

Temperature-dependent growth of the blue crab (*Callinectes sapidus*): a molt process approach

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Abstract: Crustaceans display discrete and biphasic growth as a result of the molting process, so the traditionally used von Bertalanffy growth model does not capture well the phenomena associated with molting-based growth. A molt-process model can predict crustacean growth, including the temperature dependence of intermolt period that can produce the extended overwintering phenomena during which growth ceases. This study parameterized a molt-process model for the blue crab (*Callinectes sapidus*; Portunidae). Crab growth histories were observed for individual crabs held in field enclosures and temperature-controlled, recirculating tanks. A growth-based temperature of torpor (T_{\min}) of 10.8 °C was determined. A mean growth per molt of 119.5% increase in carapace width was observed. The average intermolt period observed was 536 ± 231 degree-days. The predictive ability of these growth parameter estimates was evaluated against growth observed in the field based on data on interannual changes in size frequencies of crabs from a winter dredge survey. The evaluated model was used to explore recruitment timing in warm (1996) and cold (1998) years. A 10% shift in the timing of juvenile crabs becoming available for legal exploitation was predicted from the simulations.

Résumé : À cause du processus de la mue, les crustacés ont une croissance discontinue et biphasique; le modèle classique de croissance de von Bertalanffy ne décrit donc pas bien les phénomènes associés à cette croissance basée sur la mue. Un modèle de processus de la mue peut prédire la croissance des crustacés, y compris la dépendance de la température de la période inter-mue qui peut produire des phénomènes de longs hivernages pendant lesquels toute croissance cesse. Notre étude estime les paramètres d'un modèle de processus de la mue pour le crabe bleu (*Callinectes sapidus*; Portunidae). Le déroulement de la croissance a pu être observé chez des crabes individuels gardés dans des enclos de terrain et dans des aquariums à recirculation de température contrôlée. La température de torpeur (T_{\min}) basée sur la croissance est estimée à 10,8 °C. La croissance moyenne observée par mue comprend une augmentation de 119,5 % de la largeur de la carapace. La durée observée moyenne des inter-mues est de 536 ± 231 degrés-jours. Nous avons évalué le pouvoir de prédiction de ces paramètres de croissance estimés par une comparaison avec la croissance en nature d'après les changements inter-annuels des fréquences des tailles de crabes dans un inventaire d'hiver à la benne. Nous avons utilisé le modèle à évaluer pour examiner la chronologie du recrutement dans une année chaude (1996) et une froide (1998). Les simulations prédisent un décalage de 10 % dans le moment où les jeunes crabes deviennent disponibles pour la récolte légale.

[Traduit par la Rédaction]

Introduction

The patterns and consequences of plant and animal growth have fascinated ecologists for more than a century (Thompson 1968). Researchers have sought to understand the consequences of differences in allocation of energy to growth among species and individuals. Such questions are at the heart of life history theory (Roff 1992). Development of much of this theory requires an accurate and quantitative description of growth. One of the most flexible and com-

monly used descriptions of growth is that of von Bertalanffy (1938).

A principal assumption of the von Bertalanffy model is that growth is continuous. However, crustaceans do not exhibit continuous growth; rather, in these animals, growth is discrete and biphasic. Their rigid exoskeleton limits external growth to the brief molting events (Hartnoll 1982). The saltatory nature of crustacean growth implies that the von Bertalanffy model is likely inadequate for defining crustacean growth dynamics. However, the biphasic nature of crustacean growth can be used as a foundation to develop a more appropriate model of crustacean growth. A saltatory growth pattern can be modeled by combining predictions of the amount of growth per molt (GPM) with estimates of the frequency of molting (the inverse of the intermolt period (IMP)) (Hiatt 1948). Such approaches are termed molt-process models (Smith 1997).

Molt-process models have been created for several crustaceans, including Alaskan king crab (*Paralithodes camtschatica*), American lobster (*Homarus americanus*), and Dungeness crab (*Cancer magister*) (McCaughan and Powel 1977; Fogarty and Idoine 1988; Wainwright and Armstrong 1993).

Received 15 March 2005. Accepted 23 November 2005.
Published on the NRC Research Press Web site at
<http://cjfas.nrc.ca> on 6 May 2006.
J18603

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The previous models estimated IMP in days, based on molting-frequency estimates. For these instances, molting is infrequent (per year or longer). However, modeling IMP as a function of time alone ignores potential environmental influences on IMP. Temperature is one example of a factor that has a well-documented effect on IMP in crustaceans (Leffler 1972; Wainwright and Armstrong 1993). For example, in some temperate-climate crustaceans, growth ceases during the cold weather months because of the inhibitory effects of cold water (*Callinectes sapidus*; Leffler 1972; Ju et al. 2001). Thus, any growth-modeling framework for crustaceans must be sufficiently flexible to include temperature-dependent variation in intermolt period if it is to accommodate the diversity of growth patterns exhibited.

Smith (1997) developed a crustacean molt-process model that is flexible enough to include both overwintering and other temperature-dependent growth phenomena. In Smith's model, GPM is assumed to be a relatively constant proportion of the premolt size. However, Smith expressed IMP in physiological time, via a degree-day function, instead of in chronological time, as used in previous models.

The use of the degree-day approach permits the effects of time and temperature to be expressed simultaneously. Degree-days are calculated by multiplying the difference between the ambient temperature and a physiological minimum for growth (T_{\min}) by the duration over which the temperature was experienced (days). Importantly, when the temperatures are below T_{\min} , no degree-days are accumulated and the IMP becomes infinitely long, thereby inherently incorporating the phenomena of diapause. Smith's model accounts for variability in intermolt period by recognizing that accumulation of sufficient degree-day exposure is a necessary, but not sufficient, condition for molting. The probability of molting is determined by an exponential error function, shifted to account for the molting threshold. To parameterize the molt-process model, three parameters must be estimated: GPM, the minimum IMP (the minimum degree-days required for molting), and T_{\min} (temperature of torpor, i.e., the lower temperature constraint below which all growth ceases). To gather the estimates of GPM and IMP, successive molts of individual animals must be observed, in either field or laboratory studies, under known physiological conditions.

Here we develop a molt-process model of the blue crab (*Callinectes sapidus*). Blue crab is distributed widely from Brazil to New England (Norse 1977). In the tropical and subtropical areas of this range, blue crab completes its life cycle within 1 year. However, from midlatitudes (~30°N), winter temperatures become sufficiently low that blue crab overwinter and thus require a minimum of 18 months to complete their life cycle (Hill et al. 1989). Throughout most of its range, blue crab supports important commercial fisheries. With recent concerns over declines in landings, there has been an increased interest in developing accurate growth models for blue crab as an aid to stock assessments (Miller and Smith 2003). There have been previously published studies on the growth of the blue crab (Tagatz 1968; Leffler 1972; Guerin and Stickle 1997). Yet, despite this earlier work, we lack data to develop the generic model of the type proposed by Smith to predict growth in blue crab.

Here, we report the results of controlled laboratory experiments conducted to provide preliminary estimates of T_{\min} ,

GPM, and IMP for the blue crab. The growth of individual crabs of a range of sizes was monitored at four temperatures. Subsequently, field-enclosure experiments were conducted to test predictions of a molt-process growth model developed from the laboratory estimates. Additionally, the model was evaluated by comparing growth predicted by the model with growth observed in the field based on data on interannual changes in size frequencies of crabs from 1990 to 1997 from a winter dredge survey (Sharov et al. 2003). As an example of the model's utility, it is used to quantify the effect of interannual temperature variation on the dynamics of crab cohort recruitment to the commercial fishery.

Materials and methods

Growth studies

Laboratory study

We conducted a three-way factorial experiment, with three size classes of crabs of both sexes and four levels of temperature, to provide data to estimate model parameters. All experimental work was conducted at the Chesapeake Biological Laboratory (CBL, Solomons, Maryland) in 1999 and 2000. Crabs used in experiments were captured by dip-netting tidally migrating animals from the CBL pier located near the mouth of the Patuxent River, Maryland. Subsequently, crabs were held in an 2-m-diameter, outdoor, flow-through tank while they were trained onto artificial food (¼-inch trout chow pellets; Zeigler Brothers, Gardners, Pennsylvania) before use in the experiment.

Crabs with no missing limbs were separated by sex and carapace width (CW) into three size classes (small, <3.8 cm; medium, 3.8–5.1 cm; large, >5.1 cm). CW was measured at the base of the lateral spines. To begin the experiment, 40 individual crabs per tank were randomly assigned to one of 32 cylindrical chambers (17.8-cm-diameter cylinders) or one of eight rectangular enclosures (30.5 cm × 61 cm) within one of three 1.2 m × 2.4 m × 0.4 m temperature-controlled tanks. Each chamber and enclosure received an individual flow of temperature-controlled water and will be considered an independent experimental unit. Only large crabs were placed in the rectangular enclosures. Because of space constraints, only three of the four necessary temperatures could be run concurrently. Thus, two experimental trials were necessary to gather sufficient data. In 1999, a trial using 16, 20, and 24 °C temperature treatments was conducted. In 2000, a second trial, using 16, 20, and 28 °C temperature treatments, was performed. The two lower temperature trials were run in both trials to increase the amount of molt data collected from the slower molting crabs held at the colder temperature treatments.

During the course of the experiment, crabs were fed ad libitum every other day with the artificial pelletized food. There was always uneaten food present in the enclosure. Tanks were regularly siphoned to remove uneaten food and fecal matter. Every other day, 50% water changes were performed in the recirculating systems to prevent buildup of nitrogenous wastes and other exogenous compounds that may affect the molting patterns of the crabs. Replacement water was heated or chilled to the desired water temperature before addition. The amount of water added and the temper-

ature of the source water were controlled so that the tank total temperature did not change by more than 2 °C.

Each crab was checked twice daily on weekdays and once per day on weekends for signs of molting or death. The presence of shell remains or a crab with an incompletely hardened new shell was used to determine a molt. After the new shell of a molted crab had hardened significantly (~48 h after observation of molt), the new CW was measured. Dead crabs were removed and replaced with animals of the same size class from the outdoor holding tank when possible. Crab mortality was highest within the first week of placement in the experimental setup. This was most likely caused by a portion of the animals refusing to eat the pelletized food. Later in the experimental trials, because of the advanced season, we were unable to procure the smaller size classes of crabs for replacement. When the abundance of crabs in the tanks was reduced to approximately 10% of capacity with no available replacement crabs, the trial was ended. This experimental plan yielded a 1999 trial of 182 days and a 2000 trial of 154 days.

Records of CW changes were processed to isolate individuals exhibiting single and multiple molts to determine the growth per molt (GPM; as a percentage of premolt CW). GPM was estimated by dividing the postmolt CW by the premolt carapace size and multiplying by 100 to get the percentage increase in crab size. Intermolt period (IMP) estimates were derived from information on both temperature exposure and number of days between observed molting events, based only on those crabs that had molted at least twice in an experiment.

T_{\min} was estimated using the Curry and Feldman (1987) back-calculation method based on chronological IMP and temperature data. The inverses of the chronological IMP estimates for each temperature were plotted against the temperature treatment. A simple linear regression was performed to estimate the intersection of the function with the x axis to estimate the T_{\min} value.

The individual chronological IMP estimates were expressed as physiological time using the estimated T_{\min} . Because the temperature was held constant, IMPs were estimated as

$$(1) \quad \text{IMP}_{\text{degree-day}} = (\text{temperature} - T_{\min})\text{IMP}_{\text{days}}$$

All statistical analyses were conducted using SAS (version 8.12; SAS Institute Inc. 2001). Although the experiment was designed as a three-way factorial, inspection of the data collected in the experiment revealed overlaps in the sizes of animals in the different groups, particularly for animals tracked for multiple molts. Accordingly, the experiment was analyzed as a two-way factorial experiment using analysis of covariance (ANCOVA) to test for significant effects of temperature and sex, with initial size as a covariate.

Field-enclosure study

The results of the laboratory experiments described above were compared with data from an independent field-enclosure experiment conducted during the summer of 1997. Crabs were captured and held before the experiment in a flow-through indoor tank and fed frozen menhaden (*Brevoortia tyrannus*) and eel (*Anguilla rostrata*). After sufficient animals were collected for the trial, the crabs were separated into three size and two sex classes. The animals were

then randomly assigned to one of three chambers within a 168 cm × 38 cm × 38 cm mesh enclosure. For the animals in the enclosures, the mesh was assumed to be sufficiently large to permit prey to enter, providing food. Ten enclosures, which could house a total of 30 crabs at any time, were deployed. The enclosures were tethered to the CBL pier in 3–5 m of water. The animals were checked weekly and measured to determine if they had molted in the previous week. Any animals that died during the trial were replaced with the same size class from the holding tank. Water temperature was recorded daily to convert chronological to physiological time.

IMP and GPM were estimated and tested as in the laboratory trials, without the tests associated with the differences among the experimental temperatures. As a result of the fluctuating temperature in the field, IMP was calculated as

$$(2) \quad \text{IMP}_{\text{degree-day}} = \sum_{\text{IMP}} \text{daily temperature} - T_{\min}$$

where T_{\min} is that estimated from the laboratory data. The IMP and GPM estimates from the field were compared with the laboratory estimates using analysis of variance (ANOVA).

Molt-process framework

Using the temperature-dependent growth parameters derived from our field and laboratory studies, we developed an individual-based molt-process model of crab growth that followed the growth of a cohort of up to 1000 individual crabs. The model predicts the growth of individual crabs using a daily time step. The individual predictions are then combined to predict the growth of the cohort. The model predicts an individual's growth using two submodels, intermolt period (IMP) and growth per molt (GPM), that in combination simulate the biphasic molting cycle of the blue crab. The IMP submodel predicts the time between molt events probabilistically, depending on the amount of physiological time elapsed since the last molt, which is tracked via a degree-day (DD) pool. The DD pool increases dependent on the daily water temperature and an estimate of the temperature of torpor (T_{\min}). The DD pool is used with a cumulative molting probability density function (CMPDF) to determine the percent chance of a crab molting on that day. The CMPDF was estimated by a maximum likelihood technique from the observed proportion molting. Multiple CMPDF forms were fitted using the available data, and a logarithmic form was determined to be the most appropriate (eq. 3). The CMPDF is given by

$$(3) \quad \text{Probability of molting} = A \log_e(\text{DD}_{\text{accumulated}}) - B$$

where A and B are the coefficients of the logarithmic model (values are given in Results). This molting probability is compared with a random number to determine if the crab should experience molt on the simulated day. This technique creates a soft-molt threshold that is reflective of the variation in intermolt periods observed in the growth studies.

When the IMP submodel determines that a molt event should occur, the GPM submodel is activated. The GPM submodel increases the crab's CW by a fixed amount, based on our laboratory and field data, and also resets the accumulated DD pool to zero. Zeroing the DD pool prevents additional molting activity until the pool has accumulated enough

Table 1. Number of observations, growth per molt (GPM) mean, chronological intermolt period (IMP), and range for each experimental temperature and sex class from a laboratory study of the growth of *Callinectes sapidus*.

Class	GPM observations	IMP observations	Mean GPM	Minimum GPM	Maximum GPM
Temperature (°C)					
16	27	1	118.1±8.7	104.44	139.8
20	50	6	121.4±6.9	105.06	141.8
24	40	17	116.1±6.3	106.43	137.8
28	30	12	121.8±6.9	101.1	141.0
Sex					
Female	79	21	120.0±8.1	105.06	141.8
Male	68	15	118.7±6.6	104.44	135.5
Overall	147	36	119.5±7.4	104.44	141.8

physiological time to increase the molting probability sufficiently.

Simulations

We used the model in a series of three different simulations.

Performance simulations

We performed simple simulations designed to explore the model's ability to predict the patterns of growth observed in the field. To explore the model's reaction to temperature extremes and to determine if overwintering was being predicted, 100-day simulations were run with constant high (25 °C) and low (9 °C) temperature histories. To examine the reaction of the model to varying temperature conditions, a hypothetical 365-day cycle of temperatures between 6 °C and 25 °C was simulated. In all simulations, a cohort of 10 crabs was used.

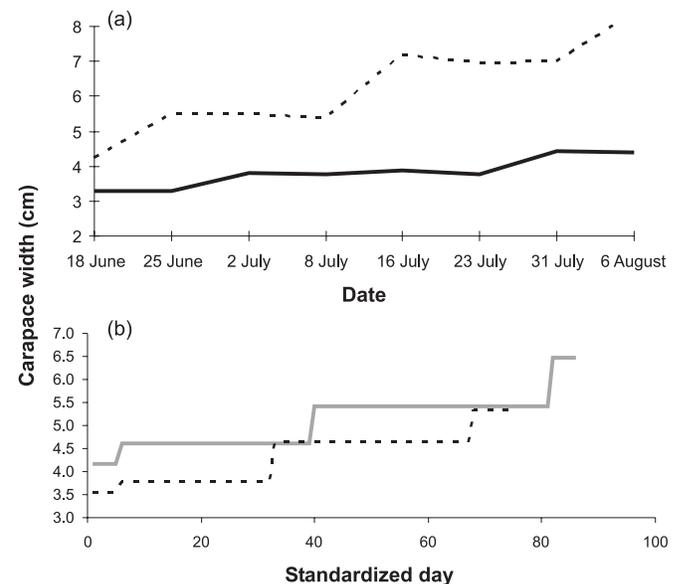
Simulations of Chesapeake Bay crab growth (1990–1997)

We conducted simulations to predict the growth of cohorts of blue crabs in Chesapeake Bay. We used the size distribution of crabs <65 mm CW observed during winter as an initial description of the size distribution in a cohort comprised of 1000 crabs. The initial size distribution was derived from the data for a particular year from a winter dredge survey that has been conducted in the Chesapeake Bay since the winter of 1989–1990 (Sharov et al. 2003). The model was used to simulate the growth of the cohort, assuming no mortality, over the next 365 days using Chesapeake Bay water temperatures recorded for the modeled year at the Virginia Institute of Marine Science (VIMS) Ferry Pier (Gloucester Point, Virginia). The predicted size distributions were compared with the observed size distributions of crabs >65 mm observed in the winter dredge survey in the following year. Simulations of growth during 1991–1997 were conducted to compare the performance of the molt-process model against population-level data.

Fishery recruitment simulations

We conducted simulations to explore the impact of variations in seasonal temperature patterns on recruitment of crabs to the hard pot fishery. Simulations were run using starting distributions of 100 crabs with a mean CW of 30 mm. The temperature history came from the 1996 (cold) and 1998

Fig. 1. Sample growth trajectories for two individual crabs from (a) field- and (b) laboratory-raised *Callinectes sapidus*.



(warm) VIMS Ferry Pier data. The output growth predictions were examined on a monthly basis to determine the partial recruitment vector. The partial recruitment vector was estimated by determining the proportion of the cohort that had attained legal size (127 mm CW) for the hard pot fishery.

Results

Laboratory experiment and field-enclosure study

Our laboratory experiment yielded 147 estimates of GPM and 36 estimates of IMP (Table 1). The GPM observations outnumber the IMP observations, as IMP estimates require sequential molts that not every experimental crab provided. Sample growth trajectories of individual crabs are shown (Fig. 1b). All observations of IMP and GPM, including repeated molts of the same animal, were used in the model parameterization and treated as independent observations in order to maximize the quantity and scope of the data. We believe that the inclusion of all data collected increases the universality of the parameter estimates as the additional

Table 2. Analysis of covariance (ANCOVA; SAS PROC Mixed; SAS Institute Inc. 2001) results for laboratory growth per molt (GPM) observations for *Callinectes sapidus*.

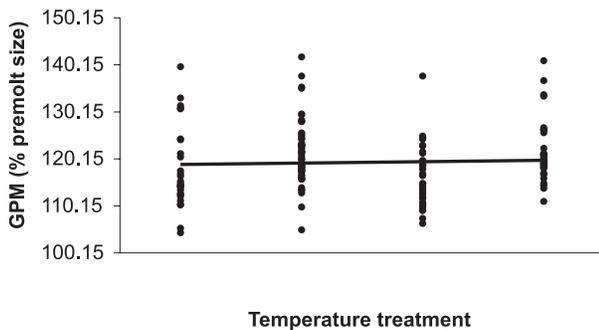
Effect	NDF	DDF	F	Probability
Sex	1	141	2.13	0.1467
Temperature	3	141	5.26	0.0018
Size (covariate)	1	141	4.19	0.0426

Note: NDF, numerator degrees of freedom; DDF, denominator degrees of freedom.

Table 3. Regression output (SAS PROC REG; SAS Institute Inc. 2001) for laboratory growth per molt (GPM) estimates as a function of temperature and *Callinectes sapidus* premolt carapace width (CW). The reported probability is for a test that the parameter = 0.

Parameter	Estimate	T	Probability
Intercept	0.142	3.74	0.0003
Temperature	-0.000113	-0.07	0.9430
Premolt CW	0.0287	2.11	0.0370

Fig. 2. *Callinectes sapidus* laboratory growth per molt (GPM) as a function of temperature treatment.



observations incorporate more sources of variability beyond the control of the experiment.

We observed molting in crabs from 2.9 to 8.5 cm CW. GPM data was highly variable. The lowest observed GPM was a 104.4% increase in CW for a 3.3 cm male crab held at 24 °C. The largest GPM was 141.8% for a 4.98 cm female crab held at 20 °C. The average GPM for the laboratory-reared crabs was 119.4% ± 7.5% (±1 standard deviation, SD) of the premolt CW. GPM estimates were normally distributed (Kolmogorov–Smirnov test, $F_{[147]} = 0.87, p = 0.09$). Average growth per molt varied among temperatures from 118.0% to 121.7% and among sexes by 118.7% to 120% (Table 1). ANCOVA analysis with sex and temperature as factors and initial size as a covariate indicated no significant difference with sex, but significant differences with initial size and temperature (Table 2). A multiple regression was performed to determine the extent of the effect of size and temperature on GPM. The slope of GPM with respect to temperature was nonsignificant (Table 3; Fig. 2). However, the GPM slope as a function of premolt CW was significantly different from zero (Table 3; Fig. 3). This result violates the molt-process model’s assumption that GPM is completely invariant. Because

Fig. 3. *Callinectes sapidus* laboratory growth per molt (GPM) as a function of premolt carapace width.

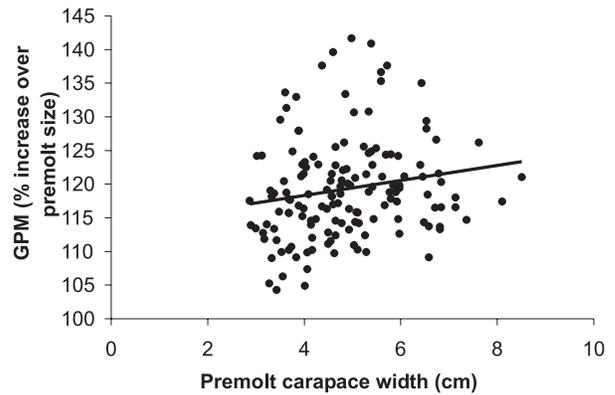
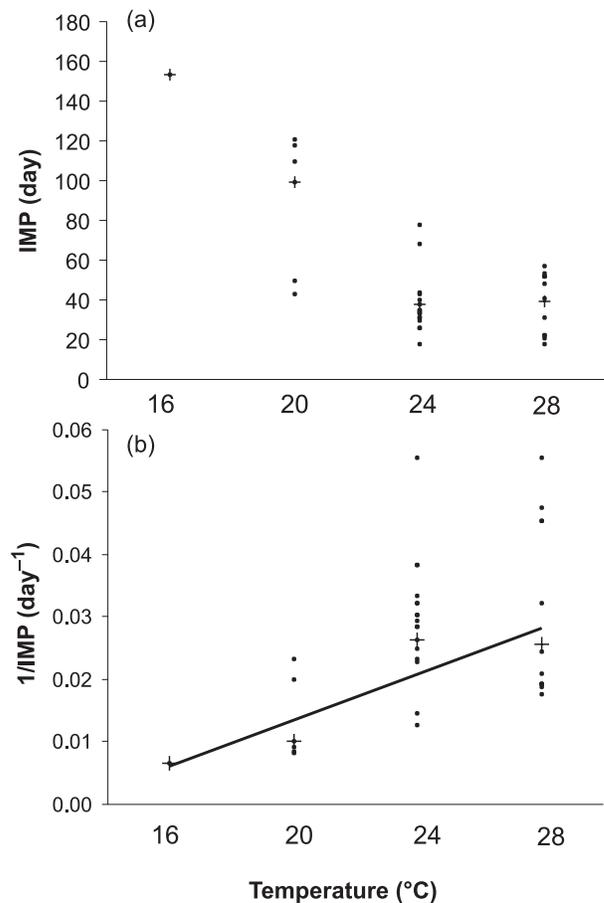
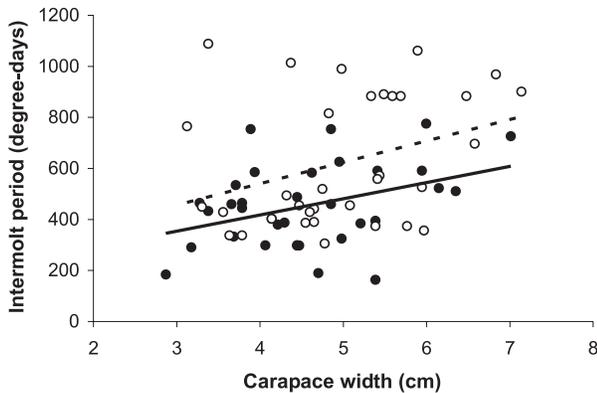


Fig. 4. *Callinectes sapidus* (a) intermolt period (IMP) and (b) inverse intermolt period (1/IMP) as a function of temperature. Regression relationship for the inverse intermolt period (b) is $IMP^{-1} = 0.00194 \times \text{temperature} - 0.02097$. The intercept of the regression line of the inverse intermolt period is the T_{min} . Mean values are represented by + signs.



the slope of the temperature – GPM relationship is minimal and not significant in the field results detailed below, we decided to accept Smith’s (1997) assumption of invariability for this model application.

Fig. 5. *Callinectes sapidus* intermolt period as a function of premolt carapace width for field-raised (solid circles) and laboratory-raised (open circles) animals. The regression lines (field, solid line; laboratory, broken line) show the expected relationship indicating longer intermolt period (IMP) durations at larger sizes; however, they are nonsignificant.



Intermolt period was significantly related to temperature (Fig. 4a); IMP decreased as temperature increased. The inverse of IMP was positively related to temperature (Fig. 4b). Extrapolation to the temperature intercept of the least squares regression fit to these data provides an estimate of T_{\min} of 10.8 ± 0.015 °C (mean \pm standard error, SE). This value was used to convert the chronological intermolt period observations into estimates of the physiological IMP. Because of a lack of data in the lower temperature trials, this T_{\min} estimate may be biased, imparting error to the physiological IMP conversion. However, it is very close to Smith's (1997) original literature-based estimate and was assumed to be adequate for this initial parameterization of the molt-process model.

We observed chronological intermolt periods ranging between 18 days in the 28 °C crabs and 153 days in the 16 °C crabs. The mean physiological IMP in the laboratory experiments was 610 ± 259 degree-days. The lab-reared animals showed a significant difference in estimated physiological IMPs among temperature treatments. ANCOVA analysis indicated that sex and initial size did not significantly affect IMP (Table 5). Although the effect of size on physiological IMP was not significant, the IMP estimates appear to increase with increasing premolt size (Table 5; Fig. 5).

The average GPM of field-raised crabs was $122.4\% \pm 7.6\%$, similar to estimates of laboratory animals. GPM did not vary significantly with sex or with initial size in the field trials (Table 4). The average IMP for field animals was 428 ± 121 degree-days. The field and lab IMP estimates are not significantly different from each other (Table 5). The field-raised animals showed no significant IMP differences among the different sizes or sexes of animals (Table 5). IMP does appear to increase at increasing premolt size (Fig. 5). GPM estimates over both lab and field varied from 104.4% to 159.7%.

The final model parameters were derived from the combined field and laboratory growth data. A combined estimate of GPM = 119.5% and $T_{\min} = 10.8$ °C was used in all simulation trials. The IMP estimates were used to derive the

Table 4. Analysis of covariance (ANCOVA) results on growth per molt (GPM) estimates of the field-enclosure-held *Callinectes sapidus*.

Effect	NDF	DDF	F	Probability
Sex	1	63	0.05	0.8167
Initial size	1	63	0.08	0.7775

Note: NDF, numerator degrees of freedom; DDF, denominator degrees of freedom.

accumulated degree-days since the last molt event for the individual crabs. These individual estimates were used to calculate the CMPDF from the proportion of the population molting as a function of accumulated degree-days (Fig. 6).

Performance simulations

The constant high and low simulations produced the expected growth parameters. The constant 9 °C temperature input resulted in no molting activity, as if the crab was overwintering. The constant 24 °C temperature simulation produced multiple molting events with slightly different intermolt period lengths between each molt. The simulation of the hypothetical temperature cycle resulted in the expected model predictions. The intermolt periods shortened at higher temperatures and were longer at the lower simulated temperatures. Molting activity also ceased completely at the lower simulated "winter" temperatures and resumed once the water had warmed in the simulated "spring". The molt-process model appears to be able to predict the crab-specific growth phenomena.

Simulations of Chesapeake Bay crab growth (1990–1997)

The Chesapeake Bay crab growth simulations produced output distributions, the means of which were compared with the winter dredge survey (WDS) data for crabs >65 mm CW in the following year (Fig. 7). Both observed and predicted size distributions were approximately normal in all years simulated. In five out of seven cases, the model underestimated the mean CW of crabs after 1 year of growth (Table 6). The extent of the underestimation ranged from 15 mm to 41.3 mm CW (~15%–45% of the observed final size). In two cases, the model overestimated the observed size (Table 6). In these cases, the overestimation was relatively small (2.6 mm and 6.5 mm CW). For all 7 years simulated, the model, on average, underestimated the mean observed CW by 19.3 mm. In contrast, the standard deviations of all the predicted final size distributions were larger than the standard deviations observed in the WDS (Table 6).

Fishery recruitment simulations

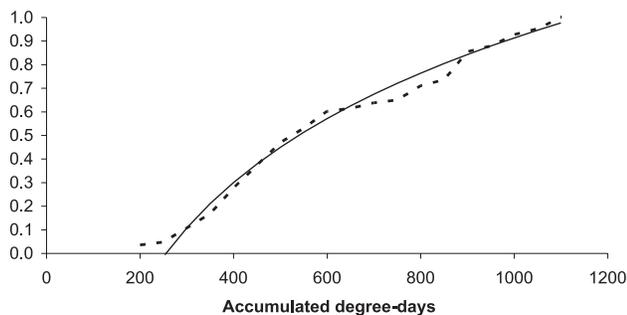
The molt-process model was used to simulate the effects of warm and cold years to explore the effects of temperature on crabs recruiting to the fishery. The two years chosen differed by 2.1 °C in mean yearly temperature. The monthly predicted percentage of crabs entering the fishery was affected by the temperature history (Fig. 8). There was no apparent difference in the timing of initial recruitment to the fishery. For both warm and cool years, crabs recruited to the fishery in August. However, in subsequent months, the partial

Table 5. Analysis of variance (ANOVA) and analysis of covariance (ANCOVA) results for tests on the observed chronological intermolt period (IMP) estimates of *Callinectes sapidus* observed in the laboratory and field.

Experiment	Effect	NDF	DDF	F	Probability
Laboratory	Sex	1	30	1.14	0.295
	Temperature	3	30	35.79	0.001
	Initial size	1	30	3.05	0.091
Field	Sex	1	31	0	0.975
	Initial size	1	31	2.92	0.974
Both	Between trials	1	67	2.83	0.097

Note: NDF, numerator degrees of freedom; DDF, denominator degrees of freedom.

Fig. 6. Proportion of the experimental *Callinectes sapidus* molting (broken line) and the estimated logarithmic cumulative molting probability density function (CMPDF; probability of molting = $0.669 \log_e(\text{DD}_{\text{accumulated}}) - 3.71$; solid line), as a function of degree-days (DD) accumulated since the previous molt event.



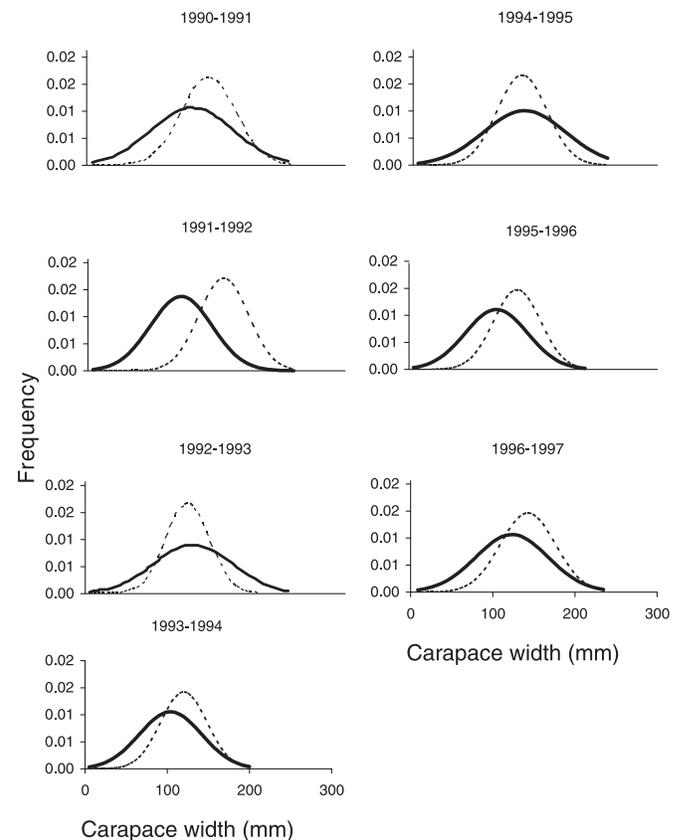
recruitment vector was on average 10% higher in any given month in the warm year than in the cool year.

Discussion

In this work, we attempted to parameterize and employ a molt-process model based on blue crab growth studies. Based on 213 molts observed under both laboratory and field conditions, the average growth per molt was estimated to increase by $119.5\% \pm 7.5\%$ of premolt size. T_{\min} was determined to be $10.8\text{ }^{\circ}\text{C}$, using the back-calculation technique described by Curry and Feldman (1987). An average intermolt period of 536 ± 231 degree-days was estimated from 69 observations of multiple molts under laboratory and field conditions.

The previous parameterization of the Smith (1997) molt-process model used meta-analysis to estimate the model parameters. There are several published experimental studies of growth in blue crab, but information on all parameters required for the molt-process model is limited. Some studies, such as Gray and Newcombe (1938), provided incomplete data required to parameterize the molt-process model. Gray and Newcombe (1938) estimated GPM to be 125%–133%; however, they did not quantify IMP or T_{\min} . Other estimates of GPM include 122% and 120.9% (Leffler (1972) and Fitz and Wiegert (1991), respectively). Our estimate of $119.5\% \pm 7.5\%$ is comparable to previous estimates. Additionally, the variation observed in our GPM estimates is similar to that seen in previous studies. Both Leffler (1972) and Tagatz (1968) reported highly variable GPM values, ranging between

Fig. 7. 1990–1997 output distributions from Chesapeake Bay *Callinectes sapidus* growth simulation trials: model predictions (solid line) and observed distributions from the censored Virginia Institute of Marine Science winter dredge survey data (broken line).



113%–139% (aggregated by temperature rearing conditions) and 107.5%–150%, respectively. However, Tagatz (1968) reported sex-specific differences in GPM for blue crab and a size-dependent effect for GPM in male blue crab, neither of which was observed in our study.

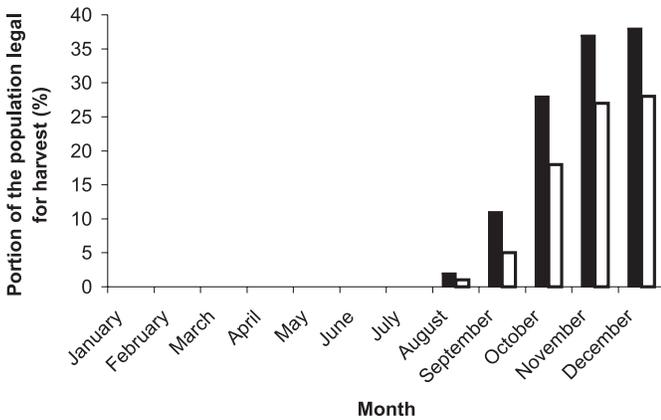
In decapods, as with all animals that molt, GPM is limited primarily by the ability of the new cuticle, formed under the old shell, to expand during ecdysis (Cheng and Chang 1994). Salinity, nutrition, limb or eyestalk ablation, and container effects have been found to alter GPM (Hartnoll 1982; Smith 1990; Cheng and Chang 1993). These factors create physiological stress that can limit the ability of the crab to inflate the new cuticle. For example, if a crab is being fed an insuf-

Table 6. Simulations of Chesapeake Bay *Callinectes sapidus* growth (1990–1997).

	Initial observed		Final observed		Predicted		Difference
	Mean	SD	Mean	SD	Mean	SD	
1990–1991	26.2	11.3	118.0	26.0	102.3	39.8	15.7
1991–1992	28.7	10.2	132.0	24.0	90.7	27.9	41.3
1992–1993	34.3	12.8	118.0	24.9	124.5	45.6	–6.5
1993–1994	29.3	12.0	120.1	28.1	104.0	37.9	16.1
1994–1995	29.8	12.7	112.0	25.5	114.6	42.2	–2.6
1995–1996	29.34	11.2	122.8	26.57	99.3	35.4	23.5
1996–1997	27.7	11.2	119.4	24.8	89.8	34.0	29.6
Sum							117.1

Note: Initial observed data are the mean and standard deviation (SD) of the initial size distribution developed from the Virginia Institute of Marine Science winter dredge survey (WDS) data for the first year of the simulation. Final observed data are the mean and standard deviation of the initial size distribution developed from the WDS data for the second year of the simulation. Statistics provided are the difference between the final observed and predicted mean carapace widths.

Fig. 8. Predicted monthly percentages of a *Callinectes sapidus* population available for legal harvest (carapace width (CW) > 127 mm) outputted from warm (solid bars) and cold (open bars) year simulations.



efficient diet or has multiple limbs to regenerate, it will not be able to devote as much energy to postmolt cuticle inflation as an unstressed crab. Thus, the similarities between the estimates of GPM likely reflect geometric constraints imposed by molting. The subtle difference between our GPM estimate results and those of the previously published studies is most likely a factor of the differing rearing conditions among the studies, combined with the natural variation in GPM between individuals.

A few estimates of T_{min} or IMP are reported in the literature. Van Engel (1958) estimated that growth ceased at 15 °C and true physiological torpor (subhibernation) occurred at 5 °C. However, these T_{min} estimates were based on physiological experiments and thus may not have a direct bearing on a minimum temperature for growth. Smith used previous estimates of IMP in a meta-analysis to generate estimates of T_{min} and IMP (Tagatz 1968; Leffler 1972; Cadman and Weinstein 1988). Smith (1997) estimated T_{min} to be 9.8 °C. The subsequent physiological IMP was 346.7–516.7 degree-days.

Variability in IMP can be due to forcing factors, other than temperature, imparted by the rearing conditions. Factors such as salinity, diet, and limb loss can significantly af-

fect the molting process in crabs (Skinner and Graham 1972; Winget et al. 1976; Guerin and Stickle 1997). Variations between rearing conditions combined with behavioral effects may explain the differences in IMP estimates between the field and laboratory portions of our study and the previously published data. In addition to direct physiological effects, such as would be created by food limitation, indirect behavioral effects such as molt cycle variations resulting from the concentrated odor of other potentially cannibalistic crabs in the recirculating system may impart bias to the IMP estimates (Moksnes et al. 1997). Because we attempted to mediate these potentially confounding variables, we assume that they are not fatally biasing the parameter estimates for this application of the molt-process model.

The variation between the meta-analysis-derived parameters and ours can also be due to the inherent error imparted by combining multiple studies. The method of measurement of blue crab growth varies greatly among the published studies. For example, the measurement of crab size is reported as either a distance between the lateral spines or as measured at the base of the lateral spines. Equally, the different studies did not raise the animals in similar conditions; thus, container or feeding effects may skew the estimated growth parameters. Moreover, experimental animals were acclimated to different experimental environments that could have affected the growth of the animal. Additionally, the crabs used in the many growth studies were from multiple sources. Accordingly, population-specific differences cannot be ruled out. Previous studies used animals captured in Florida, Louisiana, and southern Virginia and yielded progressively larger T_{min} estimates with increasing latitude. Though the parameter estimates determined in this study may not fully reflect the growth dynamics of crabs in the field, they are rigorous enough to parameterize a preliminary molt-process model.

Our model was used to predict the growth of individual crabs and cohorts. The model is able to account for the crab-specific phenomena of discrete temperature-dependent growth and overwintering lacking in the currently used von Bertalanffy growth models. In the evaluation trials, observed and model-predicted increases in mean CW over one year differed by an average of 19.3 mm CW. This represents a sizeable error (~20%), suggesting that factors important to determining the observed distribution of crabs in the wild

may have been left out. The deviations between the predicted and observed distributions in the Chesapeake Bay crab growth simulations most likely have three causes: inappropriateness of the temperature history inputs, error in censoring the WDS data, and error in parameterization of the model.

The temperature field used in the model may be an important source of the discrepancies between observed and predicted annual growth. As the temperature history drives the model through additions to the DD pool, it can drastically affect the output of the simulation. Crabs sampled in WDS have been living in a variety of temperature habitats, so there is no single best temperature for modeling. However, for practical reasons, we employed a temperature history in the model from a single geographic location, the VIMS Ferry Pier. This data set was chosen because it was complete for all simulation years and had daily temperature observations with very few missing data points. Though the data set was appropriate for evaluating in the molt-process model, it may lead to some of the deviation. Differences among the temperatures observed at one limited geographic location and the range of temperatures observed throughout the Chesapeake Bay will introduce error in the estimated output. We suggest that interannual differences in the degree of the mismatch in temperatures between the data used in the model and the temperature history of the bulk of the sampled crabs could be responsible for the variations observed in the degree of fit of observed and predicted size distributions.

A second possible source of error in the model simulations comes from the censoring technique used in the trials. We assumed that crabs under 65 mm CW were juveniles of the previous year and used their WDS distribution to provide the starting cohort for the simulation. We used the following year's size distribution of crabs over 65 mm CW as our basis for comparison. Our logic was that juvenile (<65 mm CW) crabs collected in the winter of one year would grow over the following year to be collected as immature and adult (>65 mm CW) crabs using the temperature history for the year of collection. The 65 mm CW cutoff was chosen because it fell at the minima between the two peaks of the bimodally distributed frequency data (Sharov et al. 2003). If this separation of the size distribution does not accurately reflect cohort dynamics, then the observed size distribution against which we compared our predictions may be biased.

A final source of error could be due to the incorrect parameterization of the model. An error in the estimation of any of the parameters could cause the deviation observed in the simulation runs. Though the experiments in this study were specifically designed to develop generalized and accurate parameter estimates, the data are limited in scope and robustness. By limiting the rearing conditions in order to isolate the effects of temperature, the dynamics of other important factors were not examined. This forced us to make assumptions, such as the invariability of GPM, that may bias the model's results. By excluding these more complex dynamics, we were forced to sacrifice some realism to create a simple model that could be widely applied. Future studies could be developed to provide the additional information necessary to include these dynamics.

A parameterization error may also be created by our inclusion of all the data collected in the experiments in the analysis and model parameterization. To maximize the scope

and quantity of the data available, all observations were included in the parameter calculations, though they are not all fully independent or attributable to the experimental treatments. For example, in the laboratory experiment, we included the first molt observation where the animals were not held in the experimental conditions for the entire molt cycle, significantly increasing the data supporting the GPM calculation. This inclusion of the first GPM estimate per crab should not impart treatment-specific bias as all crabs were held in identical conditions before the experiment, although it incorporates more sources in intrinsic variation, increasing the robustness of the estimate. Similarly, we treated IMP estimates from crabs that exhibited multiple molts as independent observations in the analysis. This practice may have imparted bias if the rearing conditions were suboptimal; however, it incorporated the dynamics of sequential molts in the T_{\min} , IMP, and CMPDF calculations. Additionally, we retained the 16 °C laboratory experiment in the determination of T_{\min} , though only one estimate of IMP was collected from it because of the exceedingly long molt intervals. This paucity of low temperature data increased the relative weighting importance of the low temperature data. We believe that the error imparted by excluding the 16 °C data would be greater than the error created by the unequal weighting of it, so it was retained in the analysis. These limitations of the model framework and parameterization do instill error, as exemplified by the discrepancy between the variances of the observed and predicted CW distributions in the Chesapeake Bay blue crab growth simulations. The predicted standard deviation is always greater than the observed standard deviation. This is most likely due to the lack of mortality and emigration estimates in the model. The effects of size-dependent mortality can have a great effect on the variation in a population's size distribution (Rice et al. 1993). In the field, size-dependent mortality tends to truncate the variation in the frequency distribution of sizes. Mortality resulting from predation of crabs tends to be the highest for the smallest members of the population (Hines and Ruiz 1995). Additionally, the mortality associated with molting caused by physical damage, physiological stress, and increased predation risk will reduce the numbers of larger crabs in the cohort as they experience more molt events (Leffler 1972). Additionally, the effects of the fishery and pre-spawning migration of females can significantly alter the population structure, as they remove larger animals selectively and can be significant but are not included in the current model form (Turner et al. 2003).

Future refinements of the model may include these additional complexities; however, despite these concerns, we believe that the model will predict crab growth accurately enough to examine some fisheries-important questions. The warm- and cold-year simulations showed the effect that temperature could have on the proportion of the population entering the fishery in a given year. The 1996 and 1998 sample history years varied by an average of 2.1 °C (709 degree-days), which resulted in a 10% shift in the timing of juvenile crabs becoming available for legal exploitation. A 10% shift in entrance to the fishery could cause potential yield to be overestimated and the fishery to be overharvested. This information can be used, in addition to traditional assessment techniques, to provide information to managers about

some of the natural variation in crab growth and subsequent recruitment to the fishery.

This application of the molt-process model can also lay the foundations for a yield-per-recruit (YPR) model (Bunnell and Miller 2005). YPR attempts to maximize the total harvest by controlling the fishing mortality and age of entry into the fishery. In teleost fisheries, mortality is controlled by limiting effort, and age at first capture is set by net mesh sizes and exclusion devices. In the blue crab fishery, the age at which the bulk of the population enters the fishery has been unknown because of the lack of usable age markers and size structure overlap. By using the molt-process model to forecast the percent of a cohort entering the fishery at multiple ages, a YPR model can be constructed. This would allow the exploration of the effects of juvenile exclusion devices (cull rings) on the pot-based hard crab fishery that has not been possible without age markers.

In future, the molt-process model may be usable directly in the stock assessment framework in place of the von Bertalanffy growth model. However, at this time, the model is faced with some limitations preventing its easy inclusion. In an assessment, the molt-process model will be used to create an aggregate population using average inputs. It will be impossible to predict the temperature history that a crab will experience in the upcoming years, so a temperature average will be used instead. This will most likely take the form of average temperatures every day of the year for the past few years. Continuously updating this average history will account for trends; however, there will still be a mismatch between the average and actual temperatures that crabs experience. In a worst-case scenario, the average temperature history can lead to errors in years with abnormal temperature patterns and inappropriate suggestions being made to managers.

The molt-process model can be a tool for predicting the effects of temperature on crab growth and can be used in place of the more complex bioenergetic model to explore ecological questions. By using a molt-process model, one can predict the answer to questions of management concern, e.g., the number of seasons it takes for a crab to reach maturity or recruit to the fishery. Though the model may not be currently suitable as a direct replacement for the growth models used in stock assessments, it is a viable companion model to aid in the management of blue crabs. Once the limitations of inappropriate temperature history inputs and zoogeographical differences have been thoroughly explored, the model may be able to form the basis of a more accurate stock assessment; however, for now, it is still a tool for exploring other fisheries-important questions.

Acknowledgments

We thank the anonymous reviewers for comments on earlier drafts of this manuscript. This work was supported by a research grant from the Hudson River Foundation to TJM (HRF 008/98A). This is contribution number 3918 of the University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory, Solomons, Maryland.

References

- Bunnell, D.B., and Miller, T.J. 2005. An individual-based modeling approach to per-recruit models: blue crabs (*Callinectes sapidus*) in the Chesapeake Bay. *Can. J. Fish. Aquat. Sci.* **62**(11): 2560–2572.
- Cadman, L.R., and Weinstein, M.P. 1988. Effects of temperature and salinity on the growth of the laboratory-reared juvenile blue crabs *Callinectes sapidus* Rathbun. *J. Exp. Mar. Biol. Ecol.* **121**: 193–207.
- Cheng, J.H., and Chang, E.S. 1993. Determinants of postmolt size in the American lobster (*Homarus americanus*). I. D_1^3 is the critical stage. *Can. J. Fish. Aquat. Sci.* **50**: 2106–2111.
- Cheng, J.H., and Chang, E.S. 1994. Determinants of postmolt size in the American lobster (*Homarus americanus*). II. Folding of premolt cuticle. *Can. J. Fish. Aquat. Sci.* **51**: 1774–1779.
- Curry, G.L., and Feldman, R.M. 1987. Mathematical foundations of population dynamics. Texas A&M University Press, College Station, Texas.
- Fitz, H.C., and Wiegert, R.G. 1991. Tagging juvenile blue crabs, *Callinectes sapidus*, with microwire tags: retention, survival, and growth through multiple molts. *J. Crustac. Biol.* **11**(2): 229–235.
- Fogarty, M.J., and Idoine, J.S. 1988. Application of a yield and egg production model on size to an offshore American lobster population. *Trans. Am. Fish. Soc.* **117**: 350–362.
- Gray, E.H., and Newcombe, C.L. 1938. Studies in moulting in *Callinectes sapidus* Rathbun. *Growth*, **2**: 285–196.
- Guerin, J.L., and Stickle, W.B. 1997. A comparative study of two sympatric species within the genus *Callinectes*: osmoregulation, long-term acclimation to salinity and the effects of salinity on growth and molting. *J. Exp. Mar. Biol. Ecol.* **218**: 165–186.
- Hartnoll, R.G. 1982. Growth. In *The biology of the crustacea*. Vol. 2. Edited by L.G. Abele. Academic Press, New York. pp. 111–196.
- Hiatt, R.W. 1948. The biology of the lined shore crab *Pachygrahus crassipes*, Randal. *Pac. Sci.* **2**: 135–213.
- Hill, J., Fowler, D.L., and Van Den Avyle, M.J. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic) blue crab. *Biol. Rep. US Fish. Wildl. Serv.* **82**(11.100). US Corps of Engineers, TR EL-82-4.
- Hines, A.H., and Ruiz, G.M. 1995. Temporal variation in juvenile blue crab mortality: nearshore shallows and cannibalism in Chesapeake Bay. *Bull. Mar. Sci.* **57**(3): 884–901.
- Ju, S., Secor, D.H., and Harvey, R.H. 2001. Growth rates and lipofuscin accumulation rates in the blue crab *Callinectes sapidus*. *Mar. Ecol. Prog. Ser.* **224**: 197–205.
- Leffler, C.W. 1972. Some effects of temperature on the growth and metabolic rate of juvenile blue crabs, *Callinectes sapidus*, in the laboratory. *Mar. Biol.* **14**: 104–110.
- McCaughran, D.A., and Powel, G.C. 1977. Growth model for Alaskan king crab (*Paralithodes camtschatica*). *J. Fish. Res. Board Can.* **34**: 989–995.
- Miller, T.J., and Smith, S.G. 2003. Modeling crab growth and population dynamics: insights from the blue crab conference. *Bull. Mar. Sci.* **72**: 537–541.
- Moksnes, P.-O., Lipcius, R.N., Phil, L., and van Monfrans, J. 1997. Cannibal-prey dynamics in young juveniles and postlarvae of the blue crab. *J. Exp. Mar. Biol. Ecol.* **215**(2): 157–187.
- Norse, E.A. 1977. Aspects of the zoogeographical distribution of *Callinectes sapidus* (Brachyura: Portunidae). *Bull. Mar. Sci.* **27**(3): 440–447.
- Rice, J.A., Crowder, L.B., and Rose, K.A. 1993. Interactions between size-structured predator and prey populations: experi-

- mental test and model comparison. *Trans. Am. Fish. Soc.* **122**: 481–491.
- Roff, D.A. 1992. *The evolution of life histories: theory and analysis*. Chapman and Hall, New York.
- SAS Institute Inc. 2001. SAS version 8.12 [computer program]. SAS Institute Inc., Cary, North Carolina.
- Sharov, A.F., Vølstad, J.H., Davis, G.R., Davis, B.K., Lipcius, R.N., and Montane, M.M. 2003. Abundance and exploitation rate of the blue crab (*Callinectes sapidus*) in the Chesapeake Bay. *Bull. Mar. Sci.* **72**(2): 543–565.
- Skinner, D.M., and Graham, D.E. 1972. Loss of limbs as a stimulus to ecdysis in *Brachyura* (true crabs). *Biol. Bull.* **143**: 222–233.
- Smith, L.D. 1990. Patterns of limb loss in the blue crab, *Callinectes sapidus* Rathburn, and the effects of autonomy on growth. *Bull. Mar. Sci.* **46**(1): 23–36.
- Smith, S.G. 1997. *Models of crustacean growth dynamics*. Ph.D. dissertation, University of Maryland College Park, College Park, Md.
- Tagatz, M.E. 1968. Growth of Juvenile blue crabs, *Callinectes sapidus* Rathburn, in the St. Johns River, Florida. *Fish. Bull.* **67**: 281–288.
- Thompson, D.W. 1968. *On growth and form*. Cambridge University Press, Cambridge, UK.
- Turner, H.V., Wolcott, D.L., Wolcott, T.G., and Hines, A.H. 2003. Post-mating behavior, intramolt growth, and onset of migration to Chesapeake Bay spawning grounds by adult female blue crabs, *Callinectes sapidus* Rathburn. *J. Exp. Mar. Biol. Ecol.* **295**: 107–130.
- Van Engel, W.A. 1958. The blue crab and its fishery in Chesapeake Bay. Part 1. Reproduction, early development, growth, and migration. *Commer. Fish. Rev.* **20**(6): 6–17.
- von Bertalanffy, L. 1938. A quantitative theory of organic growth. *Inquiries on growth laws. II. Human Biol.* **10**: 181–213.
- Wainwright, T.C., and Armstrong, D.A. 1993. Growth patterns in the Dungeness crab (*Cancer magister* Dana): synthesis of data and comparison of models. *J. Crustac. Biol.* **13**(1): 36–50.
- Winget, R.R., Epifanio, C.E., Runnels, T., and Austin, P. 1976. Effects of diet and temperature on the growth and mortality of the blue crab, *Callinectes sapidus*, maintained in a recirculating culture system. *Proc. Nat. Shellfish Assoc.* **66**: 29–33.