

MODELING CRAB GROWTH AND POPULATION DYNAMICS:
INSIGHTS FROM THE BLUE CRAB CONFERENCE*Thomas J. Miller and Steven G. Smith*

Over recent decades, we have learned a great many details of the behavior and ecology of the blue crab (Epifanio, 2001, this volume). Regrettably, we have yet to develop similar deep insights into blue crab population dynamics. However, until we can express this ecological knowledge mathematically to describe the dynamics of populations it will be difficult, if not impossible, to understand the implications of our hard won insights. Simply stated, population dynamics represents the glue that can bind the rich data base on blue crab ecology together. However, we should not view the link between the behavior and ecology of individual crabs and the resulting dynamics of the population as a one-way exchange. Individual-level events certainly impact population-level processes. Yet, population-level constraints may similarly limit the flexibility of individuals to modify their behavior or ecology. Thus, all researchers may benefit greatly from an increase in efforts to understand and model the dynamics of crab populations.

The study of population dynamics is a two step process. The first step involves estimation of vital rates, such as growth, fecundity and mortality. In the second step, one examines the consequences of the vital rates on patterns of population abundance and structure over time. One seeks to ask, "How many will there be?" or "How many crabs of this size can I expect?" given the vital rates hypothesized. Clearly these questions have ramifications for both our fundamental ecological understanding and for the applied area of fishery management. Sixteen presentations at the conference considered population dynamic processes from both fundamental and applied viewpoints. Four presentations dealt specifically with estimation of growth functions, two dealt with estimating mortality rates and the remaining nine examined whole population models.

Understanding growth is important for many ecological processes, which are often size-dependent. Whether a crab is a predator or a prey will depend upon its growth history. The benefits of an improved understanding of growth will not be restricted only to questions of ecological concern. An accurate growth model is fundamental to any stock assessment. Growth translates recruitment into fishery production. Fishery management strategies that are based on the results of stock assessments usually involve assumptions about growth. Thus errors and biases in the growth model cause similar inaccuracies in recommended levels of exploitation.

Two aspects of crab growth have hindered our ability to understand growth in the field. First, crabs grow discontinuously, yet traditional growth models are inherently continuous. In addition to the fundamentally saltatory nature of crustacean growth, blue crab populations from the mid-Atlantic northwards are exposed to sufficiently low temperatures during the winter months that growth ceases. The second aspect of crustacean growth that has hindered our understanding is related to the first. Since crabs shed their carapace at each molt, individuals lack calcified hardparts which have been used in other taxa to estimate age. Presentations at the conference outlined several approaches to overcoming these hurdles. Smith and Ault (unpubl. data) presented a stochastic molt-process model of crab growth. Their model combined a degree-day framework which predicts the time between molts (intermolt period) with an empirically-based growth per molt

model to construct complete growth trajectories. Their paper extended Smith's original work in this area (Smith, 1997). Sharov (unpubl. data) used a similar approach which incorporated stochastic variation to examine the development of population size structure during the growing season in the Chesapeake Bay. Brylawski and Miller (2001, this volume) presented a bioenergetics-based model of blue crab growth. This approach links patterns of consumption to growth, and when coupled with models such as those presented by Smith and Ault (unpubl. data) and Sharov (unpubl. data), may allow for more integrated ecological growth models to be developed. It is clear from the number of presentations at the conference that there is a renewed interest in developing a fuller understanding of crab growth. The new approaches represented growth as a discontinuous process, thereby overcoming many of the problems associated with earlier attempts. We cannot overstate the importance of an accurate growth model and encourage research to this end. We believe that developing an accurate growth model for blue crab is the single most important step in developing a deeper understanding of their population dynamics. We also suggest that comparative studies of patterns of growth throughout the range of the blue crab may provide useful insights into environmental regulation of crab growth.

Many presentations noted the numerous difficulties that arise because crabs can not be aged by routine methods. Ju et al. (1999, 2001) have developed a fluorometric approach to quantifying an age pigment, lipofuscin, which builds up in nervous tissue over time. At the conference, Ju and colleagues (unpubl. data) presented results that validated the approach in both laboratory and field settings. This new approach offers important potential insights into the ecology of blue crab. Initially, it may appear that lipofuscin ageing would have its biggest benefits on growth estimation. However, we conclude that the wide variation in size at presumed age (Sharov, unpubl. data), and the precision of the methodology mean that it may not yet be of sufficient precision to aid in growth directly. We suggest that it is not the ability to age crabs that stands in the way of more accurate models of growth, rather it is the form of the model itself that is deficient. Viewed in this light, obtaining age estimates will not overcome errors introduced by application of an unsuitable growth model. Yet, the ability to age crabs does present significant opportunities. Lipofuscin ageing may have its biggest impact by improving our ability to identify cohort dynamics within blue crab populations. Additionally, we anticipate that lipofuscin ageing will have substantial impact on the estimation of mortality rates in the field where length-based approaches have been questioned. However, even here, the discontinuous nature of growth needs to be taken into account. Most traditional methods of estimating mortality assume that mortality is constant. It may vary among life stages. The mortality rate of zoea is certainly different from that of adults. However, most frameworks for estimating mortality assume that, within the zoeal or adult lifestage, mortality rates are constant (but see Miller, 2001, this volume). Yet, there is strong ecological evidence that mortality, like growth, is discontinuous. Mortality is higher for newly molted soft shell crabs than for hard shell crabs. However, we have yet to develop a more complete empirical understanding of the pattern of mortality in blue crab. Until we do, we will lack the data against which alternative models of mortality can be compared. We encourage continued research into documenting the sources, patterns and consequences of mortality rates in the field. This can only be achieved by combining long-term fishery independent surveys with smaller more targeted studies (Sharov et al., this volume). We also recommend continued research into modeling mortality, in parallel to the efforts in the field.

Fecundity received little attention in the conference from a vital rate estimation

and modeling standpoint. Understanding the timing and total number of spawns that a female can potentially produce over her lifespan, as well as size-dependent batch fecundity, are fundamental to accurately modeling the reproductive capacity of blue crab populations. It was encouraging that a number of presentations addressed basic biological and ecological aspects of blue crab reproduction (Hines et al., 2001, this volume). These studies are the prerequisites for more realistic modeling of female reproductive dynamics and how these may be impacted by harvesting of both female and male crabs.

Despite the uncertainties in important vital rates discussed above, whole population models of blue crab were presented at the conference. Several approaches were showcased including stage-based models (Miller, 2001, this volume) and cohort-structured simulations (Smith and Ault, unpubl. data) that addressed both fundamental and applied management issues. Kahn and Helser (unpubl. data) and Helser et al. (unpubl. data) presented detailed risk-based stock assessment models of the Delaware Bay stock. The entire life cycle was represented in each approach and hence, each included estimates of growth, mortality, fecundity and in one case migration. Moreover, each explicitly dealt with uncertainty in parameter estimates. Yet, despite these superficial similarities, the models differed fundamentally in scope and inference. The stage-based approach sought to project the consequences of the current population structure on future population growth. Miller (this volume) extended the stage-based model to incorporate spatially-explicit population processes. The cohort-based simulation sought to predict the development of population abundance and size-age structure over time. Smith and Ault (unpubl. data) used a simulation model to estimate the sustainability of different levels of exploitation. The risk-based stock assessment models presented by Kahn and Helser (unpubl. data) and Helser et al. (unpubl. data) were extensions of traditional deterministic stock assessments that incorporate both parameter and process uncertainty. Thus this model would provide managers guidance as to the likely outcome and associated uncertainties of different management options.

The question over "Which approach is best?" is not appropriate as each model focuses on different aspects of crab population dynamics. No two models are designed to do the same thing. Each of the modeling approaches presented made different assumptions regarding important population characteristics, such as structure, density-dependence and time lags (Fig. 1). Which framework is most suitable often depends upon the question under consideration. However, there is a great deal to be gained from careful examination of the areas in which the models differ. For example, stage-based models often do not include density-dependence, whereas the stock-recruitment relationship that underlies many stock assessments is explicitly density-dependent. We suggest that comparing predictions from modeling approaches may yield insight into the potential role of density-dependence in crab populations. A second example relates to the importance of including growth and mortality as discontinuous processes. Smith and Ault (unpubl. data) showed that traditional stock assessment models which assume continuous growth and mortality processes overestimate sustainable mortality rates when compared to models that assume the two processes to be discontinuous. While the more general concern of conference participants over parameter accuracy is justified, and was recognized by the population dynamicists at the meeting, the challenge to modelers is to collaborate with ecologists in overcoming these deficiencies in our understanding of vital rate processes.

Overall, we encourage a diversity of modeling approaches as we believe they provide important insights into the processes that regulate crab population dynamics. These insights, in turn, should lead to future development of more realistic

models of greater utility incorporating key features of previous models. For example, developing a class models that incorporate molt-process growth and mortality dynamics, bioenergetics growth, density-dependent and spatially-explicit processes, and uncertainty would be a concrete step towards a more comprehensive understanding of blue crab populations. Thus, we strongly encourage development of a variety of whole population models, since we believe modeling is currently the best approach to compare and contrast alternative hypotheses regarding important life history traits, ecological processes and anthropogenic and environmental impacts regarding blue crab populations.

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LITERATURE CITED

- Epifanio, C. E. 2003. Spawning behavior and larval ecology: a brief summary. *Bull. Mar. Sci.* This volume.
- Hines, A. H., P. R. Jovoff, P. J. Bushman, J. von Montfrans, S. A. Reed, D. L. Wolcott and T. G. Wolcott. 2003. Evidence for sperm limitation in blue crab, *Callinectes sapidus*. *Bull. Mar. Sci.* This volume.
- Ju, S.-J., D. H. Secor and H. R. Harvey. 1999. Use of extractable lipofuscin for age determination of blue crab *Callinectes sapidus*. *Mar. Ecol. Progr. Ser.* 185: 171-179.
- , ——— and ———. 2001. Growth rate variability and lipofuscin accumulation rates in the blue crab, *Callinectes sapidus*. *Marine Ecology Progress Series* 00: 000-000.
- Miller, T. J. 2003. Incorporating space into models of the Chesapeake Bay blue crab population. *Bull. Mar. Sci.* This volume.
- Sharov, A. F., G. R. Davis, B. K. Davis, R. N. Lipcius and M. M. Montane. 2003. Estimation of abundance and exploitation rate of the blue crab (*Callinectes sapidus*) in Chesapeake Bay. *Bull. Mar. Sci.* This volume.
- Smith, S. G. 1997. Models of crustacean growth. Ph.D. dissertation, University of Maryland.

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