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# BIOENERGETIC MODELING OF THE BLUE CRAB (*CALLINECTES SAPIDUS*) USING THE FISH BIOENERGETICS (3.0) COMPUTER PROGRAM

*Bryce J. Brylawski and Thomas J. Miller*

## ABSTRACT

To understand better the ecology and growth dynamics of the blue crab (*Callinectes sapidus*), we developed a bioenergetic model based upon the Fish Bioenergetics 3.0 computer program. We summarized and analyzed existing data from published studies on the ecology and physiology of both blue crab and closely related species to parameterize the model. The respiration and excretion components were estimated directly from published studies. Parts of the consumption component were estimated indirectly. The resulting model was evaluated for applicability against known growth trajectories from field and laboratory studies. The model predicted observed growth and consumption to a first approximation. Inspection of model results suggest that improvements in our knowledge of temperature- and size-dependant consumption are required before a more predictive model can be developed. However, at this point the model is sufficiently accurate to explore some fishery-related questions.

The blue crab (*Callinectes sapidus*) is a benthic predator of ecological and economic importance. It feeds principally upon shellfish and scavenges for carrion, filling an important niche within estuarine ecosystems (U.S. Fish and Wildlife Service, 1989). In turn, the blue crab is prey for several important estuarine fishes, such as striped bass (*Morone saxatilis*). Thus, blue crab may represent an important link between the benthic and pelagic food webs (Baird and Ulanowicz, 1983). National Marine Fisheries Service data indicate that between 1980 and 1998 blue crab fisheries harvested an annual average of 41,200 Metric Tonnes (MT) nationally, worth more than \$43.6 Million per year (dockside value). Thus, understanding the dynamics of blue crab is important for ecological and economic reasons.

Blue crab catches have remained relatively stable in the face of increasing fishing effort (Rugolo et al., 1994; Briggs, 1998; Stehlik et al., 1998), and blue crab fisheries to date have not experienced the catastrophic declines that have occurred in some finfish fisheries. The dramatic declines in abundance of many exploited populations have motivated an interest in ecosystem-based management (Fogarty and Murawski, 1998). Bioenergetic modeling has become an important tool in ecosystem-based approaches, as it allows individual growth, population productivity, and trophic demand to be estimated (Baird and Ulanowicz, 1983). For teleosts, bioenergetic approaches have been used to explore the scope for growth (Rice et al., 1983; Chipps et al., 2000), life history trade-offs (Jensen, 1998), diel migrations (Caulton, 1978), patterns in seasonal feeding (Kitchell and Breck, 1980; Baldwin et al., 2000), predatory demand (Stewart et al., 1983; Baldwin et al., 2000), and contaminant uptake and bio-magnification of toxins (Thomann and Connoly, 1984). In addition, bioenergetic models have been used to examine predator-prey interactions in order to improve management by linking physiology to population dynamics for use in the more complex models used in multi-species and ecosystem management (Robel and Fisher, 1999).

Bioenergetics considers the flow and fate of energy within an organism (Grodzinski et al., 1975). The basic framework tracks the energy consumed by an animal as it is transformed into new somatic or reproductive tissue mass, once

physiological costs have been subtracted. The framework can be modified extensively to include a variety of biological and abiotic factors that affect organisms provided the factors can be expressed in terms of energy addition or loss (Grodzinski et al., 1975). Bioenergetic approaches thus offer an alternative to traditional growth models, such as the von Bertalanffy model, that do not directly incorporate the influence of environmental parameters such as temperature or salinity. Failure to incorporate environmental variables into growth models may lead to unreliable management advice.

Bioenergetic approaches have had limited application in crustacean fisheries, and have not been applied to the blue crab fishery. A bioenergetic framework has been employed previously to model the scope for growth of crabs under differing conditions of salinity, temperature, hypoxia, crude oil, and levels of cadmium (Guerin and Stickle, 1992, 1995, 1997a, 1997b; Das and Stickle, 1993; Wang and Stickle, 1987). However, because these models were developed to address the specific objectives of individual studies, they are not broad enough to form the foundation of a general, flexible model of crab bioenergetics. Hewett and Johnson (1987) developed a computer-based bioenergetics package for finfish that was sufficiently flexible to be used for many different species and regulating factors. This model has been expanded and revised (Fish Bioenergetics 3.0) (Hanson et al., 1997). We have adapted this framework for blue crab by developing species-specific estimates of key physiological parameters. By using a general model as a foundation, we hope to create a framework that can be modified to explore a variety of topics.

### MODELING APPROACH

We have developed a bioenergetics model for juvenile blue crabs (>10 mm carapace width). In this paper, we focus on crab size and temperature, the major factors affecting crab growth and consumption (Leffler, 1972). Model simulations were conducted at a constant salinity of 12.5 psu, a value typical of blue crab habitats in many estuaries. This limitation was imposed to reflect the data available for parameterization and calibration of the model. However, we note that variation in salinity and other effects can be easily added to our basic framework when requisite data are obtained. The model predicts the bioenergetic response to environmental conditions of a single crab. However, the model can be expanded to yield cohort and population level predictions by scaling food availability to the population level.

The basic bioenergetic equation equates growth resulting from the difference between energy gains and losses such that:

$$\text{Growth (G)} = \text{Consumption (C)} - [\text{Respiration (R)} + \text{Excretion (U)} + \text{Egestion (F)}]$$

(Grodzinski et al., 1975). Each term in the equation represents an individual sub-model that predicts the energy use or production from size- and temperature-dependent functions. All terms were parameterized with the data from previously published physiological studies. Some parameters, such as the lethal temperature, were estimated from the literature values directly. Other parameters, such as the parameters that define the respiration function, had not been previously estimated and thus were developed by combining information from various published sources. The unknown variables were estimated by non-linear and linear techniques. All data were converted to equivalent units used in the model.

Here we develop and parameterize each component of the bioenergetics model. Data sources used to provide parameter estimates are shown in Table 1. The calibrated parameter estimates for each compartment are provided in Table 2.

**CONSUMPTION.**—In specifying consumption we adapted the approach to estimate the proportion of the maximum consumption ( $p$ ) required to produce the observed growth (Rice and Cochran, 1984). Consumption varies with crab size and temperature. Maximum consumption ( $C_{\text{MAX}}$ , the amount an animal can possibly eat under ideal conditions) was predicted from a simple exponential mass-dependent model ( $C_{\text{MAX}} = CA \cdot W^{\text{CB}}$ ). We parameterized this function from available consumption estimates (Fig. 1, Table 2). A point estimate of consumption, given in the literature, was used to estimate the intercept (CA). A generalized allometric function that typifies many warm water aquatic predators was used to approximate the slope of the function (CB).

Table 1. Sources of data used in parameterization of blue crab bioenergetics model divided by compartment.

Process	Data source
Excretion and egestion	Guerin and Stickle, 1992
Respiration	Leffler, 1972
	Booth and McMahon, 1992
	Laird and Haefner, 1976
	Batterson and Cameron, 1978
Consumption	Das and Stickle, 1993
	Hanson et al., 1997
	Passano, 1960
Length weight key	Newcombe et al., 1949
Dry weight	Jorgensen et al., 1991
Caloric content	Akpan, 1997
	Lucas, 1996

The predicted maximum consumption at the optimal temperature was scaled to the daily-simulated temperature by a temperature-dependant relationship  $F_C(T)$ . No reliable data on which to base  $F_C(T)$  were available. Thus, the function was constrained to the lethal, optimal, and zero consumption points and the slope (CQ) was adjusted until the resulting equation best explained a set of growth-based consumption estimates (Passano, 1960; U.S. Fish and Wildlife Service, 1989). The growth estimates were computed using a derivation of Smith's (1997) molt-process model because of its inclusion of temperature as a forcing function. We modeled temperature-dependent growth by combining estimates of growth per molt (molt size = 116% pre-molt size) and temperature-specific estimates of intermolt periods (Leffler, 1972; Brylawski and Miller, unpubl. data). We simulated growth over 100 days from a fixed initial size of 10 mm at four different temperatures. The final size of crabs at each temperature was used to calculate the temperature-specific increases in size. The increase in size was converted to joules, via a length-weight key and estimates of crab energy density (Newcombe et al., 1949; Akpan, 1997; Lucas, 1996). We then estimated the minimum energy consumption needed to support the projected level of growth (Guerin and Stickle, 1992). These growth-based consumption estimates were then set proportional to the maximum temperature's value in order to convert data into the form used in the temperature function. An iterative nonlinear estimation technique was then used to estimate the slope of the function from the growth-based consumption values (Fig. 2).

RESPIRATION.—Respiration was modeled as two separate terms: specific respiration (R) and specific dynamic action (SDA). Specific respiration represents the temperature- and mass-dependent metabolism that fuels maintenance and activity. R is composed of three different parts, a mass-dependent equation ( $RA \cdot W^{RB}$ ), a temperature-dependent equation ( $F_R(T)$ ), and an activity multiplier (ACT). These equations are multiplied together to describe the full range of possible animal responses such that:

$$R = (RA \cdot W^{RB})F_R(T) \cdot ACT$$

The mass-dependent term was estimated from Laird and Haefner's (1976) work on the effect of

Table 2. Blue crab bioenergetic model parameters for use in the Fish Bioenergetics 3.0 computer program. The equation numbers refer to the function forms selected for the computer program, see Hanson et al., 1997 for equation details.

Consumption		Egestion and excretion		Respiration	
Equation	2	Equation:	1	Equation	2
CA:	0.35 g/g/d	Fa:	0.378	ACT:	4.6
CB:	-0.39	Ua:	0.019	RA:	0.00464 gO <sub>2</sub> /g/d
CQ:	2°C <sup>-1</sup>			RB:	-0.29
		Energy densities			
CTM:	39°C	Joules/g		RQ:	5.32°C <sup>-1</sup>
CTo:	31°C	Blue crab		RTM:	39°C
			2,416	RTO:	34°C
				Sda:	0.175

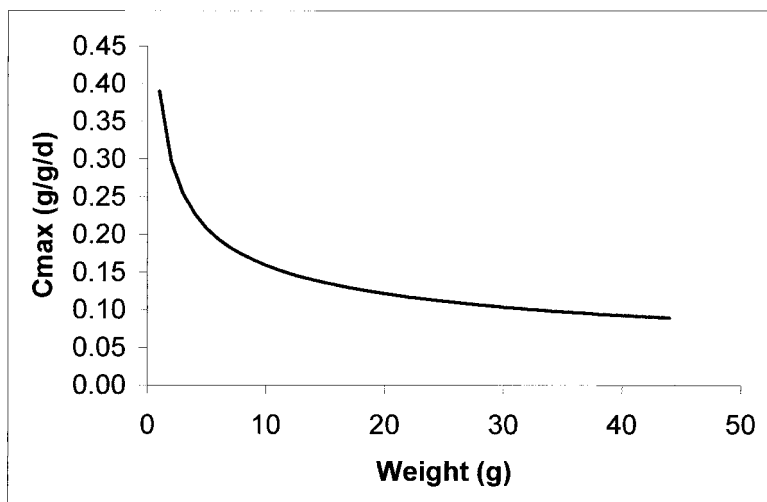


Figure 1. The relationship between maximum consumption of the blue crab, at the optimal temperature, ( $C_{max}$  = grams prey consumed per gram wet weight of crab) and the wet weight of the animal.

body size and temperature on the metabolism of blue crabs (Fig. 3). Laird and Haefner estimated the proportional decrease in oxygen consumption with increased wet weight. From these estimates, we calculated the mass-dependent respiration parameters (Table 2).

As with the consumption model, we used a temperature-dependent function for a generalized aquatic predator (Kitchell et al., 1977). The model predicts exponentially increasing metabolism, up to an optimal temperature (RTO), beyond which metabolism declines to zero at the lethal or maximum temperature (RTM). We fitted the respirometry data published by Leffler (1972) and Batterson and Cameron (1978) to the three parameter temperature function (Fig. 4). Parameter estimates are provided in Table 2.

The ACT coefficient or Winberg multiplier is estimated from standard and active metabolism measurements. The ACT coefficient represents energetic costs of activity as a fixed multiplier of the

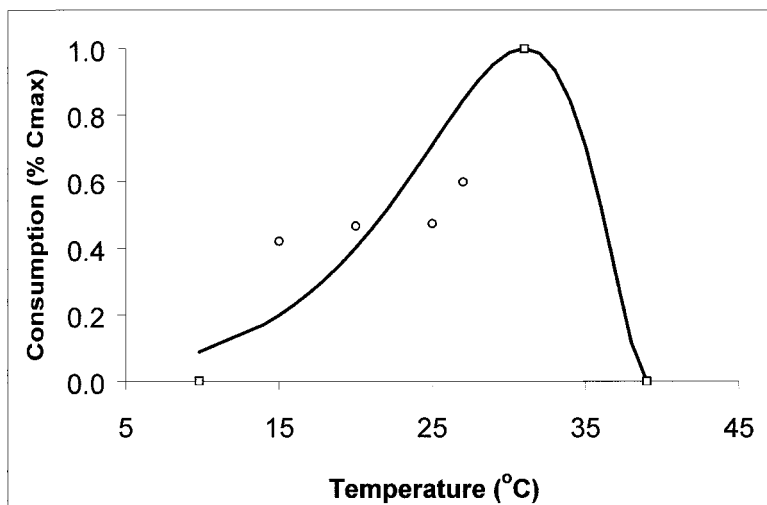


Figure 2. The blue crab consumption temperature scaling function. The predicted function (solid line) was derived from constrained points (open squares), and growth-based consumption estimates (open circles) calculated as described in the text.

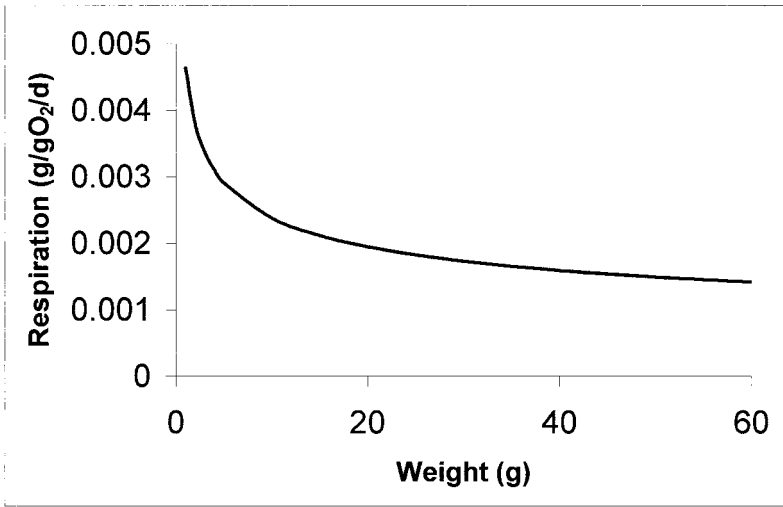


Figure 3. Allometric specific respiration function for the blue crab, at the optimal respiration temperature, based on data compiled from respirometry studies.

specific metabolism. The multiplier was estimated from Booth and McMahon's (1992) data from forced swimming experiments, which were assumed to be equivalent to peak activity levels. Parameter estimates are provided in Table 2.

SDA, the energy an animal uses in digesting a meal, is assumed to be a set proportion of the consumed energy left after egestion ( $SDA = S_{SDA}\{C - F\}$ ). The  $S_{SDA}$  value is assumed to be similar to the values for other species of crabs; yielding a loss to SDA of 17.5% of the assimilated energy (Rudstam, 1989; Paul and Fuji, 1989).

EXCRETION AND EGESTION.—Excretion (U) and egestion (F, defecation) are assumed to be directly proportional to the amount of consumption. This is a standard assumption in bioenergetics modeling (Kitchell et al., 1977). Temperature and mass effects are not included directly in the U and F terms, and only influence U and F through their influence on consumption. Thus the influences of temperature and mass are expressed as second order effects. Sensitivity analyses of fully parameterized bioenergetic models suggest that the model is relatively insensitive to these terms (Grodzinski et al., 1975; Bartell et al., 1986).

Both factors are calculated directly from the energy budget developed by Guerin and Stickle (1992).

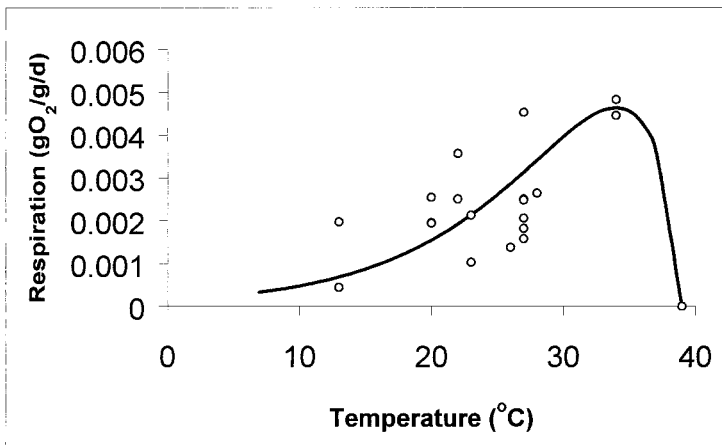


Figure 4. The blue crab specific respiration temperature function, derived from respirometry data shown (open circles).

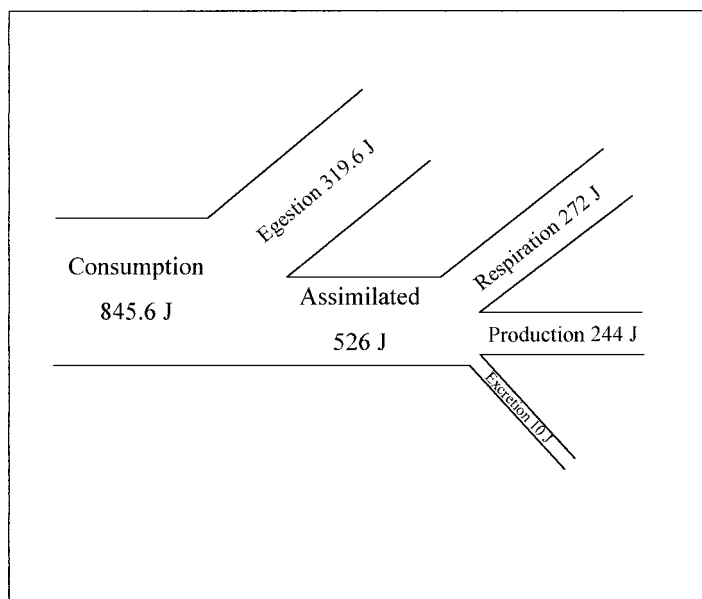


Figure 5. Energy budget for a 1 g blue crab held at 31°C developed from the parameters estimated for the bioenergetic model.

The  $F$  is calculated as one minus the assimilation efficiency. The estimated egestion loss is 37.8% of all consumed food. The loss to excretion is proportional to the remaining energy after egestion multiplied by a coefficient (UA), and is 1.85% of the remaining energy.

**ENERGY DENSITIES.**—To use the model, energy densities for both the crabs and the prey consumed are required. For simulations involving laboratory-reared crabs fed on commercial feed (Zigler Brothers  $\frac{1}{4}$ " trout pellets), we used a food energy density provided by the manufacturer. The energy density for the crabs themselves was gathered from the percent composition information determined in the seafood industry and calculated using the component equivalencies (Akpan, 1997).

The softshell clam (*Mya arenaria*) was selected to represent a typical natural prey, since it is both a preferred prey type and good calorimetry data are available (Ebersole and Kennedy, 1995; Jorgen et al., 1991). The energy density (J/g) was calculated from the percent contents reported in the literature and the published energy concentrations for each component (Lucas, 1996).

**ENERGY BUDGET.**—To check the adequacy of the parameter estimates an energy budget was calculated. If the parameter estimates are valid, the energy budget should balance to yield a positive production compartment. We estimated the energy budget for a 1 g (initial weight) crab held at 31°C, the optimal temperature for consumption (Fig. 5). The calculations estimate that production available for somatic and reproductive tissue growth should be 29% of the consumed energy.

## SIMULATIONS

We report two categories of simulations. The first, termed growth-consumption calibrations, sought to explore the variation in the proportion of maximum ration ( $p$ ) consumed by crabs under a variety of conditions. The second, termed growth-consumption fisheries simulations, sought to explore the consequences of three different growth models used in recently published stock assessments.

**GROWTH-CONSUMPTION CALIBRATIONS.**—Using the model parameterized as described above, we calibrated the model with respect to  $p$ -values (the proportion of maximum ration) by examining the agreement between model simulations and three independent empirical growth estimates. The model was run to simulate the results of laboratory studies of crab growth over 100 days, when individuals were fed commercial trout pellets ad libitum, at a constant 24°C. To examine the performance of the model under variable conditions, we simulated growth of blue crab over 141 and 35 days in field enclosure trials conducted in the Patuxent River near Chesapeake Biological Lab, Maryland, and in the Potomac River at Point Lookout, Maryland. For these simulations we used an estimated diet of half clam and half crab. To examine model performance over an extended time series, including an over-wintering period, we simulated the growth of pond reared crabs from the Choptank River, Mary-

land, over 375 days (Se Jung Ju, David H. Secor and Roger Harvey, Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, P.O. Box 38, Solomons, Maryland 20688, unpubl. data). For all simulations, we used a weight-length regression (Wet weight (g) =  $0.000335 \cdot \text{Length} \{ \text{mm} \}^{2.571}$ ) to convert laboratory and field measures of length to weight. In each simulation, we adjusted p-values incrementally until observed and predicted growth was in closest agreement, judged visually for goodness of fit. Subsequently, we used the model with the calibrated p-value to predict the seasonal pattern in daily growth rates of blue crabs.

**GROWTH-CONSUMPTION FISHERY SIMULATIONS.**—The results from stock assessments often form the basis of advice to management agencies. The growth model used in the stock assessment, which describes how growth translates new recruits to the fishery to harvestable biomass, is of fundamental importance. To explore the differences among the growth models, we used the bioenergetic model to simulate the consumption required to produce the growth predicted by three different growth models from three stock assessments for two adjacent stocks (Rugolo et al., 1997; Helser and Kahn, 1999; Smith and Ault, submitted). The first two assessments employed von Bertalanffy growth models. Helser and Kahn (1999) developed growth parameter estimates for the Delaware Bay blue crab population that suggest that crabs reach legal size (120 mm CW) after one growing season. Rugolo et al. (1997) used estimates for assessment of the Chesapeake Bay population suggesting two growing seasons are required. In contrast, Smith and Ault (submitted) did not use the von Bertalanffy growth model, but rather used a molt-process model (Smith, 1997) in their work on the Chesapeake Bay. Since the two estuaries are similar in climatic conditions, concern has been expressed regarding the discrepancy between the estimates. Simulations were set to run over a 91-day summer growing season with a temperature curve that approximated the pattern seen in the Patuxent River, Maryland. Crabs were assumed to be eating equal proportions of clam and crab.

## RESULTS

**GROWTH-CONSUMPTION CALIBRATIONS.**—The model was able to predict to the outcome of all the independent growth estimates but required different p-values for each rearing condition (Fig. 6). Though statistical comparisons are impossible, the model appeared capable of fitting the observed growths regardless of field or laboratory origin. The model predictions bisect the individual predictions when scaled with individually derived p-values, and the simulation tracked the mean growth of the individual estimates when combined using an averaged p-value for the simulated experiment (Fig. 6).

The model predicted a variable pattern of daily growth. The model produced reasonable, temperature-dependent patterns in daily growth over the course of a full year, including the over-wintering phenomena (Fig. 7). The pattern in growth rates also reflects the allometric limitations on growth at greater crab masses.

Overall, we conclude that with the p-values set appropriately the model performs consistently and accurately in the prediction of crab growth within the constraints of the assumptions of the model.

**GROWTH-CONSUMPTION FISHERY SIMULATIONS.**—The bioenergetic model was used to estimate the consumption necessary to support the growth over a summer season predicted by the three growth models used in different stock assessments (Fig. 8). Because the trial is run for only a quarter of a year the differences in the growth models are not as pronounced as they would be over a full annual cycle. The difference between the final sizes predicted by the two von Bertalanffy models is only 8% for the 91-day simulation. The molt process model growth prediction appears to track the Chesapeake Bay growth function for the first 60 days and then switches to relate more with the Delaware Bay predictions. This is due to the effect of the temperature forcing function altering the intermolt period. There is a 7 g (21%) difference in consumption between the 2 von Bertalanffy models (Fig. 9). The deviation in estimated consumption between the Delaware Bay parameterized von Bertalanffy growth model and molt process model final size predictions is very small, with a difference of only 0.2 g (>1%) over the entire 91-day period.



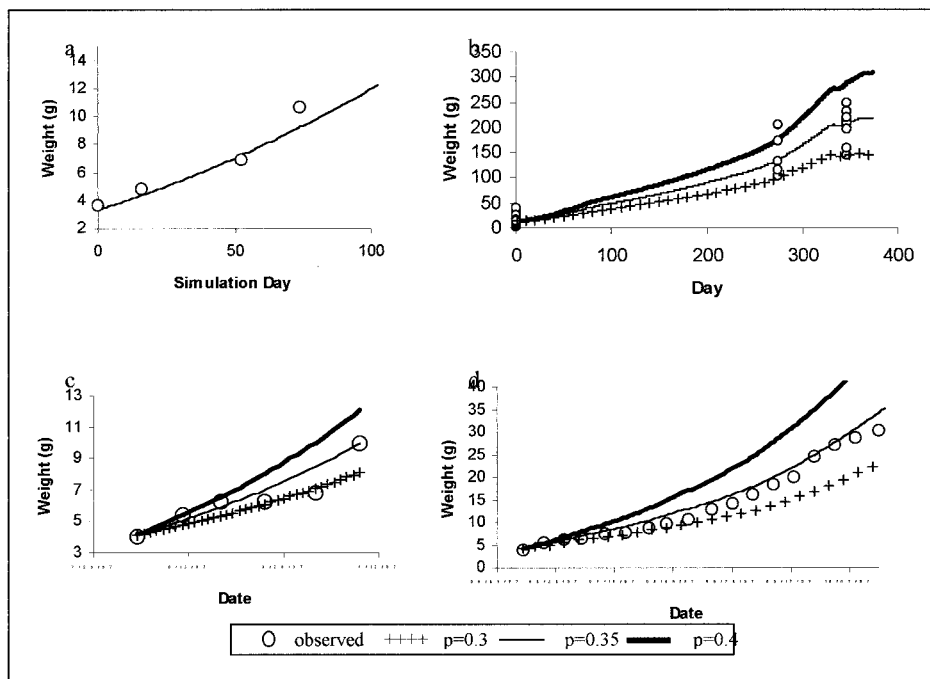


Figure 6. Predicted, from the calibrated bioenergetic model, and observed blue crab growth from different environments. All show close fit of the predicted growth to the average observed growth when the correct "p" value term is selected. See text for explanation of "p" value use and selection. (A) Laboratory growth observations fitted with a bioenergetic model estimate using a p value of 0.065. (B) Pond-reared Choptank River, Maryland, growth observations (open circles) and three bioenergetic model predictions using differing "p" value terms. (C) Enclosure-reared Point Lookout, Maryland, crabs' mean observed growth (open circles) and three bioenergetic model predictions using differing "p" value terms. (D) Enclosure-reared Patuxent River, Maryland, mean observed growth (open circles) and three bioenergetic model predictions using differing "p" value terms.

## DISCUSSION

The blue crab bioenergetics model is able to predict the growth of crabs when adjusted with a p-value appropriate to the rearing conditions. The low p-values in all simulations may be symptomatic of some discrepancy in the parameters. However, even with this caveat, the model can match known growth trajectories. When appropriately calibrated, the model should be able to address important physiological, ecological and fisheries-related questions of growth, habitat selection, spatial distribution, and population energetic demand.

The p-values estimated for each simulation were possibly different because of the differences in the rearing conditions, though there were some patterns. The laboratory simulation required a much lower value ( $p = 0.067$ ) than either the pond-reared ( $p = 0.35$ ) or enclosure-raised ( $p = 0.35$ ) crabs. This effect is likely due to the differences in food quality and activity of the crabs in each environment. The lab-reared crabs may have a low p-value because the food quality is much higher than in nature and the crabs are extremely limited in their movement. Additionally, the model may have overestimated the feces produced and associated energy lost due to the unnaturally high food quality used in the laboratory study. Moreover, the restricted movement meant that the respiration of the animals was at a minimum and the model's prediction would remove too much energy in

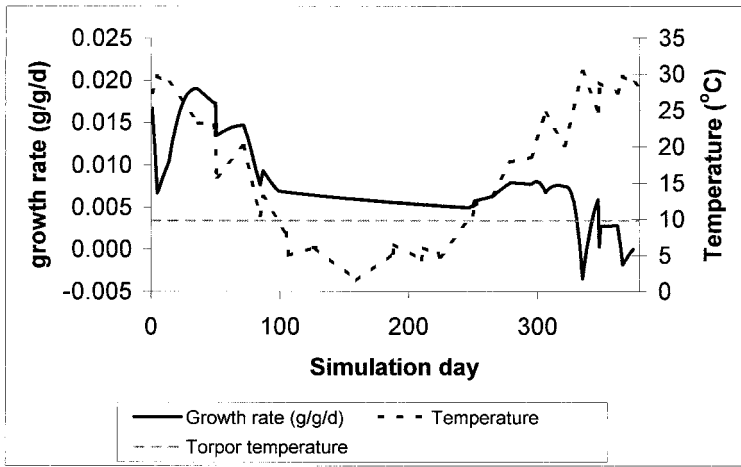


Figure 7. Model predicted daily growth rate and corresponding temperature time-series of the Chop-tank River simulation. The growth rate tracks the temperature as expected with a decrease in the magnitude of the function as the simulated crab gets larger, due to the allometric growth limitation inherent in the bioenergetics model.

the respiration compartment. The pond- and enclosure-reared crabs were raised on lower quality food and had greater opportunities for activity. Accordingly, the p-values for the field-based simulations were higher than the laboratory-based simulations.

The simple fisheries example shows the usefulness of the bioenergetics approach. The different growth models may have important population dynamic consequences (Miller, in press), and our simulations suggest that the bioenergetic consequences of the different environments are greater than the difference between the simple growth model estimates, making it appear that the Chesapeake and Delaware Bay environments may be more different than originally hypothesized.

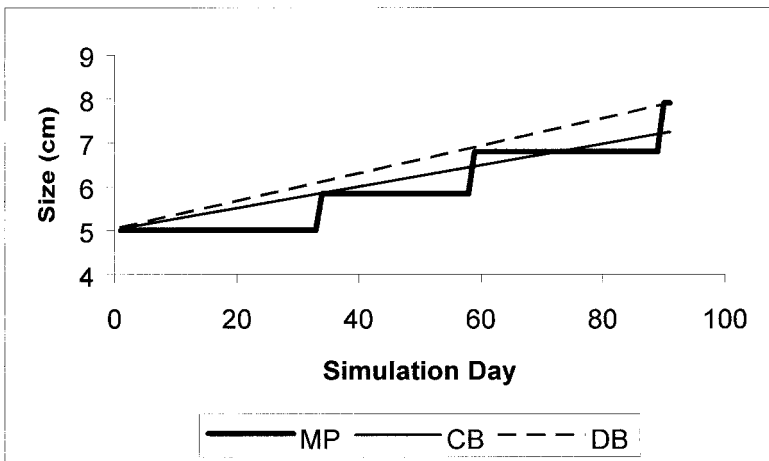


Figure 8. Growth curves for a simulated 91-day summer season produced by three different growth models: the von Bertalanffy growth models used in the Chesapeake Bay (CB) and Delaware Bay (DB) stock assessments; and the Smith molt-process model (MP).

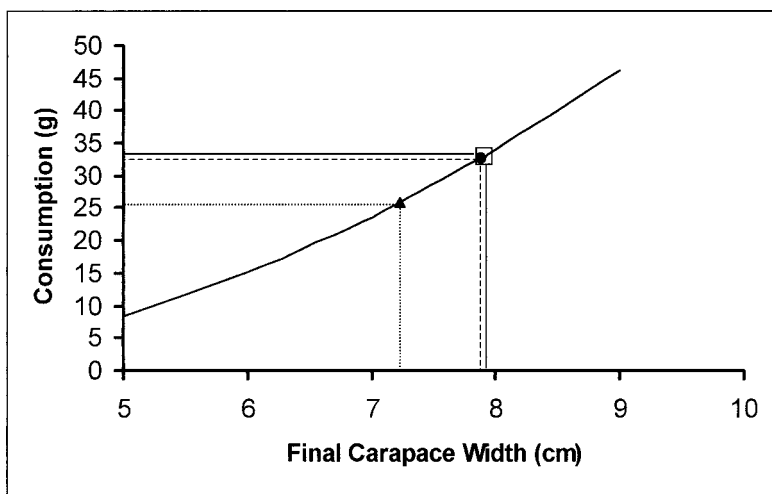


Figure 9. Total weight of prey consumed by an individual blue crab, initial carapace width of 5 cm, over a 91-day summer growing season as a function of the final carapace width achieved. The three specific growth/consumption corresponding to the predicted final sizes of three growth models are indicated: triangle (dotted lines), Chesapeake Bay estimate; circle (dashed line), Delaware Bay estimate; square (solid line), Chesapeake Bay molt-process model estimate.

An interesting result of the fisheries application example is the closeness of the final size estimates of the molt-process model (Smith, 1997; Smith and Ault, submitted) to the Delaware Bay model (Helser and Kahn, 1999). The molt-process model was calibrated to Chesapeake Bay temperature conditions, so it represents the expected growth achievable in this system. The similarity of the molt-process model and the Delaware Bay model lends support to the suggestion that Rugolo et al.'s (1997) growth model for Chesapeake Bay blue crab may underestimate their actual growth trajectory at the end of the first growing season and beyond. These results are not sufficiently rigorous to draw final conclusions; however, they do show the usefulness of a flexible bioenergetics model in fisheries management.

Bioenergetic models can be used to explore other questions concerning the exploitation of blue crabs that are difficult to examine by more traditional techniques. For example, bioenergetics approaches can be used to quantify the predatory demand of a blue crab. In the Chesapeake Bay blue crabs preferably feed on the soft shell clam (*Mya arenaria*) (Ebersole and Kennedy, 1995), which is also an exploited animal. If the current trend toward multi-species or ecosystem-based management continues (NMFS Ecosystem Principals Advisory Panel, 1999), information such as the predatory demand of crabs will be invaluable. The amount of clams consumed by the crab population is essentially unknown, since the fishery and other predators' removals confound traditional catch survey techniques. Bioenergetic modeling combined with electivity information can be used to reexamine catch data, in order to explore the predatory interaction of the species. By combining the theoretical consumption of crabs necessary to support growth with the population estimates of the crab stock, the amount of clams consumed can be calculated and then incorporated into multi-species management frameworks.

Bioenergetic models have applications beyond examining management questions. The crab model can be useful for increasing the efficiency of aquaculture production. The cost of food is a substantial component of operating expenditures

in aquaculture (Landau, 1992). Bioenergetics can be used to calculate the optimal amount of food required at a given temperature. This would allow focused feeding, thereby reducing waste due to unconsumed food at low temperatures, and maximizing growth at higher temperatures. Alternatively, the model could also be used to predict the temperature at which most efficient use of the provided food is achieved.

Bioenergetics models also have applications for fundamental issues in the ecology of blue crabs. Applications of bioenergetics could be used to predict habitat choice and patterns of distribution of adult blue crabs. For example, in the Chesapeake Bay crabs are distributed along the main axis of the Bay with more males in the northern areas, and more females in the southern waters (Norse, 1977). The reasons behind the distribution are not known; however, it is theorized that the males inhabit the less saline northern waters to increase their growth rate. The male crabs should select habitats to maximize their growth as male size is theorized to be one of the major determining factors in the ability of a male to successfully guard a pre-molt female and deliver a sufficient sperm load (Kendall and Wolcott, 1999). In contrast, adult females remain in the southern waters to possibly reduce the energy lost in the reproductive migration to more saline waters necessary for zoeal survival. The less distance the female has to travel, the more energy is available to go into egg production. Bioenergetic simulations could be useful to predict scope for growth to determine if the male habitat selection really maximizes growth, and whether female habitat selection maximizes egg production and larval survival.

Although the uses of bioenergetic models are numerous, several problems limit the creation of a more inclusive, robust model. The lack of detailed physiological information for some parameters is a major limiting factor. Data on the respiration, egestion, and excretion are adequate, though additional studies would strengthen the model. However, there are almost no studies on consumption. Only one study (Das and Stickle, 1993) has estimated the effects of environmental factors on consumption. Yet the environment-consumption interaction is central to the accuracy of the model (Bartell et al., 1986). Because of the lack of this information we were forced to use indirect estimation techniques (Passano, 1960). Though this does not affect the utility of the model for comparative experiments, it does lead to increased inaccuracy. We believe that improving the consumption term in the current model represents the single most important limitation to further improvement in the model's accuracy and applicability.

There is also a lack of reliable data on the energy density of different crab tissues. A large amount of information is available on the edible portions of the crab; however, almost nothing has been published about the energy densities of other body tissues. Without exact estimates of the energy density as a whole, the model is hampered. The lack of energy density information also prevents the model's including the significant effect of molt shell loss. Since the energy discarded with the shell during ecdysis is not lost in this model it is corrected by the proportional consumption term. In addition a modification of the framework may be necessary to include the energy loss from the act of molting itself beyond the physical loss of the old shell. Consumption and respiration are both effected by the molt cycle, altering the bioenergetics of the animal depending on its molt stage (Passano, 1960). However there is not enough information available to model this phenomenon. We believe that the inability to model molt stage effects and shell loss is a major contributor to the low proportional consumption term.

The lack of detailed physiological data on the costs of reproduction is another major area that precludes development of a full life cycle model. Accurate esti-

mates of the energy density of male and female reproductive tissue, and the energy cost of its creation are needed. In most applications of the model to finfish the physiological costs of reproduction in males are negligible (Hanson et al., 1997). If one is willing to adopt a similar simplifying assumption for blue crabs, it may be possible to develop a whole life cycle model by simply estimating the energy density of sponges on mature females. However, as discussed in Kendall and Wolcott (1999), reproduction by male crabs can be substantial as it involves both sperm production and mate guarding behaviors. The implications of these additional costs to growth and bioenergetics of male crabs are unknown.

However, despite the lack of data for some important bioenergetic relationships, the model we developed does represent a solid foundation on which future elaborations can be based. A principal advantage of the model is that considerable experience already exists to identify the components of the model to which its output is most sensitive from its application in other species. In addition, it is straightforward to compare and contrast patterns in energy allocation among widely different taxa on an equivalent basis. More studies need to look at the basic physiology of blue crabs to develop a robust model that can be used to explore physiological, ecological and fishery-related questions. But a model such as the one developed in this paper is a good start toward bringing bioenergetic approaches to bear on the ecology and exploitation of this important species.

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