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## **SIZE FREQUENCY ANALYSIS AND INSTAR DETERMINATION IN CLAYOQUOT SOUND AND FRASER RIVER DELTA DUNGENESS CRAB (*CANCER MAGISTER*)**

**by**

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## Abstract

Crustaceans grow discontinuously by moulting, and each moult stage is called an instar. Instars cannot accurately be aged, as no hard structures which might show growth rings are carried through a moult. Small instars cannot be tagged, and neither field moult increments nor intermoult periods can be accurately determined from tank-rearing studies. Consequently, total instar number in a crustacean's life cycle, moult increments, and intermoult periods are typically estimated from observing the progression of modes in size frequency distributions (SFDs), which are presumed to represent specific instars, in consecutive field population samplings. A problem with this approach is that as instars become larger, their intermoult periods become longer, which coupled with the cumulative effects of slow and fast growing individuals, means they become less definable using only modal observations. With Dungeness crab (*Cancer magister*), to date estimation of instar size ranges has been done primarily by visual identification in SFDs. Here, we present an analytical approach using both SFD data and field data on the size of moult increments. The analytical model we describe is available for use by other researchers with similar data as a Visual Basic © application. Results indicate that for Clayoquot Sound, most newly recruited legal crab are two-year-old, instar 12, crab, i.e., in their third year of life. This is 1-3 instars sooner than previously published studies have estimated. Being able to assign a probability that a crab of known carapace is within a particular instar category means that crab growth and mortality dynamics can be better measured and predicted.

## Introduction

Unlike for some invertebrates, e.g., sea urchins (Vadas et al. 2001), the age and growth of crustacea are difficult to determine because there are no permanent hard structures which survive a moult and record age. All hard structures are cast away with the discarded exoskeleton. Growth of individual Dungeness crab (*Cancer magister*) can be followed to some extent through use of anchor tags in the episuture line which are retained through a moult, but this requires recapture of tagged crabs, and to achieve a sufficient rate of return, this often necessitates the cooperation of fishers. The problems with this approach are 1) the smallest crabs are too small to hold visible tags, 2) tags can be lost during a moult, 3) the crab may be harmed over the long term by the tag (thus tags might remain on a live, healthy crab for only a few moults), and 4) the largest, legal crabs are mostly removed by fishing before they have had an opportunity to moult. The overall result is that tagging in the field can only provide measures of moult size increments for intermediate size (80-155 mm notch-to-notch carapace width (CW)) crab instars. Crab growth and instar size ranges for crabs outside that size range have typically been inferred from size frequency analyses.

A crab instar is usually described by a statistical distribution of crab sizes within a SFD. Instars are generally assumed to be composed of a normal (Gaussian) distribution of crab sizes with the distribution being described by its mean and SD of CW. Crustaceans grow by moulting into an instar with a larger mean CW, and so their growth is not continuous, but rather proceeds in a step-wise manner. Thus, modes in a SFD can often be visually followed through sequential sampling over time of the same population. However, growth rate of a single crab is a function of two events, the size increment at a moult and the length of the intermoult period. Not all individuals in a cohort grow at the same rate, so that over time, the CWs of a cohort of young, newly settled crab will overlap a range of sizes in later instars, and the modal pattern can become increasingly difficult to discern visually. This is exacerbated by the fact that while early instar moults are large enough (relative to the SD of CWs in instar) and frequent enough to be distinct,

later moults occur only every year or two, which tends again to diffuse the population's instar composition.

If instar growth and mortality rate estimates are available, and there is now evidence that such rates may be quite instar-specific (Fernandez et al. 1993), possible applications of this information include estimation of the time when a particular instar is likely to recruit to the fishery, and the magnitude of this recruitment. What complicates crab size frequency analysis is the fact that crustacean growth is discontinuous, and that overlap exists among instar size ranges. Thus there is not a 1:1 relationship between instar size and instar age. With many juvenile instar moults occurring each calendar year, each year-class can be composed of several instars. Smaller instars tend to be more distinct than larger ones, since crabs in the former moult frequently and are often the result of large, discrete settlement events. This distinction becomes progressively blurred over time, so that a population of crabs just below legal size may actually consist of a number of different instars and year-classes (Jamieson 1996).

To challenge this difficulty, we use an analytical approach that incorporates data obtained from moult increments observed for tagged crabs and from numerous SFDs collected over seasons and years from the same location. The tagging data provide information on crab growth at the level of the individual, while the SFD provide information on crab growth at the population level. Together both data sets can be used to interpret instar composition for the individual, seasonal SFDs. Small instars tend to be more distinct than larger ones and thus age can often be assigned *a posteriori* to these young instars. Ageing of older instars is more problematic and must be inferred from the results of both the size frequency analyses and from estimated intermoult durations.

Wainwright and Armstrong (1993) reviewed previous observations of growth of Dungeness crab, and compared different models for describing growth. However, their analyses considered five procedures to estimate moult increments: 1) measurement of newly moulted crabs and their cast shells in nature, 2) observation of moulting in held crab, 3) observation of laboratory-reared individuals, 3) distance between instar modes in SFDs, and 5) recapture of tagged animals. They estimate growth rate, but presented no rigorous analysis of suggested number of instars and their size ranges. They projected average instar size and size at age using a combination of the bent-line model for moult increment and a degree-day model if intermoult period for three different temperature regimes, and suggested that 14 instars would be required to reach legal size. At 15° and at 5-15°C, they suggested average growth to legal size would take about 27 and 40 months, respectively.

The rate at which individual crabs increase in size has important implications for the study of crab population dynamics, the fishery and its management. For example, these data can be used to estimate the ages at which crab are breeding and recruiting to the fishery, the year-class of a particular cohort of crab, and how different instars are being impacted by environmental and fishery events.

The technique of inferring crab growth by considering the frequency of moulting and the moult increment is most successful with older crab, for reasons mentioned above. Earlier studies addressing size frequency analysis and growth in crabs, and the different models and techniques used, have been reviewed by Wainwright and Armstrong (1993). Predicting the size range of large instar crab from trap SFDs is difficult, since traps tend to poorly sample crab abundance below about 135 mm CW, and seldom retain crab less than 80 mm CW. Trawl SFDs better

represent crab <135 mm CW, but poorly represent larger crab, since these latter crab can often avoid a trawl because of their greater mobility. Different instars appear to have specific habitat requirements, and habitats where smaller instars occur are difficult to sample with these gear, which may not sample them well.

The objectives of this study are to interpret growth increment and SFD data in order to: 1) evaluate which Dungeness crab instars straddle the current minimum legal size and estimate the proportion of these instars which are taken by the fishery, 2) follow trends or changes in instar age structure, 3) characterise seasonal SFDs by instars likely to be present, and 4) assess how fisheries may be impacting instar age structure. Jamieson (1996) and Jamieson et al. (1998) used instar data in their evaluation of possible selective effects of fishing on Dungeness crab population dynamics. To achieve these objectives we developed a mathematical model for jointly analysing moult increment and SFD data. We introduce the model, explain its use for our data, and evaluate the reliability of the model using simulation. The model is available for use by researchers with similar data on the internet as a Visual Basic © application.

## **Methods**

### ***A. Study Sites***

Site descriptions (Fig. 1) and research sampling protocols have been previously described by Jamieson et al. (1998). The only data used here were obtained from beam trawling. Briefly, sites were:

**Clayoquot Sound:** Trawling was conducted in relatively shallow (about 5-15 m in depth), well-mixed nearshore locations around Tofino. Annual seawater temperature ranged from about 6 to 12°C. Substrate varied from sand in stronger current areas to mud in the quiet waters at the upper end of Lemmens Inlet.

**Fraser River delta:** Trawling locations around Vancouver were Sturgeon and Roberts Banks on the delta of the Fraser River. Waters were 0-15 m depth, with a pronounced year-round near surface pycnocline (most pronounced near river outflows) and a summer thermocline at about 10 m depth. Annual temperature ranges above and below the thermocline were about 6-20°C and 6-9°C, respectively (Thomson 1981). Substrate varied from sand in areas of strong water flow to mud in more sheltered areas.

### **B. Size frequency distributions**

Male and female Dungeness crabs were collected by beam trawl (Gunderson et al. 1985). In Tofino, during summer, 1985, more than 50 tows were made to assess spatial distribution throughout the study area. Then, in selected areas where crabs were abundant, tows were made approximately monthly from June 1985 until January 1987, and approximately quarterly from then until 1995, when they became annual. Fraser delta samples were not collected as systematically (samples were mostly June and September) and varied in time from year-to-year. They were also not as numerous, and fewer crab were caught per tow.

For each crab caught, sex, notch-to-notch carapace width, shell condition, injuries, date and location fished were recorded. The exception was with the smallest crab (probably first instar), which were all called “male” in the Clayoquot Sound data and when in doubt, “unsexed” in the Fraser River data set. Some of these crab were identified as “female” in the latter data, though, which allowed us to use these data in later analyses.

### **C. Moulting increments**

British Columbia male and female moulting increment data were from mark-recovery data from Tofino (Smith and Jamieson 1989a) and Dixon Entrance (Butler 1961), all data combined. The latter were re-analysed by converting spine-to-spine CW measurements to the equivalent notch-to-notch CW measurements by multiplying by the factors 0.94 and 0.95 for males and females, respectively (Smith 1988). In addition, female moulting increments from California were incorporated into the moulting increment data set (Diamond 1983). Moulting increment data from local tank-reared young-of-the-year crabs were available and used in preliminary analyses, but were not used in the final analyses (see below). These increments came from hard-shelled crab taken from Clayoquot Sound.

### **D. Growth increment and size frequency model**

We used a generic polynomial model of order  $J$  to describe the growth increment in CW of an individual crab by moulting as a function of pre-moulting size  $l_{i,k}$ , such that

$$(1a) \quad \hat{g}(l_{i,k}) = \sum_{j=0}^J \beta_j l_{i,k}^j$$

$$(1b) \quad g(l_{i,k}) = \hat{g}(l_{i,k}) + \varepsilon_k,$$

where we add normally and independently distributed variation in growth ( $\varepsilon_k$ ) to recognize that the growth increments for a population of crabs with the same carapace width would vary among crabs. Additionally, we also recognize that growth rate might depend proportionately on a crab's relative size within an instar

$$(2a) \quad \hat{g}(l_{i,k}) = \sum_{j=0}^J \beta_j l_{i,k}^j \left( 1 + \omega \left( \frac{l_{i,k} - \mu_i}{\sigma_i} \right) \right)$$

$$(2b) \quad g(l_{i,k}) = \hat{g}(l_{i,k}) + \varepsilon_k .$$

In Eqs. 1 and 2 size is represented by  $l_{i,k}$  where there are  $i=1, \dots, I$  consecutive instars and  $k=1, \dots, K$  growth increment records, described by their mean size ( $\mu_i$ ) and SD ( $\sigma_i$ ). This structurally over-parameterized, but flexible, model that relates moult increments to pre-moult size suits most of the data sets we have encountered to date, however, often a simple linear model ( $J=1$ ; the classical Hiatt model (Hiatt 1948, Botsford 1985)) is sufficient for a narrow size range of pre-moult sizes. The equivalent and familiar Hiatt model equivalent to Eq. 2, which relates post-moult CW to pre-moult CW, is

$$(3) \quad l_{i+1,k} = l_{i,k} + \hat{g}(l_{i,k}) + \varepsilon_k .$$

If individual crabs providing growth increment data cannot be assigned to an instar, but the proportional contribution ( $\zeta_i$ ) of instars within the population from which crabs providing growth increment records were drawn is known, then Eq. 2a can be expressed as

$$(4a) \quad \hat{g}(l_{\bullet,k}) = \sum_{j=0}^J \beta_j l_{\bullet,k}^j \left( 1 + \omega \sum_{i=1}^I \zeta_i \left( \frac{l_{i,k} - \mu_i}{\sigma_i} \right) \right) .$$

$$(4b) \quad g(l_{i,k}) = \hat{g}(l_{i,k}) + \varepsilon_k$$

This completes the description of growth, by moulting, of an individual. Note that this model produces a bivariate normal distribution of observed increments within an instar when  $l_{i,k}$  is drawn from an instar whose individuals are normally distributed with respect to size and  $\varepsilon_k$  is independent of  $l_{i,k}$ .

We now modify our notation to write the equivalent instar growth model for the size frequency data, where a normal distribution of individuals in instar  $i$ , is characterised by its mean ( $\mu_i$ ) and SD ( $\sigma_i$ ), such that the expectations

$$(5a) \quad E[l_{i+1,k}] = l_{i,k} + E[g(l_{i,k})]$$

$$(5b) \quad V[l_{i+1,k}] = V[g(l_{i,k})],$$

become

$$(6c) \quad \hat{\mu}_{i+1} = \hat{\mu}_i + g(\hat{\mu}_i)$$

$$(6d) \quad \hat{\sigma}_{i+1}^2 = \hat{\sigma}_i^2 + V[g(\hat{\mu}_i)],$$

where we now treat size,  $l_{i,k}$ , as a random variable. Equation 6d is more explicitly expressed as

$$(7) \quad \hat{\sigma}_{i+1}^2 = (1 + \hat{\beta}_1)^2 \hat{\sigma}_i^2 + \sum_{j=2}^J \hat{\beta}_j^2 \hat{V}[l_{i,\bullet}^j] + \hat{\sigma}_k^2$$

where  $\sigma_k$  represents the SD of moult increments for individuals moulting at the mean size of instar  $i$  ( $\mu_i$ ). To avoid the tedium of numerically calculating the variance of products of the polynomial in Eq. 7 we more simply calculate the average slope,  $\lambda_i$ , of the growth rate (Eq. 2a) from  $\mu_i$  to  $\mu_{i+1}$ . This gives

$$(8) \quad \hat{\lambda}_i = \left( \frac{\hat{\mu}_{i+1} - \hat{\mu}_i}{\hat{\mu}_i - \hat{\mu}_{i-1}} \right).$$

For a linear growth model (i.e.,  $J=1$ ), the slope of the growth increment versus pre-moult CW is simply  $\lambda_i \equiv \beta_i$ ; or for the Hiatt model  $(1+\lambda_i) \equiv (1+\beta_i)$ .

Thus our complete model for stochastic instar growth is:

$$(9a) \quad \hat{\mu}_{i+1} = \hat{\mu}_i + g(\hat{\mu}_i)$$

$$(9b) \quad \hat{\sigma}_k = \sum_{t=0}^2 \hat{\tau}_j \left( \sum_{j=0}^J \beta_j l_{i,k}^j \right)^t$$

$$(9c) \quad \hat{\sigma}_{i+1}^2 \approx (1 + \hat{\lambda}_i)^2 \hat{\sigma}_i^2 + \hat{\sigma}_k^2 + 2(1 + \hat{\lambda}_i) \text{Cov}[l_{i,k}, \varepsilon_k]$$

$$(9d) \quad \text{Cov}[l_{i,k}, \varepsilon_k] = \hat{r} \sqrt{\hat{\sigma}_i^2 \hat{\sigma}_k^2},$$

where the covariance  $\text{Cov}[l_{i,k}, \varepsilon_k]$  accounts for any correlation between the relative size of an individual within an instar, and the deviation of a predicted moult increment at  $l_{i,k}$  from the predicted moult increment at the instar mean ( $\mu_i$ ). As suggested by experience with data, our model was designed to allow  $\sigma_k$  to be as complex as a quadratic polynomial function of the expected growth rate at the instar mean (Eq. 9b). Equation 9c is an approximation for two reasons. First, we use the slope approximation  $\lambda_i$  instead of calculating the variance of products. Second,  $\sigma_k$  is ultimately a function of  $l_{i,k}$ , and typically would not be a constant as required for independent variances to be additive. However, our use of  $\sigma_k$  near the mean ( $\mu_i$ ) of a normally distributed instar (Eq. 9b) will tend to minimize the inaccuracy of Eq. 9c. Our use of Eq. 9c, rather than relating  $\sigma_k$  to the mean of an instar is predicated on our being limited to only probabilistically assigning a crab to an instar. The model described by Eq. 9 requires two parameters in addition to those already introduced to represent the mean of virtual instar zero ( $\mu_{i=0}$ ) and the SD of instar one ( $\sigma_{i=1}$ ). The means and variances of the larger instars can then be calculated sequentially starting with these two values.

One can infer from the above consideration that estimates for  $\omega$  (growth increment data) and  $r$  (size frequency data) both measure the correlation ( $-1 < \omega < 1$ ;  $-1 < r < 1$ ) between the relative size of a crab within an instar and the relative growth increment at that size. If  $\omega$  can be well estimated by the growth increment data, then ideally,  $r$  should not differ significantly from zero,

and be fixed at zero, since the role of  $\omega$  is to measure the relationship between a crab's relative size within an instar and the size of a moult increment. However, a significant positive (negative) value for  $r$  indicates that for the size frequency data instar variance is increasing at a rate greater (lesser) than predicted by our growth increment data. If the growth increment data do not facilitate an estimate of  $\omega$  (i.e.,  $\omega=0$ ), then a positive or negative estimate of  $r$  suggests that one could potentially estimate a value for  $\omega \neq 0$  if there were sufficient and informative growth increment data. If there are too few data to estimate  $\omega$ , i.e., either the moult increment or SFD data are (probabilistically) uninformative of the instar to which a crab might belong, then an estimate of  $r$  might be the only parametric option. Note also that if  $\omega=0$ , then the  $\zeta_i$ s no longer contribute to growth increment model structure.

Once a final estimate for  $\omega$  or  $r$  has been settled upon, then one could infer from a positive value for  $\omega$  or  $r$  that a population of crabs tends to be composed of individuals having consistently either larger (or smaller) than average moult increments. A negative value for  $\omega$  or  $r$  suggests that moult increments are compensatory; i.e., smaller than average moult increments tend to be followed by larger than average moult increments. One might also consider that a negative  $r$  could be an indication that individuals toward the extremes of the instar's distribution were less likely to survive and thus occurred less frequently in the larger, older, instars.

### E. Data analysis

Following the general concept and design of Schnute and Fournier (1980), the growth analysis used the above model to describe the progression by moulting of the mean sizes of male and female instars and their variance. The above model defines the expected frequencies of individual crabs in each cell  $h=1, \dots, H$ , defined by its midpoint  $CW_h$  and width  $w$ , for each instar  $I$ , in each sequential SFD  $s=1, \dots, S$  as:

$$(10) \quad P_{s,h} = \sum_{i=1}^I \frac{v_{s,i}}{\sqrt{2\pi\sigma_i^2}} \int_{CW_{h-\frac{w}{2}}}^{CW_{h+\frac{w}{2}}} e^{-\frac{(CW_h - \mu_i)^2}{2\sigma_i^2}} \partial CW$$

where  $v_{s,i}$  is the estimated proportion of crabs of instar  $i$  in SFD  $s$ . In a computer application, the estimates  $v_{s,i}$  can either be determined independently of each other, or be constrained within a SFD  $s$  to conform to a robust mortality function such as the Weibull function (Walpole et al. 1998). A parsimonious option is to estimate the values of  $v_{s,i}$  independently for the younger, smaller and clearly identifiable instars, but constrain the values of  $v_{s,i}$  for the older, larger, overlapping and obscure instars to conform to a mortality function.

A maximum-likelihood function, the separation statistic ( $\Theta_1$ ) of Schnute and Fournier (1980), was used to measure the discrepancy between observed ( $C_{s,h}$ ) and predicted ( $P_{s,h}$ ) frequencies for all size frequency cells  $h=1, \dots, H$  in each sequential SFD  $s=1, \dots, S$ :

$$(11a) \quad \Theta_1 = 2 \sum_{s=1}^S \sum_{h=1}^H C_{s,h} \ln \left( \frac{C_{s,h}}{P_{s,h}} \right) \text{ for all } C_{s,h} > 0,$$

subject to the constraint that



$$(11b) \quad \sum_{h=1}^H C_{s,h} = \sum_{h=1}^{\infty} P_{s,h} \text{ for each SFD } s \text{ not subject to truncation, or}$$

$$(11c) \quad \sum_{h=1}^H C_{s,h} = \sum_{h=H_{<}}^{H_{>}} P_{s,h} \text{ for each SFD } s \text{ subject to truncation below } H_{<} \text{ and above } H_{>}.$$

The value for  $\Theta_1$  at the maximum-likelihood estimates is always zero or positive, is conveniently zero only when  $P_{s,h}=C_{s,h}$  in all frequency cells, and approximates the  $\chi^2$  statistic when sample size is large and the fit is good. For our analyses we aggregated the crab CW frequencies into 1 mm cells with midpoints beginning at 0.5 mm.

The SFD likelihood function was complemented by a likelihood function for the growth increment data ( $\Theta_2$ ) assuming a Gaussian distribution of random deviates ( $\varepsilon_k$ ) and where  $\zeta_i$  represents the independently estimated proportion of crabs of instar  $i$ :

$$(12) \quad \Theta_2 = 2 \sum_{k=1}^K \ln \sum_i^I \left( \frac{\zeta_i e^{-\left(\frac{(O_k - \hat{g}(I_{i,k}))^2}{2\sigma_k^2}\right)}}{\sqrt{2\pi\sigma_k^2}} \right).$$

The overall likelihood ( $\Theta_3$ ) is simply  $\Theta_3=\Theta_1+\Theta_2$  since the SFD data and the growth increment data are assumed to be statistically independent data sets; i.e., no crab that provided a growth increment record also occurs in a SFD.

Parameter estimates for the maximum-likelihood solution to the instar composition analysis, i.e., obtained by minimizing  $\Theta_3$ , were obtained with either the Simplex algorithm (Mittertreiner and Schnute 1985) or Marquardt's algorithm (Press et al. 1986) implemented in a robust Visual Basic © application available from BDS. Standard errors were calculated by Mittertreiner's and Schnute's (1985) approximate numerical technique. A  $X^2$  computer algorithm modified from Roff and Bentzen (1989) was used to test model goodness-of-fit for both the size frequency and growth increment data. In both cases randomised Pearson deviates were calculated from the expected frequencies of individuals within each cell of the size frequency distributions and 0.5 mm cell widths for the growth increment data. The value of  $X^2$  for the observed data was then probabilistically compared with those values generated by the randomisation algorithm. Candidate models passing the goodness-of-fit diagnostic were compared, ranked and adjudicated in descending order of their fit to the data based on  $AIC_c$  (Burnham and Anderson 1998).

Analysis of a SFD created using data from a single sampling was in most cases insufficient for a meaningful estimation of growth parameters, therefore we chose to simultaneously analyse several SFDs from samples collected regularly over a few years. Before performing our analyses we combined all SFDs for a single study site by sex and by season (roughly every three months, or quarterly). Although unsexed individuals were used in both female and male analysis, unsexed individuals above 80 mm CW were excluded from our SFDs.

Combining SFDs should not distort the underlying instar composition because Dungeness crabs grow discontinuously by moulting over a short time period from instar  $i$  to a larger instar  $i+1$ , thus instars are simply superimposed upon one another. A disadvantage of this treatment of the data is that otherwise distinct instars might be partially obscured by adjacent and partially overlapping instars when the data are combined, and thus become more difficult to identify. However, an important practical advantage to combining SFDs is a reduction in the number of proportion parameters ( $v_{s,i}$ ) requiring estimation. Too many such parameters can be problematic for an estimation algorithm and so an analysis must trade-off between too many parameters and a loss of information on instar composition. We judged our choice of a simultaneous analysis of all SFDs grouped within seasons to be a reasonable compromise between resolution of instar composition and an unmanageable number of parameters. For males, the SFDs and their predicted size frequency densities were truncated above the minimum legal size limit of 153 mm to account for the intense rate of removal of male crab larger than 153 mm CW by fishing (Smith and Jamieson 1989a). Means and variances for instar sizes were then estimated by simultaneously analysing the SFD data with the growth increment data described above. The growth parameter estimates obtained from this analysis were then held fixed for subsequent analyses run on those seasonal beam trawl SFDs that had enough individuals to permit a meaningful estimate of the proportion of each instar present. Year-classes were inferred by following shifts in instar pattern over time.

## Results

Variation in the number of crabs caught in the beam trawl over time resulted from variable annual settlement rates, and variable and high male (Smith & Jamieson 1989b) and female (Hankin et al. 1985) mortality, changes in spatial distributions of crabs over time (Smith 1988), and uneven trawling effort over time. Appendix A gives the raw data for each sampling date.

### **A. Moulting Increments:**

Figures 2-4 give the fit for increments analysed in conjunction with quarterly grouped Tofino SFDs. We did not know the mean size, SD or instar number the instar to which a crab yielding a growth increment record belonged, so not surprisingly our preliminary analyses suggested that we could not fruitfully consider instar number in our analysis of growth. Thus we choose to estimate  $r$  rather than  $\omega$  in all analyses. We were comfortable with this decision because our growth increment data provided no visual evidence of the importance of instar number as a covariate. The increment data are most useful in the upper range of sizes when separation of instars became difficult because of increased range in instar size. The increment data from smaller, tank-reared crab did not produce an acceptable fit (Table 1, Fig. 4). Monitoring growth of small individuals reared in tanks yielded smaller moulting increments than those observed in SFDs for field data.

### **B. Size frequency analysis:**

Parameters for all the models are presented in Table 1.

**Clayoquot Sound:** Instar means and SDs for male and female crab are presented in Table 2.

**Males:** Two analyses were performed using SFDs. The first used only increment data from field recovery of apparently healthy, moulted, tagged crab (mark-recapture), and gave an optimal solution with 12 instars (Tables 1, 2). A plot of calculated instar CW size ranges against the

actual data is shown in Fig. 5. The model predicted 12 instars with a good fit on three of the seasonal data sets, but the fit was poorer with the fall set (October-December) due to few clear modes, possibly because this was the time of year most larger crab moult in the Tofino area. Table 1 gives the probability of a  $>\chi^2$  for the different model runs; lower values for p indicating less probable models. Table 4 gives the proportion of each instar in each CW size category. Appendix B shows plots of each SFD with numbered vertical lines representing the mean sizes of each consecutive instar.

A second analysis with the Tofino male SFDs included additional increment data from small, tank-reared crab (Table 1). Here, 12 instars did not yield a minimum solution, but a run with 13 instars did. However, the fit was relatively poor, suggesting that the increment data from tank-reared individuals may not be representative of what would have occurred under field conditions. A plot of calculated instar CW size ranges against the actual data is shown in Fig. 6.

*Females:* There were no very small individuals, i.e., identifiable first instar female crab (males and females could not be separated since all individuals looked like males) in the female SFD. As a result, the best solution predicted 11 instars (Table 1), with the first at about 9 mm, corresponding to the second male instar size (Table 2). The mean first instar size was back-calculated from the above best-fit parameters, given in Table 1. For instars below 80 mm in mean size, mean female instar sizes are within 1 or 2 mm of the respective male instar sizes. This is in agreement with most other studies which found that males and females grow at the same rate until puberty. A plot of calculated instar CW size ranges against the actual data is shown in Fig. 7.

**Fraser River Delta:** Instar means and SDs for male and female crab are presented in Table 3.

*Males:* It was more difficult to obtain a statistically acceptable solution for Fraser River males than it was for Clayoquot Sound males since the size frequency data available were more limited (Fig. 8). The number of years sampled was fewer, but it has also proven to be quite difficult to capture mid-sized juvenile Dungeness crab in the delta. Waters accessible by boat have been quite well surveyed, but habitats higher up in the very extensive intertidal zone have proven difficult to survey, and this is where these juvenile crab may be present in abundance. Table 3 shows the means and standard deviations (SDs) for male instars of different model runs, whose parameters are presented in Table 1. Analysing SFDs without incorporation of moult increment data gave the best fit. There was also a fairly good fit obtained with 11 instars, but the low probability of  $>\chi^2$  values in all three instances where Tofino moult increment data were used argues for rejection of use of Tofino moult increment data in Fraser River delta crab growth analyses. Effort is now needed to obtain field moult increment data for Fraser River delta crab. The worst fit occurred when the Tofino growth polynomial was forced on the Fraser River delta SFDs. A plot of calculated instar CW size ranges using the best solution statistically against the actual data is shown in Fig. 8.

*Females:* Analysis of Fraser River females produced a better solution (Table 1) than did analysis of males, and here available moult increment data were used. However, moult increment data (Fig. 3) were only for crab  $>80$  mm CW, unlike the male data (Fig. 2). The same problem occurred with these data as with the Clayoquot Sound data in sexing first instar crab, but here, data were labelled male, unsexed or female. Since there were some female data, it was analysed, but the value (4.8 mm CW) generated for the mean size of this instar appears inaccurate since no

crab that small have been found in field sampling. A plot of calculated instar CW size ranges using the best model against the actual data is shown in Fig. 9.

## Discussion

The maximum likelihood procedure described here is similar to one used previously (Smith and Jamieson 1989; Jamieson et al. 1998) to identify probable instar frequencies in Dungeness crab SFDs. However, the previous analyses did not extend the instar series to include the whole range of instars present in a population. Rather, these analyses focused only on the last 2-5 instars. Here, we present estimated instar size ranges for a full Dungeness crab instar series, and suggest that from settlement to legal size in Clayoquot Sound, there are 12 Dungeness crab instars. This conclusion differs from some of the very first studies which used eye-identification of modes in SFDs to suggest that 13-16 instars were required to reach legal size. We believe our approach is more defensible, since it used empirical data and repeatable analytical procedures, but that does not necessarily mean that other studies are not correct. There may be geographical growth differences between populations because of different ocean climate factors.

Tank-reared crab were not always soft-shelled when brought to the holding tanks, so we believe our moult increment data obtained in this manner were biased. Captive or laboratory increment tend to be smaller than those observed in nature, even for recently captured animals (Butler, 1961; Hartnoll, 1982; Mackay, 1934).

In Fig. 10, we plot pre-moult and post-moult instar sizes against each other, and it is evident that all published data series are similar, not surprising really, since many used the same original moult increment data of Butler (1961) and Diamond (1983). However, these data are not a measure of growth rate, even if they are of growth, as there is no time component to the data. This also becomes evident when mean instar size is sequentially plotted (Fig. 11), which shows that previous studies suggest that adjacent instars differ less in absolute size that we have suggested in this study. It should be noted that our estimates of mean instar size in instars 1- 5 are on the upper side in comparison to other studies, and that for instars 6-10, our estimates are comparable in size but differ in the instar number that size of crab is assigned to. These differences may relate to the relative lack of credible moult increment field data for smaller instars in the literature, and hence possible biases in earlier data extrapolation.

Although a polynomial function probably does not show as distinctly the size at which maturity occurs as with a Hiatt diagram, the advantage of the former is that it describes growth over the whole size range of the species. This allows us to evaluate instar presence and abundance after sexual maturity, when instar modes from our usual size frequency data source, traps, are less distinguishable because of the consequences of gear selectivity and instar size ranges.

While we are quite confident with our interpretation of Clayoquot Sound crab size frequency data, we are less so with the solution for the Fraser River delta. To improve future analyses, we need two things: 1) more accurate population SFDs over time, which means first identifying the location of the preferred habitat for older juveniles and then obtaining larger samplings of the entire population (females included), and 2) acquisition of moult increment data from Fraser River delta crab, particularly for smaller instars. The fact that the best fit of our model with Fraser delta crab was achieved without use of increment data suggests that the increment data available, which was from outer coast crab, may not best describe the growth of Strait of Georgia crab. Jamieson et al. (1993) document behavioural differences between outer coast and Strait of

Georgia crab in the larvae which affect growth, and it is not unreasonable to assume that additional physiological and/or behavioural differences which affect growth in juveniles and adults may also exist. Certainly, the ocean climates each population experiences are different.

It is difficult to assign age to any crustacean instar because no hard structures, which show growth rings, are carried through a moult. However, by following the progression of a mode through several SFDs sequential in time, and incorporating field data on moult increments, it is possible for us to estimate instar age by observing the movement of modes through a probable instar size range series (Appendix A). Our analyses indicate that with male crab in Clayoquot Sound, the instar at recruitment to the fishery is the 12<sup>th</sup>; mean size of this instar is 156 mm CW (Table 2), near the minimum legal size limit of 155 mm CW (= 165 mm CW, spine to spine). In the Fraser River delta in the Strait of Georgia, the recruiting instar may be the 13<sup>th</sup>, since the predicted 12<sup>th</sup> instar had a mean size of only 143 mm CW (Table 3). A difference was not unexpected, since the minimum legal size limit in both areas is the same (it is a coast-wide regulation), yet the sizes at which the larvae settle from the plankton differ significantly (DeBrosse et al. 1990). At settlement, outer coast megalopae average 6.0-6.2 mm carapace length (CL), while Georgia Strait megalopae average 4.6-4.8 mm CL. Timing of settlement of Georgia Strait and outer coast megalopae also differs, being mostly July-August and May-June, respectively. This affects the opportunity for growth during the warmer summer and fall months, and outer coast crab likely overwinter at a larger size than do Strait of Georgia crab. Data interpretation of this type was not possible with the Fraser River data, as we do not have sufficient confidence in the data to justify further extrapolation.

Environmental conditions may affect the relative ages at which crab from the two sites reach both sexual maturity and recruitment to the fishery, with Strait of Georgia crab being somewhat older. Evaluating frequency of moulting was not part of this study per se, although it can be inferred in part by following the relative occurrence of large modes in sequential samplings (Appendix A). Male Tofino crab which settled in June, 1987, reached instar 8 by January, 1988, and instar 9 by April, 1988. A similar pattern was observed in 1989 and 1990. Inter-moult duration then appears to increase significantly, with moulting to instar 10 by the following September, i.e., just after turning 1 y old (see year 1985). Instar 11 is mostly reached by the following February (see year 1986). The trawl data series in Appendix A does not adequately reflect instar 12 abundance because of gear selectivity, but we know that there was a large recruitment to the fishery in the spring, 1987, which would be instar 12 (Jamieson et al. 1998). This suggests a one year intermoult duration between instars 11 and 12, and that first recruitment of a year-class around Tofino was at about 33 months old (2<sup>+</sup> years). As discussed by Jamieson et al. (1998), not all instar 12 crab are above the minimum legal size, and since the intermoult period of pre-recruit instar 12 crab may be two years, final recruitment of a year-class may be instar 13 as 4<sup>+</sup> year-old crab. Given the above scenario, the large 1987-88 Dungeness crab recruitment in Clayoquot Sound appears to have been from the 1984 year-class. This is of interest, because it has been speculated that the large year-class resulted from the relatively large El Nino of 1983. This appears to have not been directly the case. A similar analysis cannot be conducted at this time for Fraser delta crab because of both limited sampling frequency and crab abundance.

In summary, while knowing the mean size and standard deviation in size of an instar does not allow assignment of any specifically-sized crab to an instar category, knowing these sizes may allow relative instar abundance to be estimated in a SFD. If sampling is unbiased, this in turn

facilitates identification of possible unexpected changes in relative instar abundance, and possible correlation of such abundance changes to potential causes. Overall, it allows better understanding of crab population dynamics.

The approach we present here allows projection of trawlable instar size ranges into the size ranges of larger instars which characterise trap catches. Size ranges of these larger instars are quite broad in absolute size, since they reflect both slow and fast growth rates over an increasing number of instars. With larger instars, many possible instar size ranges potentially exist, and if the model was run without incorporating moult increment data, many functions could be postulated to fit SFDs. Using our model, greater confidence has been achieved in determining likely instar definition.

The utility of being able to assign crab to a probable instar is shown by Jamieson (1996) and Jamieson et al. (1998), which consider mortality rates and fisheries implications in the context of instars.

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## Figure Legends

Fig. 1: The study locations in (A) BC, (B) around Vancouver Island, (C) around Tofino (Clayoquot Sound), and (D) on Roberts and Sturgeon Banks on the Fraser River delta near Vancouver.

Fig. 2. The fit of moult increments to pre-moult carapace widths (CW) for male Dungeness crab using all Clayoquot Sound SFDs. The increment data are from Masset Inlet, Queen Charlottes Islands (Butler 1961) and from Tofino (Smith & Jamieson 1989a).

Fig. 3. The fit of moult increments to pre-moult carapace widths (CW) for female Dungeness crab using all Clayoquot Sound SFDs. The increment data are from Masset Inlet, Queen Charlottes Islands (Butler 1961), from Tofino (Smith & 1989a) and from California (Diamond, 1983).

Fig. 4. The fit of moult increments to pre-moult carapace widths (CW) for male Dungeness crab using all Clayoquot Sound SFDs. The increment data are as in Fig. 1 plus tank reared juveniles.

Fig. 5. All Clayoquot Sound SFD trawl data, with estimated instar (superimposed) and total abundance distributions, using moult increment data in Fig. 2, for male crab caught in the time intervals of A. January-March, B. April-June, C. July-September, and D. October-December. N = sample size;  $\chi^2$  = Chi-square probability.

Fig. 6. All Clayoquot Sound SFD trawl data, with estimated instar (superimposed) and total abundance distributions, using moult increment data in Fig. 4, for male crab caught in the time intervals of A. January-March, B. April-June, C. July-September, and D. October-December. N = sample size;  $\chi^2$  = Chi-square probability.

Fig. 7. All Clayoquot Sound SFD trawl data, with estimated instar (superimposed) and total abundance distributions, using moult increment data in Fig. 3, for female crab caught in the time intervals of A. January-March, B. April-June, C. July-September, and D. October-December. N = sample size;  $\chi^2$  = Chi-square probability.

Fig. 8. All Fraser River delta SFD trawl data, with estimated instar (superimposed) and total abundance distributions, using no moult increment data, for male crab caught in the time intervals of A. January-March, B. April-June, C. July-September, and D. October-December. N = sample size;  $\chi^2$  = Chi-square probability.

Fig. 9. All Fraser River delta SFD trawl data, with estimated instar (superimposed) and total abundance distributions, using moult increment data in Fig. 2, for female crab caught in the time intervals of A. January-March, B. April-June, C. July-September, and D. October-December. N = sample size;  $\chi^2$  = Chi-square probability.

Fig. 10. Plots of post-moult vs. pre-moult size for A. male and B. female Dungeness crab from the studies indicated. Instars are identified as points on the lines.

Fig. 11. The same data for A. male and B. female Dungeness crab as in Fig. 9, with instar number plotted against mean instar size. However, Smith and Jamieson (1989) and Diamond (1983) did not specify instar numbers, since they estimated only larger instar mean sizes, and so their data are excluded. Regressions are not as overlapped as those in Fig. 9 because here, total number of estimated instars, and indirectly, intermoult intervals, are factors. Analyses presented in this study suggest fewer instars are present than do other studies.

## Tables

Table 1. Estimated growth model parameters (see Methods) and the probabilities of a  $>\chi^2$  value (for simultaneous analysis of four Dungeness crabs SFDs grouped by season (winter, spring, summer and fall). Unless indicated by an \*, all size analyses used only field moult increment data; in other cases, moult increment data from cultured crab were added. <sup>1</sup> = not directly comparable with other analyses because number of parameters was different. AIC<sub>c</sub> = Akaike Information Criterion.

Parameters	Clayoquot Sound			Fraser River delta					
	Male		Female	Male				Female	
	12 instars	13 instars*	12 instars	12 instars (no increment data)	11 instars	12 instars	13 instars	12 instars (Tofino model imposed)	12 instars
$\mu_0$	3.3067	5.4127	5.8454	3.9127	0.9683	5.6425	3.4696	3.3065	1.1802
$\beta_0$	3.2140	3.4333	2.9696	2.4946	4.0255	3.0241	3.2108	3.2140	3.6435
$\beta_1$	1.0855	0.9825	1.1277	1.1881	1.1207	1.1173	1.0530	1.0855	1.0740
$\beta_2$	5.17E-03	5.41E-03	5.29E-03	4.14E-03	4.43E-03	3.51E-03	5.29E-03	5.17E-03	5.88E-03
$\beta_3$	-5.12E-05	-4.18E-05	-7.12E-05	-6.64E-05	-4.85E-05	-3.35E-05	-4.95E-05	-5.20E-05	-7.41E-05
$\beta_4$	1.38E-07	9.29E-08	2.20E-07	2.29E-07	1.38E-07	8.24E-08	1.29E-07	1.38E-07	2.27E-07
$\sigma_1$	0.4462	1.6657	1.5800	1.1688	0.0190	1.9863	1.0705	0.4462	1.7166
$\tau_0$	0.8922	0.1584	0.7344	-0.5852	2.7446	-0.7651	1.0411	0.8922	0.9728
$\tau_1$	0.0000	0.1020	-0.0131	0.1399	-0.1294	0.2160	-5.73E-03	0.0000	-1.40E-02
$\tau_2$	2.52E-03	0.0000	5.92E-03	1.60E-03	4.84E-03	-3.06E-03	2.57E-03	2.52E-03	4.89E-03
$\omega$	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
$r$	-1.96E-02	1.45E-03	-0.0803	0.1639	-0.2456	-0.0345	-0.0774	-0.0194	-0.1653
AIC <sub>c</sub>	2444	3049	2119	640	2442	2419	2428	2608	1976
p[ $>\chi^2$ ] Jan-Mar	0.76	0.03	0.09	0.39	0.35	0.17	0.18	0.48	0.32
p[ $>\chi^2$ ] Apr-Jun	0.26	0.53	0.34	0.39	0.00	0.05	0.07	0.10	0.09
p[ $>\chi^2$ ] Jul-Sep	0.67	0.00	0.44	0.54	0.53	0.69	0.54	0.00	0.65
p[ $>\chi^2$ ] Oct-Dec	0.05	0.07	0.20	0.35	0.56	0.33	0.60	0.08	0.54

Table 2. Estimated means ( $\mu_i$ ) and SDs ( $\sigma_i$ ) for carapace widths (CW, mm) for successive instars of Dungeness crabs in Clayoquot Sound. \* = not estimated in the analysis as there were no first instar crab in the SFDs; i.e., it was calculated from the values obtained in instars 2-12.

Instars	Male		Female	
	$\mu_i$	$\sigma_i$	$\mu_i$	$\sigma_i$
1	6.9	0.5	5.8*	
2	10.9	1.1	9.7	1.6
3	15.6	1.5	14.4	2.0
4	21.2	2.1	20.1	2.5
5	28.1	2.7	27.2	3.2
6	36.7	3.5	36.2	4.1
7	47.7	4.7	47.8	5.4
8	61.9	6.1	62.3	6.8
9	80.0	8.0	79.8	8.4
10	102.4	10.0	99.3	8.5
11	128.4	11.9	118.6	9.6
12	156.2	13.0	135.6	8.6

Table 3. Estimated mean instars sizes (mm CW) ( $\mu_i$ ) and SDs ( $\sigma_i$ ) for successive instars of Dungeness crab in the Fraser River delta. \* = analysis with best fit (best AIC<sub>c</sub>).

Instars	Male								Female	
	12 instars* no increment data		11 instars		12 instars		13 instars		12 instars*	
	$\mu_i$	$\sigma_i$	$\mu_i$	$\sigma_i$	$\mu_i$	$\sigma_i$	$\mu_i$	$\sigma_i$	$\mu_i$	$\sigma_i$
1	7.2	1.2	5.1	0.02	9.4	2.0	6.9	1.1	4.8	1.7
2	11.2	1.4	9.9	2.2	13.8	2.3	10.7	1.5	9.1	2.0
3	16.3	1.8	15.5	3.0	19.1	2.7	15.1	2.0	13.8	2.3
4	22.7	2.4	22.3	3.7	25.4	3.3	21.1	2.5	19.4	2.8
5	30.8	3.3	30.6	4.5	33.2	4.1	26.2	3.1	26.2	3.4
6	41.3	4.5	41.3	5.6	42.8	5.2	33.6	3.8	34.6	4.2
7	54.7	6.1	54.8	6.9	54.9	6.6	42.8	4.8	45.1	5.2
8	71.0	8.1	72.0	8.5	70.2	8.5	54.5	6.2	58.1	6.4
9	89.8	10.1	93.4	10.2	89.2	10.7	69.4	7.9	74.0	7.6
10	109.4	11.4	118.4	11.6	112.0	13.1	88.3	10.0	92.1	8.6
11	127.9	11.4	145.6	12.2	138.2	15.1	111.2	12.2	110.9	8.9
12	144.7	10.9			166.2	16.4	137.3	13.9	128.3	8.2
13							165.2	14.9		

Table 4. Maximum-likelihood proportions of total (A) male and (B) female crab abundance in Clayoquot Sound for different instars of each sex, respectively, by sampling period. N = sample size for that time period. Values below instar stage are mean CW (mm) for that instar stage.

**A**

Date	N	1 6.9	2 10.9	3 15.6	4 21.2	5 28.1	6 36.7	7 47.7	8 61.9	9 80.0	10 102.4	11 128.4	12 156.2	$\chi^2$
Jun 85	138	.00	.00	.00	.02	.01	.02	.00	.01	<b>.41</b>	.30	.07	.15	.95
Jul 85	343	.01	.09	.01	.00	.00	.06	.06	.00	.07	<b>.62</b>	.02	.06	.23
Aug 85	204	.00	.00	.00	.01	.00	.00	.18	.06	.07	<b>.56</b>	.06	.05	.22
Sep 85	153	.00	.00	.01	.01	.03	.00	.01	.14	.03	<b>.64</b>	.07	.05	.43
Oct 85	307	.00	.00	.00	.00	.01	.01	.00	.00	.02	<b>.56</b>	.39	.00	.14
Dec 85	171	.00	.00	.00	.01	.01	.03	.10	.00	.03	<b>.41</b>	.40	.02	.58
Jan 86	210	.00	.00	.00	.00	.00	.01	.01	.01	.02	.36	<b>.59</b>	.00	.33
Feb 86	244	.00	.00	.00	.00	.00	.00	.01	.00	.00	.24	<b>.52</b>	.23	.60
Mar 86	563	.00	.00	.00	.00	.00	.00	.00	.00	.00	.08	<b>.83</b>	.08	.23
Apr 86	275	.00	.00	.00	.00	.00	.00	.00	.00	.00	.10	<b>.70</b>	.20	.56
May 86	317	.00	.00	.00	.00	.00	.00	.00	.01	.02	.10	<b>.77</b>	.10	.59
Jun 86	203	.00	.00	.00	.00	.00	.00	.00	.00	.00	.16	<b>.71</b>	.07	.55
Sep 86	112	.00	.00	.00	.00	.01	.02	.12	.14	.04	.06	<b>.31</b>	.30	.76
Jan 87	85	.00	.00	.00	.00	.00	.00	.00	.00	.00	.15	<b>.74</b>	.11	.22
Jul 87	93	.00	.01	<b>.47</b>	.15	.00	.09	.06	.02	.04	.00	.13	.03	.86
Jan 88	45	.00	.00	.00	.00	.00	.02	.00	.18	<b>.74</b>	.06	.00	.00	.64
Apr 88	79	.00	.00	.00	.00	.00	.00	.00	.00	<b>.55</b>	.39	.00	.06	.13
Jun 88	24	.00	.05	<b>.42</b>	.00	.00	.04	.00	.00	.00	.27	.22	.00	.64
Oct 88	125	.06	.13	<b>.19</b>	.10	.00	.00	.00	.10	.13	.00	.17	.12	.14
Nov 88	241	.00	.00	.00	.00	.00	.01	.27	.02	.02	.09	<b>.56</b>	.02	.92
Jan 89	175	.00	.00	.00	.00	.00	.00	.02	.26	.00	.03	<b>.53</b>	.16	.46
Sep 89	177	.00	.00	.04	.12	.26	<b>.40</b>	.01	.05	.05	.01	.07	.00	.62
Jan 90	426	.00	.00	.00	.00	.00	.00	<b>.52</b>	.40	.00	.00	.04	.03	.92
Apr 90	294	.00	.00	.00	.01	.00	.00	.02	<b>.62</b>	.23	.00	.03	.09	.30
Jul 90	461	.00	.00	.00	.00	.00	.16	.06	.00	<b>.37</b>	<b>.37</b>	.00	.04	.02
Nov 90	159	.00	.00	.00	.00	.01	.00	.03	.00	.01	<b>.61</b>	.33	.00	.17
Jan 91	95	.00	.00	.00	.00	.02	.01	.00	.06	.00	.33	<b>.58</b>	.00	.09
Jul 91	127	.00	.00	.00	.00	.02	.08	<b>.29</b>	.03	.06	.08	.25	.19	.45
Jul 92	346	.00	.01	.05	.27	.13	.02	<b>.29</b>	.12	.05	.03	.01	.02	.34
Nov 92	158	.00	.00	.00	.00	.01	.04	<b>.71</b>	.18	.02	.02	.03	.00	.37
Feb 93	82	.00	.00	.00	.00	.00	.00	.01	<b>.86</b>	.11	.00	.02	.00	.79
Apr 93	71	.00	.00	.00	.00	.00	.00	.00	.08	<b>.59</b>	.12	.04	.16	.18
Jul 93	220	.00	.00	.01	.03	.04	.06	<b>.37</b>	.15	.09	.20	.04	.00	.61
Oct 93	95	.00	.00	.00	.00	.00	.00	.01	.14	.19	<b>.38</b>	.24	.04	.89
Feb 95	104	.00	.00	.00	.00	.00	.02	.11	<b>.63</b>	.10	.07	.00	.07	.57
Oct 96	152	.00	.00	.00	.00	.00	.22	<b>.51</b>	.09	.03	.01	.09	.04	.53

**B**

Date	N	1 9.7	2 14.4	3 20.1	4 27.2	5 36.2	6 47.8	7 62.3	8 79.8	9 99.3	10 118.6	11 135.6	$\chi^2$
Jun 85	110	.00	.00	.00	.06	.01	.00	.10	.23	<b>.39</b>	.11	.11	.22
Jul 85	257	.00	.00	.00	.00	.00	.08	.02	.00	<b>.73</b>	.15	.02	.19
Aug 85	217	.00	.00	.00	.00	.00	.07	.13	.02	<b>.74</b>	.01	.03	.32
Sep 85	165	.00	.00	.00	.00	.01	.02	.14	.05	<b>.40</b>	.39	.01	.20
Oct 85	182	.00	.00	.00	.00	.01	.01	.02	.02	.34	<b>.60</b>	.00	.41
Dec 85	125	.00	.00	.00	.00	.01	.02	.01	.03	.30	<b>.63</b>	.00	.86
Jan 86	97	.00	.00	.00	.00	.00	.00	.01	.00	.07	<b>.91</b>	.00	.67
Feb 86	65	.00	.00	.00	.00	.00	.02	.03	.00	.06	<b>.83</b>	.06	.79
Mar 86	58	.00	.00	.00	.00	.02	.01	.00	.00	.00	<b>.98</b>	.00	.52
May 86	78	.00	.00	.00	.00	.00	.00	.00	.01	.00	<b>.96</b>	.03	.34
Jun 86	39	.00	.00	.00	.00	.00	.00	.03	.03	.01	<b>.87</b>	.05	.46
Sep 86	214	.00	.00	.00	.00	.00	.04	.04	.00	.02	.12	<b>.76</b>	.36
Jul 87	119	.00	<b>.32</b>	.18	.00	.08	.04	.00	.06	.00	.01	.29	.54
Apr 88	57	.00	.00	.00	.00	.00	.00	.00	.39	<b>.46</b>	.00	.15	.98
Jun 88	25	.01	<b>.45</b>	.00	.00	.00	.04	.00	.03	.10	.20	.17	.39
Oct 88	167	.12	.13	.09	.00	.00	.00	.00	.20	.05	<b>.39</b>	.00	.34
Nov 88	132	.00	.00	.00	.01	.00	.40	.00	.02	.05	<b>.51</b>	.01	.39
Jan 89	44	.00	.00	.00	.00	.00	.06	<b>.87</b>	.00	.05	.00	.02	.69
Apr 89	75	.00	.00	.00	.00	.01	.00	.10	.03	.00	.12	<b>.74</b>	.52
Sep 89	132	.00	.00	.04	.21	<b>.49</b>	.00	.06	.07	.00	.10	.04	.83
Jan 90	253	.00	.00	.00	.01	.00	<b>.52</b>	.43	.00	.00	.02	.03	.43
Apr 90	207	.00	.00	.00	.00	.01	.09	<b>.53</b>	.25	.01	.05	.07	.38
Jul 90	323	.00	.00	.00	.00	.19	.08	.00	.27	<b>.43</b>	.00	.03	.09
Nov 90	99	.00	.00	.00	.00	.00	.06	.00	.01	.36	<b>.57</b>	.00	.31
Jan 91	50	.00	.00	.00	.03	.01	.00	.00	.00	.29	<b>.65</b>	.01	.58
Jul 91	67	.00	.01	.00	.03	.12	<b>.52</b>	.06	.00	.00	.13	.12	.82
Jul 92	292	.00	.03	.24	.11	.15	<b>.27</b>	.09	.00	.08	.02	.01	.16
Nov 92	103	.00	.00	.00	.00	.08	<b>.60</b>	.24	.00	.05	.03	.00	.44
Feb 93	70	.00	.00	.00	.00	.00	.03	<b>.73</b>	.21	.01	.02	.00	.75
Apr 93	60	.00	.00	.00	.00	.00	.00	.13	<b>.50</b>	.12	.00	.25	.82
Jul 93	237	.00	.00	.00	.04	.04	.29	.21	.03	<b>.33</b>	.02	.04	.85
Oct 93	98	.00	.00	.00	.02	.04	.00	.10	.17	.24	<b>.43</b>	.00	.96
May 94	49	.00	.00	.00	.00	.00	.00	.00	.00	.05	<b>.90</b>	.05	.21
Feb 95	89	.00	.00	.00	.00	.04	.00	<b>.84</b>	.01	.09	.02	.00	.39
Oct 95	46	.00	.00	.00	.00	.08	.17	.00	.00	.04	<b>.70</b>	.00	.73
Oct 96	140	.00	.00	.00	.00	.14	<b>.68</b>	.09	.02	.02	.02	.03	.12

## **Appendices**

Appendix A. Raw SFD data for each crab sampling date.

Appendix B. Plots of each SFD with vertical lines showing the calculated mean sizes of each instar.