F_{1,107}^*$ ,  $P<0.001$  and lines L:  $F=812.9 \sim F_{1,130}^*$ ,  $P<0.001$ ).

The 95% predictive intervals were computed for observed data (Figure 4). The standard errors of prediction,  $\text{sepred}(\tilde{y}_*|x_*)$ , at  $x_*$  for joined regression lines S and L are

$$1.86 \cdot \left[ 1 + \frac{1}{109} + \frac{(x_* - 83.6)^2}{10,685.6} \right]^{1/2} \text{ and}$$

$$2.15 \cdot \left[ 1 + \frac{1}{132} + \frac{(x_* - 118.9)^2}{24,461.9} \right]^{1/2},$$

respectively. The residual degrees of freedom are respectively 107 and 130. Fitted growth equations provide predictions of NCW given a new ICW that are accurate to within  $\pm t(0.025; df) \cdot \text{sepred}(\tilde{y}_*|x_*)$  with a confidence level of 95%. The 95% predictive intervals of NCW predicted for the 12 crabs collected in 1993 covered the corresponding observed NCW (Figure 4).

### Carapace Width Versus Chela Height

Graphical examination of premolt and postmolt measurements (CW, CH) of the crabs with both chelae ( $n=237$ ) reveals that growth of the chelae becomes highly variable at approximately 125 mm CW postmolt (Figure 5A). A graphical examination of the relationship between the percent change in carapace width and percent change in chela height clearly shows two distinct groups (Figure 5B): one dense group on the left side of the figure and one group on the lower half of the figure. These two groups roughly correspond to the lower and upper groups in Figure 5A. The group on the left side of the graph (Figure 5B) is comprised predominantly of small crabs with small chelae. This group is characterized by a slight, but predictable, percent increase in carapace width with a percent increase in chela height. The group on the lower half of the figure represents the large-clawed crabs, or those with an approximate 45% or greater increase in chela height (Figure 5B). This group shows no clear trend, except a possible slight percent increase, in carapace

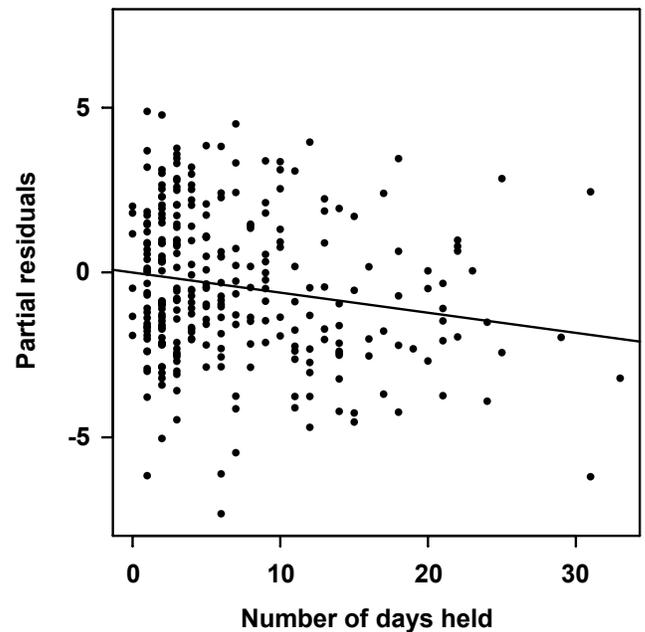


Figure 2. Partial residual plot for number of days held in the laboratory prior to ecdysis. Partial residuals were computed as residuals from the regression of new carapace width (NCW) on initial carapace width (ICW), Pre-LL, and Day plus the estimated coefficient for Day multiplied by Day (Weisberg 1985). The partial residual plot is also called the residual plus component plot (Weisberg 1985). Pre-LL=number of limbs lost prior to ecdysis; Day=number of days held in the laboratory prior to ecdysis.

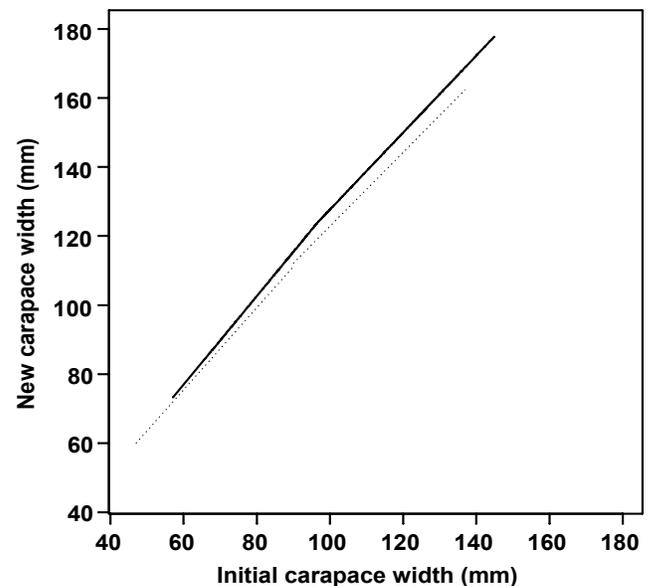


Figure 3. Joined growth lines estimated for crabs in this study ( $n=241$ ; solid line) and the unjoined growth lines estimated by Donaldson et al. (1981) from their data (dotted lines).

width in relation to chela growth (Figure 5B). These data indicate that among large-clawed crabs, percent increase in chela height appears to be independent of percent change in carapace width.

## DISCUSSION

Regardless of statistical method used to model growth, growth rates (CW increment per molt) for both small and large male Tanner crabs measured in this study are greater (2.3% to 6.2%) than those measured for the Kodiak Island area (Donaldson et al. 1981). In the Kodiak Island study, premolt crabs were collected in shallow water (< 23 m) in several northern Gulf of Alaska bays and held in situ until ecdysis occurred. This process was undertaken during several consecutive years (November 1973 through November 1977), and growth was estimated from pooled growth data. Interannual differences in growth were not examined. In this study, we found no interannual difference in growth rate during consecutive years within one population of Tanner crabs.

Differences in growth rate between Southeast Alaska and Kodiak Island may be due to differences in water temperature. Water temperatures in the near-shore waters of Southeast Alaska are generally 1°C to 2°C warmer than those near Kodiak Island (McLain

et al. 1979). For example, water temperatures measured for a two-year period in Fritz Cove, Southeast Alaska were generally 1°C warmer throughout most of the year than in Trident Basin near the study site of Donaldson et al. (1981) (Figure 6). Another possibility is that growth rates at the two geographically disparate locations (1,100 km) are indeed the same and have increased concomitantly throughout the Gulf of

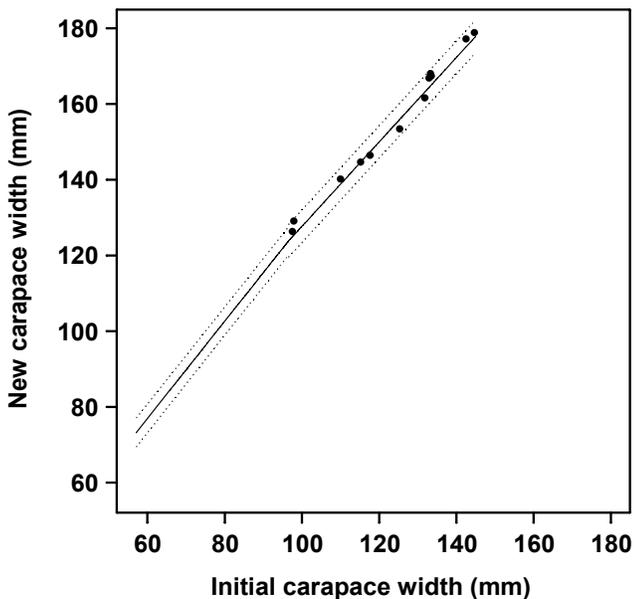


Figure 4. Growth (molt increment) for 12 crabs collected at the study site in 1993 (Stone, unpublished data). Joined growth lines (solid lines) and 95% predictive intervals (dotted lines).

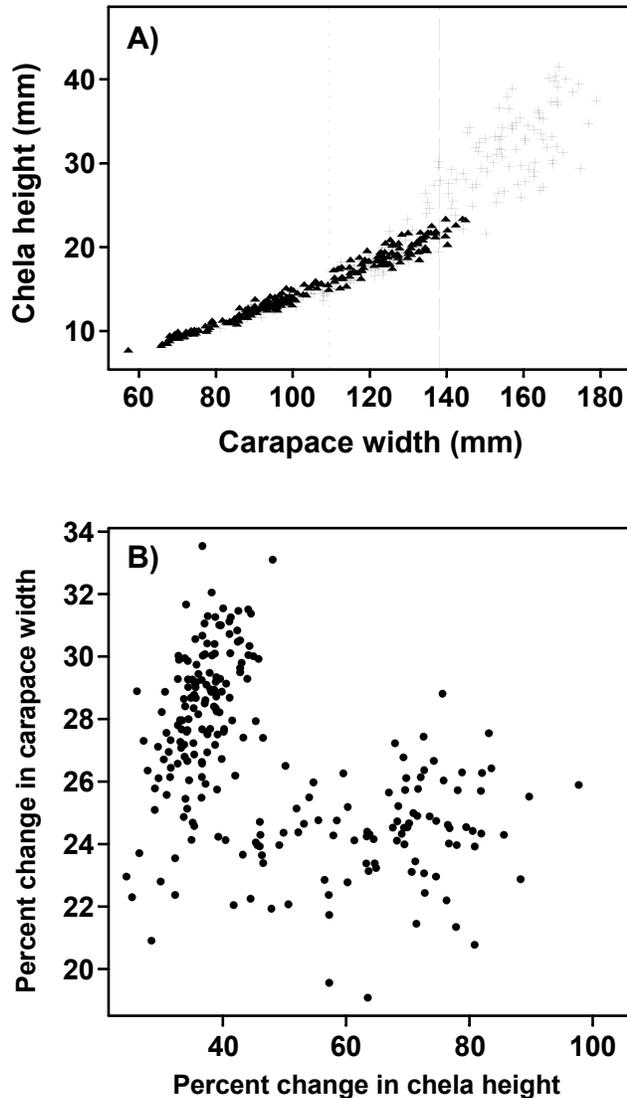


Figure 5. A) The allometric relationship between chela height and carapace width of crabs prior to ecdysis ( $\blacktriangle$ ) ( $n=237$ ) and after ecdysis ( $+$ ) ( $n=237$ ). Based on the point prediction from growth line L, crabs with carapace width > 109.3 mm (dotted line) will recruit to the fishery. Legal-sized crabs measure 138.0 mm (CW) (dashed line). B) The relationship between percent change in carapace width and percent change in chela height. Note that the x- and y-axes are not on the same scale.

Alaska with water temperature between the periods 1974 to 1977 and 1999 to 2000 (Hare and Mantua 2000). There is some evidence that water temperature increased in Trident Basin between the periods 1975 to 1976 and 1989 to 1990 (Figure 6). Studies of growth rate conducted simultaneously at both locations could test that hypothesis. Low levels of genetic diversity exist among *C. bairdi* populations of the Bering Sea, Gulf of Alaska, and Southeast Alaska (Merkouris et al. 1998), so differences in growth rates among these disparate locations are likely not controlled by genetic factors.

Moriyasu et al. (1987) found that male *C. opilio* (60 to 70 mm CW) molting in the laboratory to the large-clawed state had molt increments about 3 mm smaller than those molting to a small-clawed state. Similarly, female Tanner crabs have decreased percentage growth during the molt to maturity when the width of the abdomen increases disproportionately (Donaldson et al. 1981). We clearly determined that growth of the chelae for male crabs in this study becomes highly variable at approximately 125 mm CW postmolt and over a wide range of sizes (approximately 125.0 to 178.9 mm CW). We were unable to explicitly test for differences in growth between large- and small-clawed crabs since we could not definitively assign crabs a priori to either group. However, we found no evidence among large-clawed crabs for a percent reduction in growth associated with a percent increase in chela height.

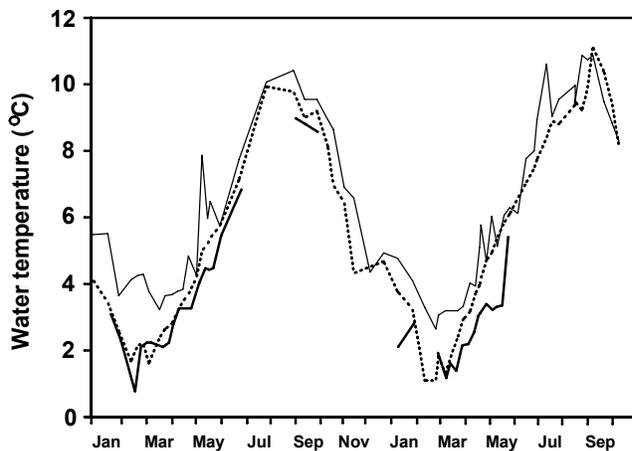


Figure 6. Water temperature measured in Fritz Cove, Juneau (top solid line), and in Trident Basin, Kodiak Island (dotted line), between December 1988 and October 1990. Water temperature data recorded in Trident Basin between January 1975 and June 1976 are also plotted (discontinuous solid line at bottom). Temperatures were recorded on the same day at a depth of 10.7 m mean lower low water. Trident Basin data is from Blau and Dooley (1995).

Using the new method of joined regression lines we determined that a decrease in growth rate occurs for male crabs examined in this study at 96.5 mm CW. Kodiak Island area crabs exhibited a change in growth rate at 90 mm CW and also at about 50 mm CW and these changes were attributed to the attainment of sexual maturity and a “change in lifestyle”, respectively (Donaldson et al. 1981). Paul (1992), however, found that males become sexually mature, as evidenced by the production of spermatophores, at much smaller sizes (40 to 60 mm CW). We believe the change in growth rate we observed at 96.5 mm CW is associated with the attainment of functional maturity. Conan and Comeau (1986) originally defined functional maturity as the ability of males to mate in situ in the presence of competition from other males. Using this definition, male crabs as small as 91 mm CW become functionally mature in Southeast Alaska (Stone, unpublished data) and as small as 83 mm CW in the Kodiak Island area (Stevens et al. 1993). The observed reduction in growth is possibly due to the additional energetic costs of functional maturity that include mate searching, mate guarding, competition with other males, and mating. Activity rate of functionally mature male crabs increases 2- to 3-fold during the spring mating season when they greatly increase their home range presumably in search of mates (Stone, unpublished data). The observed reduction in growth may or may not be related to differentiation of the chelae. Certainly some crabs in the size range of the inflection point (pre-molt) attain large-claw status but we found no evidence among large-clawed crabs that a percent increase in chela height was associated with a percent decrease in carapace growth.

Several species of crabs exhibit reduced growth for individuals missing several limbs prior to ecdysis (Smith 1990—four limbs in *Callinectes sapidus*; Sainte-Marie et al. 1995—three or more limbs in *C. opilio*). In this study, we similarly observed reduced growth for crabs missing three or more limbs before ecdysis. We are unaware, however, of any studies other than ours that have demonstrated reduced growth for crabs that have lost limbs during or immediately after ecdysis.

Laboratory conditions may affect both molt increment (NCW–ICW) and intermolt period of crustaceans (Kurata 1962; Hartnoll 1982; Castro 1992). Several studies have shown that growth is reduced for crustaceans molting in the laboratory compared to those molting in situ even when laboratory conditions are meticulously controlled to follow natural conditions (MacKay and Weymouth 1935—*Cancer magister*; Hiatt 1948—*Pachygrapsus crassipes*; Kurata

Table 2. Recruit classes of male Tanner crabs in relation to the legal size of 138 mm carapace width (spines exclusive) using different growth models. EC equals exoskeleton condition (from Stone 1999).

Recruit Class <sup>a</sup>	EC	Carapace Width (mm)		
		Donaldson et al. (1981)	This study based on the point prediction.	This study based on 95% predictive intervals.
Prerecruit 2+	1-3	< 114.3	< 109.3	< 113.2
Prerecruit 1	1-3	114.3–137.9	109.3–137.9	113.2–137.9
Recruit	1, 2	138.0–163.3	138.0–169.9	138.0–174.2
Postrecruit 1	3	138.0–163.3	138.0–169.9	138.0–174.2
Postrecruit 1	1, 2	> 163.3	> 169.9	> 174.2
Postrecruit 2+	3	> 163.3	> 169.9	> 174.2

<sup>a</sup>Prerecruit 2+ crab will recruit to the fishery in 2 or more molts; prerecruit 1 crab will recruit to the fishery in 1 molt; recruit crab recruited to the fishery during their most recent molt; postrecruit 1 crab recruited to the fishery a minimum of one year ago; and postrecruit 2+ crab recruited to the fishery more than 2 years ago.

1962—*Hemigrapsus sanguineus*). Kurata (1962) also showed that the growth of larger crabs was affected more by laboratory confinement than the growth of smaller crabs and that these effects were detectable after five weeks of confinement. In this study, we detected decreased growth after only 13 days of laboratory confinement.

Tanner crab fishery managers have been concerned in recent years about the high exploitation rate (percentage of all legal-sized crab caught in a season) estimated for the Southeast Alaska fishery (Clark et al. 2001). High harvest rates of recruit crab (i.e. 138.0–169.9 mm CW with EC ≤ 2) and a steady decline in catch rates as a season progresses are indicators of a high exploitation rate. Recruit crab have accounted for an estimated 42% to 58% of the total commercial landings between 1996 and 2001 (Clark, personal observations), indicating that the fishery relies heavily on newly recruited crab each year. Using the growth rate estimated in this study, recruit crab accounted for an estimated 53% to 70% of the harvest during the same period (Table 2). Using the relatively conservative 95% predictive interval (Table 2) would have yielded an even higher estimate of recruit crab (138.0 to 174.2 mm). Obviously, a recruitment failure would be devastating to the fishery. Counter to this negative effect on the fishery outlook from our results, preseason estimates of crabs that will grow to commercial size in one molt are underestimated by 5.5% using the growth rate measured by Donaldson et al. (1981).

Since growth rates probably differ markedly throughout the Tanner crabs' range, growth studies on male crabs should be conducted from additional geographical locations where populations sustain commer-

cial fisheries and are managed separately. Based on the results of this study, we recommend that future growth studies, especially those designed for application to dynamic models of natural populations, consider four general criteria: 1) crabs should be collected from one geographical or fisheries management area, 2) premolt and postmolt limb loss should be accounted for in the analysis, 3) holding time of animals in the laboratory should not exceed 14 d, and 4) when experimental animals are held in the laboratory, the conditions should be similar to conditions that the crabs are subjected to in situ. Ideally, studies of growth should be conducted in situ as in the Donaldson et al. (1981) study.

Based on results of this study and the historically stable nature of the Southeast Alaska Tanner crab fishery, we are reluctant to recommend changes to current minimum harvest size restrictions. Managers should be aware, however, that male Tanner crabs in Southeast Alaska have larger increments per molt and apparently mature (at least functionally) at a larger size than was measured for crabs from the Central Gulf of Alaska during the period from 1973 to 1977. Exploitation rates of recruits are consequently higher than previously calculated because the population of recruits is a larger proportion of the legal population than previously thought. Yield per recruit is higher for Southeast Alaska crabs than for central Gulf of Alaska crabs since they reach commercial size at a younger age and are therefore subject to natural mortality for a shorter period of time. Until maturity studies have been conducted in situ for Southeast Alaska male Tanner crabs, we can say little about how this will affect spawning biomass estimates.

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