ECOLOGY OF JUVENILE AND ADULT BLUE CRABS: SUMMARY OF DISCUSSION OF RESEARCH THEMES AND DIRECTIONS

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INTRODUCTION

Complex ecological interactions for juvenile and adult blue crabs include extensive movement among patchy estuarine habitats, differential sources of mortality, and shifting use of resources for foraging, refuge, molting/growth, and reproduction. After an initial period of growth to about instar 7 (approximately 20 mm CW) in their settlement habitats in the polyhaline zone, juvenile blue crabs disperse throughout the estuary. The triggering mechanisms, routes and behavior of post-settlement dispersal are poorly understood. Post-settlement dispersal allows juveniles to rapidly exploit habitats in upper reaches (lower salinities) of estuaries, where food resources appear to be rich and the diversity of predators relatively low compared to higher salinity regions (Hines et al., 1987). Juveniles in the upper estuary undergo further growth over a period of 1–2 years to attain maturity, depending on timing of settlement and latitude of the site. In Chesapeake Bay, USA, mating occurs in late spring or summer in these nursery habitats through out the estuary, while at lower latitudes mating occurs from early spring through summer. Following mating, females migrate back down estuary and produce eggs in high salinity waters, releasing larvae for dispersal out to sea in the surface plume of the estuary. Depending on the size of the estuary, latitude and winter severity, males and juveniles may move short distances to over-winter in deep water, while females may migrate up to 250 km to high salinity waters, where they produced broods of eggs that hatch larvae into the water column in late spring through fall. This pattern of juvenile dispersal, and adult migratory movement result in the crabs partitioning the estuarine habitat by size, molt stage, gender and sexual maturity (Hines et al., 1987, 1990).

A wide-ranging discussion resulted from the session of the blue crab symposium that considered juvenile and adult ecology (nine oral presentations, which produced four papers in this section of the proceedings). Often the discussion carried over to broad topics of other sessions (e.g., fisheries, reproduction, parasites and disease) in the symposium, and no constraints were placed on these important links. The discussion brought out logistical/technical difficulties that must be overcome to address some of the research questions, but it also showed technological advances that have allowed new opportunities for progress. Importantly, the discussion showed a new emphasis on cooperation and teamwork to address some of the priorities for large spatial scales. As the latest in a series of meetings spanning nearly two decades (e.g., Smith et al., 1990; Olmi and Orth, 1995), this symposium shows that blue crab researchers have long demonstrated this spirit of collaboration, which was particularly evident in the larval sampling network that produced a unique set of papers on recruitment over large geographic scale (see Olmi and Orth, 1995, and associated papers). However, this discussion also highlighted improved cooperation among ecologists and fishery managers that is developing new models and conceptual understanding of population and ecosystem dynamics. This discussion emphasized many areas of active research and indicated priorities for new investigation. The purpose of this summary is to provide an overview of the main discussion points with an introduction to the literature associated with those points; however, it is not intended as a literature review or a comprehensive survey of blue crab research.

DISCUSSION OF RESEARCH PRIORITIES

MORTALITY.—Identification of sources of blue crab mortality is of great concern to both ecologists and fishery managers, due to the difficulty in directly measuring mortality of a highly aggressive species that molts and inhabits turbid subtidal habitats. Mortality also may be difficult to assess because of the variable impacts of physiological stresses in estuaries, and because diseases of crabs are poorly understood. Cannibalism is acknowledged to be a major source of juvenile mortality by the symposium group. Much research over the past 10–15 years has focused on agonism between size/age classes of blue crabs, with juveniles suffering intense cannibalism by large adult blue crabs, which attain a size refuge from predation (e.g., Hines and Ruiz, 1995; Dittel et al., 1995). These studies show the role of juveniles obtaining refuge from cannibalism and predators in key habitats, especially those with structure (submerged aquatic vegetation, oyster reefs, and coarse woody debris), but also shallow nearshore water (Ruiz et al., 1993).

Evidence against the importance of fish predation and for the impact of cannibalism includes several examples. In a subestuary of upper Chesapeake Bay, tethering experiments over a 13-year period recorded no instances of fish predation on tethered juvenile blue crabs, while more than 92% of the mortality was attributed to cannibalism (Ruiz et al., 1993; Hines and Ruiz, 1995; Dittel et al., 1995; Hines, unpubl. data). The long-term decline in tether mortality during decline of crab abundance and the increase in abundance of potential fish predators like striped bass (*Morone saxatilis*) is consistent with the hypothesis that large blue crabs are important predators while striped bass are not. Otherwise, increases in the fish predators would have produced higher mortality of juvenile crabs and tethering studies would have detected frequent incidences of successful predation by fish. While fish predators attacked juvenile crabs with fractional success at sites in the lower Chesapeake Bay, 100% of video-taped attacks by cannibalistic *C. sapidus* were successful (Moody, 1994).

At the same time, considerable spatial and temporal variation in consumption of blue crabs results from opportunistic foraging by some of the key predatory fishes. Fish stomach contents often include blue crabs, but the percentage that blue crabs comprise of stomach contents is often low and only occasionally high (Guillory and Elliot, 2001; Guillory and Prejean, 2001). Although anecdotal reports from fishermen note instances of *Morone saxatilis* (striped bass) stomachs full of small blue crabs (Hines, pers. obs.), Austin and Walter (1998) found that blue crabs (mainly juveniles averaging 41 mm CW) occurred in only 9.4% of relatively larger (>45 cm) striped bass (n = 2,009 fish) collected from fish processing houses. In another study (Tupper and Able, 2000), the diet of striped bass varied spatially within tidal creeks of New Jersey, USA salt marshes, where blue crabs comprised a major portion of the fish stomach contents overall, but with crabs forming as much as 50% occurrence and 60% of weight of stomachs in one creek and zero occurrence in another creek.

In one lower Chesapeake Bay sea grass bed, abundance and stomach contents of fish were measured simultaneously over two short periods (12 h) to estimate predator impact (Orth et al., 1999). Gut content analysis showed that 100% of *Scieaenops ocellatus* (red drum) had an average of 4.5 juvenile blue crabs, while 60.5% of striped bass held 2.3 crabs, and 35.7% of *Micropogonias undulatus* (croaker) consumed 1.4 crabs on average. Of the remaining striped bass and croaker that did not consume blue crabs, 14.5% and 39.3%, respectively, had empty stomachs, and 13.2% and 25%, respectively, contained food only food

items other than crabs. By integrating diet and fish abundance with sea grass aerial cover, predation impacts were estimated for the 1.6×10^9 blue crabs within this habitat as 7.35×10^7 crabs per 12 h (4.6%) by striped bass, 3.06×10^5 crabs per 12 h (0.42%) for croaker, and 1.20×10^4 crabs per 12 h (0.017%) by red drum. However, only one sampling period captured these large numbers of fish feeding upon blue crabs, while other sampling did not capture fish. Thus, in combination, fish predators could be estimated as much as consuming as much as 5% of the blue crab population per 12 h period; but when averaged over several sampling periods that had much lower fish densities and much lower percentages of crabs in stomachs, this impact would be much lower. Although it is clear that blue crabs may be important in the diet of certain species of fish in particular habitats, and that some fish species are effective predators on blue crabs, there is little quantitative data demonstrating rigorously that predation by fish directly regulates blue crab populations.

While both fish predation and crab cannibalism appear to be important sources of mortality for blue crabs, most of studies of blue crab mortality have dealt with intermolt crabs and have not assessed mortality of molting crabs. Even though crabs seek special refuges such as marsh creeks and SAV for ecdysis, when they are thought to be highly vulnerable to predators (Hines et al., 1987; Shirley et al., 1990; Wolcott and Hines, 1990; Ryer et al., 1997), mortality of molting crabs is generally believed to be high. There are virtually no quantitative estimates of mortality during molting (but see Ryer et al., 1997), probably because mortality is technically difficult to estimate realistically or even comparatively for organisms that shed their exoskeletons.

At higher latitudes, winter mortality may be limiting blue crab populations. Anecdotal information in Chesapeake Bay and Delaware Bay indicates that severe winters cause increased mortality of blue crabs (Pearson, 1948; Krantz, 1977; Kahn et al., 1998; Helser and Kahn, 1999). Cold temperature mortality may depend interactively on salinity (especially low salinity) and life stage (especially for mature females that migrate to higher salinities in advance of brood production (Truitt, 1934; MacGregor, 1950; Tagatz, 1969; van Heukelem and Sulkin, 1990).

Disease may be a major source of blue crab mortality that is not well measured or understood. In particular, the blood parasite *Haematodinium* spp. is being reported at high prevalences in high salinity zones of some areas (Shields et al., 2003) and is suspected to cause high levels of blue crab mortality along the southeast coast of the U.S. The discussion group speculated that blue crabs are more vulnerable to diseases when under pollution stress. More systematic analysis of prevalence of *Haematodinium* and other diseases needs to be pursued, because technical aspects of estimating disease mortality have resulted in relatively few large-scale surveys of spatial and temporal patterns. Several ecologists are concerned that prevalences may be much higher than thought and may be impacting much larger segments of the blue crab population, especially in response to such variables as low oxygen stress resulting from excessive nutrient loading in wet years and salinity shifts during drought.

Most ecological experiments (e.g., Heck and Wilson, 1987; Hines and Ruiz, 1995; Dittel et al., 1995) produce relative indices of mortality, yet estimates of true rates of morality are crucial for models of population dynamics and fisheries. The Chesapeake Bay winter dredge survey provides one such estimate of annual mortality for the two main age-classes of the population (Bi-State Blue Crab Advisory Committee, 2001). By sampling 1,500 sites in a stratified random design throughout the entire Chesapeake Bay during winter when crabs are moving very little, the program produces Bay-wide estimates of the abundance and size struc-

ture of crabs that can be compared each year. These estimates still require fishery statistics and models to partition natural from fishing mortality. Many population ecologists are skeptical of natural mortality rates estimated by fishery modelers because they are sometimes based on unrealistic estimates of maximum age (e.g., Rugulo et al., 1998). The symposium discussion acknowledged, however, that ecologists must accept responsibility to generate more realistic estimates of mortality rates and how they vary in space and time.

HABITAT.—In Chesapeake Bay, the loss of crucial submerged aquatic vegetation (SAV), especially during the 1970s, is considered to have major impact on blue crabs, which utilize this habitat for both structural refuge from predation upon juveniles and molting individuals, and for its food resources (Heck and Orth, 1980; Heck and Thoman, 1984). However, the symposium group questioned whether the blue crab's life history dependence on SAV in Chesapeake Bay is a good reflection for habitat requirements in other estuarine systems. In some other systems like North Carolina and the Gulf of Mexico, blue crabs apparently use alternative nursery habitats, such as shallow detritus and salt marshes (Minello and Webb, 1997; Etherington and Eggleston, 2000). Delaware Bay has never had extensive SAV habitat, and the marked decline of SAV in Chesapeake Bay in the 1970s did not result in concomitant declines in the blue crab population, which did not decline until the 1990s when increasing fishing pressure and concomitant low recruitment led to an 85% decline in the spawning stock (Lipcius and Stockhausen, 2001).

There are other critical habitats in addition to SAV that are necessary for other life stages of the blue crab. Seitz et al. (2003) present evidence that bivalve prey are crucial food resources for blue crabs that provide "bottom-up" control of crab distribution and abundance. In turn, bivalve abundance appears to be associated with detrital carbon inputs. Thus, unvegetated habitats that are near marshes and characterized by high clam density appear to be critical to blue crab populations in Chesapeake Bay. However, the traits and features that make habitats valuable may be difficult to evaluate. Measures of habitat value include: blue crab abundance and correlation with resource variables (e.g., Seitz et al., 2003); relative index of survival (e.g., using tethering techniques) (e.g., Heck and Wilson, 1987; Ruiz et al., 1993; Hines and Ruiz, 1995); and growth rates (e.g., Perkins-Visser et al., 1996). The studies by Rakocinski et al. (2003) and Seitz et al. (2003) raise the question of the relative importance of critical but often concentrated habitat, such as SAV, versus more marginal but widely distributed, extensive habitat, such as shallow unvegetated sediments. These patterns of habitat use by blue crabs are likely to vary among regions which have fundamentally different combinations of habitats: mangroves are not found north of Cape Canaveral; SAV is generally missing in some large systems like Delaware Bay; extensive marshes dominate some regions like the South Atlantic Bight and Gulf Coast, but are essentially absent from upper Chesapeake Bay; oyster reefs have been removed from other systems; low oxygen levels may make large areas of habitat uninhabitable for days to months. Symposium participants emphasize the need for much more comparative analyses of habitat use by the blue crab.

MOVEMENT.—Blue crabs exhibit a migratory life cycle, with juveniles dispersing to lower salinities to feed and grow, often reaching maturity in the upper reaches of estuaries, and with inseminated mature females then migrating down the estuary to return to high salinities to incubate and hatch broods of eggs (van Engel, 1958). Recent research has focused on female migration. In large systems like Chesapeake Bay, females may migrate distances of 200 km or more, and studies presented in the symposium considered the timing of female migration

with respect both to time lapsed since molting/mating and to season. Initial studies (Turner, 2000) indicate that following mating females remain in upper Chesapeake subestuaries to feed, and that migration occurs only later in the fall, typically weeks to three months after mating. The mechanism of migration remains poorly understood but involves two phases (Tankersley et al., 1998). Phase I migration involves movement of inseminated females down the estuary from the mating area to higher salinities, where brood incubation can be initiated. Phase II involves movement of brooding females to hatch their eggs at the mouth of the estuary or out onto the shelf (Tankersley et al., 1998). The discussion group raised questions concerning the mechanisms of Phase I migration, such as: what are the migration routes and habitat? what are energetic costs for active swimming or walking versus passive transport on tidal currents? and what is the orientation behavior used to navigate in migration? These questions require use of new technology (biotelemetry or data-logging tags) applied in the field rather than more conventional mark-recapture techniques or laboratory studies to distinguish ''normal movement'' from migration (Wolcott, 1995; Wolcott and Hines, 1996). Understanding migratory behavior is important for improved management actions to conserve inseminated females that are highly vulnerable to the fishery while they are in route to the protected spawning sanctuaries in certain U.S. states. Lipcius et al. (2003) indicate the importance of corridors of protected habitats to conserve spawning stocks of blue crabs.

Factors regulating juvenile dispersal and movement are also poorly understood, and symposium researchers posed several alternative hypotheses about mechanisms and stimuli for dispersal behavior. Intrinsic behavior and activity patterns appear to change during juvenile ontogeny, and early instars may exhibit the propensity to swim up in the water column (Blackmon and Eggleston, 2001), while at about instar J6–7 crabs swim less and become more benthic. If swimming is timed with tidal rhythms, then selective tidal stream transport is an effective mechanism for dispersing juveniles up estuary (e.g., Tankersley and Forward, 1994). However, this would not explain the apparent sequence of juvenile dispersal at about instar J6–7 after initial post-larval settlement into polyhaline sea grass beds. Instead, dispersal may be stimulated by density-dependent agonistic interactions of post-settlement juveniles that achieve high densities in SAV patches (Pile et al., 1996; Moksnes et al., 1997). In North Carolina sounds, juvenile dispersal from the settlement habitat appears to be strongly influenced by tropical storms and hurricanes that create major disturbance and push water, broken sea grasses, and crabs across the sound and into shallows along the mainland (Etherington and Eggleston, 2000). In these sound systems, juvenile dispersal by storms thus may be much more episodic than the typical estuarine conceptual model of seasonal dispersal along the salinity gradient.

PHYSIOLOGICAL STATE.—Blue crabs demonstrate in spectacular fashion that physiological state is a strong variable influencing ecological relationships and outcome of experiments. Much variation in blue crab ecology, such as habitat use and migration, is attributed to differences in gender (Van Engel, 1958). Molt stage affects such key ecological considerations as blue crab movement and activity level, feeding, habitat use, energetic demands, and susceptibility to predation/cannibalism (e.g., Wolcott and Hines, 1990; Shirley et al., 1990; Hines and Ruiz, 1995). Similarly, many aspects of these behaviors change during ontogeny (Pile et al., 1996; Moksnes et al., 1997). Autotomy in blue crabs also affects the outcome of ecological interactions (Smith and Hines, 1991; Juanes and Smith, 1995). Other variables of physiological state that are not so evident morphologically as molt stage, autotomy or life stage also may have profound effect on behavior and

ecology—hunger level and reproductive condition are good examples that symposium participants used for illustration. Researchers emphasized that the complex potential interactions of several such key physiological states as life stage, molt stage, and hunger level are rarely considered in combination in blue crab ecology, yet may have dramatic effects on more simplistic considerations of physiological states (see Hines et al., 1987, as one example). Improved models are needed to integrate such complex factors, and Brylawski and Miller (2003) evaluate the application of a fish physiological model to blue crab bioenergetics.

SCALE.—Symposium participants articulated the urgent need to "scale-up" results of ecological experiments to larger populations and fishery stocks. While funding and logistical considerations usually constrain the scale of controlled field experiments, a number of new approaches increasingly allow researchers to address larger scale processes. Geographic Information Systems (GIS) is an increasingly valuable tool for characterizing and analyzing habitat use/availability and movement. Modeling approaches, such as those assessing the relationship between source/sink subpopulations and metapopulation dynamics, provide new ways of integrating variation among demographic variables across large spatial scales.

Broad scale comparisons are increasingly important as more becomes known about the details of blue crab ecology in systems other than the long-standing paradigm of Chesapeake Bay: increasingly refined studies have developed rapidly in recent years in, for example, Delaware Bay, North Carolina sounds, Mobile Bay, and several other sites. While most aspects of blue crab ecology are, of course, similar among systems, there do appear to be some fundamental differences at large scales. At a very large scale, blue crab recruitment dynamics of larval settlement rates and postlarval predation rates appear to differ by at least an order of magnitude between Gulf Coast and East Coast estuaries, with higher larval ingress, settlement rates and rapid predation on post settlement juveniles by more diverse predators on the Gulf Coast (Heck and Coen, 1995; Rabalais et al., 1995; Morgan et al., 1996; Spitzer et al., 2003). At another large scale, migration patterns of female blue crabs appear to differ between East Coast systems with little migration away from the "home estuaries" and Floridian Gulf Coast systems with long distance migration out of estuaries and along shore toward Appalachicola Bay (Steele, 1991). Drivers to dispersal and habitat use in large, deeper, "drowned river valley estuaries" like Chesapeake or Delaware Bays may differ substantially from those in large, shallow sound systems like those of North Carolina, where tropical storms and hurricanes dramatically alter recruitment dynamics (Etherington and Eggleston, 2000). Blue crabs may exhibit much different scales of movement across the size range of bays and estuaries, where, for example, Phase I migration of females may range from <5 km in small systems to 200+ km in large estuaries. Seitz et al. (2003) found that blue crab density is driven by both food availability and hydrodynamic transport of larvae at broad spatial scales (10–50 km), whereas food availability is a primary control at smaller spatial scales (1–10 km) within a Chesapeake subestuary.

Many questions about scale of ecological processes are difficult to determine because of technical limits to sampling methods such as gear catch efficiency that is often unknown yet changing as a function of habitat, life stage or crab size, and density, especially for juveniles that require small mesh size. Biotelemetry provides some technical ways around these problems, but these approaches are typically expensive and constrained to small numbers of relatively larger (>60 mm CW) crabs (Wolcott, 1995; Wolcott and Hines, 1996). Nevertheless, researchers all acknowledge the need to evaluate processes across habitats and over larger spatial scales (Eggleston et al., 1998; Hovel and Lipcius, 2001), especially when

densities may be high in limited habitats (e.g., SAV) but may be low in habitats with vast spatial extent (e.g., non-vegetated sediments) (e.g., Seitz et al., 2003).

MODELING APPROACHES.—An increasingly diverse array of modeling approaches is being applied to blue crab research, including: conceptual models; individual based models; dynamic optimization models; stochastic models; spatially explicit models; and life-stage based models. The symposium group expressed excitement about using these approaches to produce models that are much more realistic and useful to address ecological problems than previous fishery population models for stock-recruit and recruit-stock relationships. Good examples include the life stage and spatially explicit model of the Chesapeake blue crab population (Miller, 2001) and the dynamic optimization analysis of foraging and movement of juvenile blue crabs (Terwin, 1999). At the same time, these modeling advances emphasized the glaring data gaps in fundamental blue crab demography, especially for key variables such as age at maturity, schedules of brood production, and longevity. The discussion group indicated that filling these demographic data gaps was a high research priority. The partnership of new modeling approaches and invigorated demographic research should guide fishery managers to develop more narrowly targeted and more effective regulations for blue crab stocks under intense fishing pressure. These models should also guide more integrative assessments of habitat value for a species with such high motility over its life cycle, emphasizing, for example, conservation of blue crab stocks through development of linked protected areas and corridors to ensure successful completion of all stages of the crab's full life cycle (Lipcius et al., 2003).

ANTHROPOGENIC IMPACTS AND ECONOMIC VALUE.—Assessing anthropogenic impacts on blue crab ecology is complicated by the many interactions of the species' life stages with a full range of coastal and estuarine habitats and the myriad of human activities affecting them all. In particular, researchers at the symposium emphasized the pervasive, interactive impacts of nutrient loading and habitat destruction, as well as fishing (considered in a separate section of this symposium issue). The pollution effects of eutrophication are well known to produce increased turbidity in the water column, increased epiphytic growth, and severe oxygen depletion (Rabalais and Turner, 2001). Turbidity along with increased epiphytic growth has destroyed much of the submerged aquatic vegetation (SAV) in estuaries, especially Chesapeake Bay (Moore et al., 2000). Because SAV is a key habitat for larval settlement, post-larval growth, and juvenile molting, the SAV loss has significant potential impacts on blue crab populations (e.g., Heck and Orth, 1980), directly through loss of this habitat or indirectly by causing blue crab and other species to shift to other habitats (Ruiz et al., 1993).

Oxygen depletion makes habitat unusable for blue crabs—especially deep channel habitat during water column stratification after periods of high freshwater runoff or summer surface heating—presumably forcing crabs to move into shallow water (Pihl et al., 1991). Low oxygen also impacts benthic food resources of blue crabs, and an important research question is how tolerance of low dissolved oxygen varies among infaunal prey species and epibenthic predators to regulate foraging dynamics in estuaries (Diaz and Roseberg, 1995). The dynamics may depend on duration and intensity of low dissolved oxygen. While prolonged anoxia typically kills infauna, creating "dead zones," infauna and epibenthic predators like blue crabs exhibit varying behavioral and physiological responses to short episodes of anoxia and degrees of hypoxia (Breitburg et al., 1997). If infauna move to the sediment surface or become less effective at escaping predators during periods of hypoxia, then crabs and other predators may exploit them at increased rates if the predators either are more tolerant of low dissolved oxygen or

are able to move rapidly back into the area of exposed prey when oxygen levels recover (Taylor and Eggleston, 2000). While adverse impacts of eutrophication on oxygen levels and SAV habitats are clear, the indirect effects of habitat loss and trophic interactions resulting from nutrient loading are complex and non-linear, requiring much more study at the ecosystem level.

Researchers at the symposium emphasized that management's valuation for the blue crab should encompass more than the dollar value of fishery landings and the cultural symbolism of the species from the mid-Atlantic to Gulf Coast. The importance of this top predator in the estuary carries major ecological value in the food web of the estuarine ecosystem, serving to transfer carbon from the benthos to the nekton (Baird and Ulanowicz, 1989). Ecosystem, community and population ecologists use the blue crab as a model system for a wide range of research problems of both theoretical and applied interest. Discussion at the symposium noted the marked increase in attention to blue crab fishery management as key stocks have suffered declines in recent years. While blue crab researchers are heartened by increased funding, they note that limited funding in past decades means many basic questions remain unanswered. Despite the current urgency for answers, newly focused research requires time to produce clear results, given the complexity of the crab's life cycle and intrinsic variability of estuarine systems that receive multiple human impacts.

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