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Natural mortality of blue crab: Estimation and influence on population dynamics

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Natural Mortality of Blue Crab:

Estimation and Influence on Population Dynamics

A Dissertation

Submitted to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

of the Requirements for the Degree of
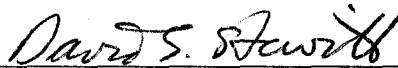
Doctor of Philosophy

by

David Allen Hewitt

2008

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the requirements for the degree of

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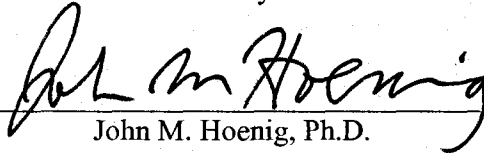
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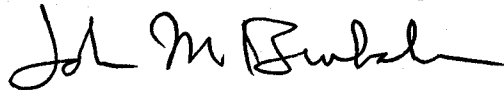
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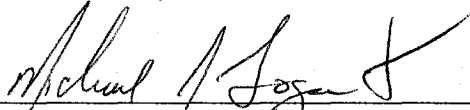
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To my wife, Mandy

"If one examines the traditional 'core' methods of fisheries stock assessment, ..., it is shocking to realize that all these methods assume that we have learned nothing from any previous experience in fisheries except perhaps that the natural mortality rate is likely to be 0.2."

HILBORN, R., & LIERMANN, M. 1998. Standing on the shoulders of giants: learning from experience in fisheries. *Reviews in Fish Biology and Fisheries*, **8**, 273-283.

"The current approach of merely assuming natural mortality to be a constant driven by unknown sources is not likely to be very informative."

CONOVER, D. 2000. Darwinian fishery science. *Marine Ecology Progress Series*, **208**, 303-307.

"Stock assessments offer great potentials—if they are rooted in correct assumptions."

CRONIN, L. E. 1998. Reactions to the blue crab symposium. *Journal of Shellfish Research*, **17**, 587.

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ABSTRACT

The blue crab *Callinectes sapidus* supports one of the most important fisheries in the Chesapeake Bay and is the leading contributor to blue crab landings in the United States. Assessment and management of blue crab stocks has been hampered by a lack of estimates of natural mortality rates, a key parameter in assessment models. In Chapter 2, we demonstrate that the approach used for estimating natural mortality that had been used in past assessments was flawed, and provide justification for a superior alternative. In Chapter 3, we synthesize our current understanding of natural mortality rates in adult blue crab and provide a suite of estimates for the Chesapeake Bay stock. Our estimates were used in the 2005 assessment for this stock, and the methods and estimates can provide guidance for assessments of the same or other species. In addition to estimates of natural mortality for adult blue crab, the short turnover time in the stock makes it necessary to consider changes in natural mortality rates with size or age. Current assessment models use an annual time step, which smooths over the changes in natural mortality that occur during ontogeny. Some crabs reach an exploitable size within the first year of life, and smaller crabs are expected to have higher natural mortality rates. In addition, natural mortality is known to vary seasonally, being highest in Chesapeake Bay during the summer months when predators are most abundant and crabs are molting frequently. To include size-dependent mortality in more realistic population dynamics models, we estimated mortality rates of juvenile crabs through field experiments (Chapter 4). In 2005 and 2006, we estimated mortality rates of seven cohorts of hatchery-reared juveniles in two tidal marsh creeks along the York River, Virginia during the summer and fall. Juvenile mortality rates were orders of magnitude higher than current estimates of adult mortality rates and were highest in the summer. Our results reinforce concerns about the adequacy of current assessment models and provide estimates of mortality that can be used to guide future work.

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Natural Mortality of Blue Crab:

Estimation and Influence on Population Dynamics

Chapter 1

Blue Crab in Chesapeake Bay: Life History and Fisheries Management

Blue crab life history

The blue crab *Callinectes sapidus* (Rathbun 1896; Decapoda: Brachyura: Portunidae) is the most widely distributed of the 15 or 16 species in the genus *Callinectes*, a genus of swimming crabs with its center of origin in the Atlantic neotropics (Williams 1974; Millikin & Williams 1984; Williams 2007). On the Atlantic coast, the blue crab has been reported from as far south as southern South America and as far north as Nova Scotia, Canada (Williams 1974). The blue crab has also been introduced elsewhere in the North Altantic and North Pacific Oceans and the Mediterranean and Black Seas (Millikin & Williams 1984).

The blue crab is an adaptable coastal species and its life history in Chesapeake Bay differs in some respects from its life history in lower latitudes (Tagatz 1968a; Hines 2007). Although blue crabs are tolerant of water temperatures as low as 0-3°C (Tagatz 1969; Williams 1974; Norse 1977), and can even continue to molt at temperatures as low as 3°C (Tagatz 1968b), individuals in temperate latitudes typically grow little and may enter a state of torpor in the winter when temperatures drop below about 9°C (Archambault *et al.* 1990; Smith & Chang 2007). During such periods crabs often aggregate and bury in muddy sediments in

deeper water (Jensen *et al.* 2005; Jensen & Miller 2005), but quickly become active again when water temperatures rise above about 9°C (Van Heukelem & Sulkin 1990). Juveniles and adults are more tolerant of temperature extremes in higher salinities (Tagatz 1969; Van Heukelem & Sulkin 1990), which may explain the greater incidence of winter mortality in the colder, less saline northern portions of Chesapeake Bay (Uphoff 1998; Sharov *et al.* 2003; Rome *et al.* 2005; Bauer 2006).

Blue crabs are tolerant of extreme salinities (Tagatz 1968a; Williams 1974; Guerin & Stickle 1992), but certain periods of their life history appear to be evolutionarily adapted to specific salinity ranges. In Chesapeake Bay, males and females mate primarily in the spring and summer in the shallow, low salinity areas of creeks and rivers (Van Engel 1958). Inseminated females throughout the Bay migrate to more saline areas near the mouth of the estuary to develop broods, or sponges (Van Engel 1958; Turner *et al.* 2003; Aguilar *et al.* 2005). Females that mate later in a given year may delay migration and spawning until the following spring (Van Engel 1958; Jivoff *et al.* 2007). Male blue crabs tend to remain in shallow, less saline regions of tributaries, sometimes as far upstream as tidal freshwater areas (Van Engel 1958; Hines *et al.* 1987). Differences in osmoregulatory capabilities between male and female blue crabs (Tan & Van Engel 1966) may in part explain female preferences for higher salinity regions of estuaries (Tagatz 1968a; Hines *et al.* 1987).

Whereas males continue to grow and molt after they reach sexual maturity and can mate more than once, female blue crabs and females of other Portunid species mate at the same time that they undergo their last molt and become sexually mature (Van Engel 1958). Females can spawn more than once using the sperm transferred from their only mating and can produce millions of eggs (Van Engel 1958; Tagatz 1968a). Fecundity is limited by and related to size (Hines 1982; Prager *et al.* 1990), and reproductive output declines with subsequent spawns (Hines *et al.* 2003). The eggs are carried attached to the abdomen and develop over a period of about two weeks, changing color from orange to black as the yolk is absorbed and the eyes develop (Sandoz & Rogers 1944).

Mated females presumably seek out higher salinities for brood production because higher salinities are required for successful hatching and larval development (Sandoz & Rogers 1944; Costlow 1967). Based on the preponderance of the laboratory and field evidence, Norse (1977) suggested that the poleward limits of the distribution of blue crab and other *Callinectes* species were not limited by cold winter water temperatures, but rather by summer temperatures below 20°C that are insufficient for egg hatching and larval molting and survival. Egg hatching in Chesapeake Bay occurs mostly during the warmer months of the late spring and summer near the mouth of the estuary or in the shallow coastal ocean (Sandifer 1973; McConaugha *et al.* 1983), and may occur in two peaks (Van Engel 1958; Jones *et al.* 1990). Larvae (zoeae) are transported out into the open water on the continental shelf (Tagatz 1968a; Sulkin *et al.* 1980; Provenzano *et al.* 1983), where development proceeds through seven (rarely eight; Sandoz & Rogers 1944; Costlow & Bookhout 1959; Costlow 1965) zoeal stages prior to metamorphosis into postlarvae (megalopa[1]) (Costlow & Bookhout 1959; Williams 1965).

Development from hatching to postlarvae takes one to two months and appears to be fastest at salinities between 21 and 28 ppt and water temperatures between 19 and 29°C (Sandoz & Rogers 1944; Costlow & Bookhout 1959; Smith & Chang 2007). Field collections have shown that larvae and postlarvae are most abundant in salinities and temperatures consistent with ranges shown to be optimal for survival, growth, and development in the laboratory (in the lower Chesapeake Bay – Sandifer (1973) and Olmi (1995); in other estuaries – Tagatz 1968a and others reviewed in Sandifer 1973). However, salinity and temperature are correlated with other factors that affect larval and postlarval distribution (Olmi 1995), and some collections have indicated that larval and postlarval survival and development are more flexible than laboratory studies have shown (Van Engel 1987; van Montfrans *et al.* 1995).

Postlarvae rely on advective transport to return to estuaries. Larval and postlarval dis-

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[1]Based on the summary in Kennedy (2007), I use the term *megalopa* to refer to the postlarval stage in both singular and plural forms.

persal from, retention in, and reinvasion of estuaries has received more research attention than any other aspect of blue crab population dynamics. In Chesapeake Bay, postlarval recruitment occurs primarily between August and November (van Montfrans *et al.* 1990; Olmi 1995; van Montfrans *et al.* 1995). River discharge, tidal range, the effects of winds on surface currents, lunar phase, and vertical migrations of megalopae all appear to play substantial and related roles in the processes leading to postlarval recruitment (McConaugha *et al.* 1983; Johnson *et al.* 1984; Johnson 1985; Goodrich *et al.* 1989; Johnson & Hester 1989; Johnson & Hess 1990; Boylan & Wenner 1993; Epifanio 1995; Johnson 1995; Olmi 1995; Perry *et al.* 1995; Rabalais *et al.* 1995; Morgan *et al.* 1996; Garvine *et al.* 1997; Roman & Boicourt 1999; Etherington & Eggleston 2000; Hasek & Rabalais 2001; Etherington & Eggleston 2003; Perry *et al.* 2003; Forward *et al.* 2004b). As a result, postlarval abundance is highly episodic and variable within and among years and sites (Mense & Wenner 1989; Olmi *et al.* 1990; van Montfrans *et al.* 1990; Boylan & Wenner 1993; Olmi 1995; Perry *et al.* 1995; Rabalais *et al.* 1995; van Montfrans *et al.* 1995; Morgan *et al.* 1996; Pardieck *et al.* 1999; Hasek & Rabalais 2001; Perry *et al.* 2003; Spitzer *et al.* 2003; Forward *et al.* 2004b).

Postlarvae may or may not actively select settlement habitats (Pardieck *et al.* 1999; Orth & van Montfrans 1987, 1990; van Montfrans *et al.* 1995; Morgan *et al.* 1996; van Montfrans *et al.* 2003), but they are typically most abundant in protective structured habitats in the lower regions of estuaries and tributaries, such as areas of submerged aquatic vegetation (SAV; Orth & van Montfrans 1987; Pile *et al.* 1996; Etherington & Eggleston 2000; Orth & van Montfrans 2002) or inundated emergent salt marsh vegetation (Morgan *et al.* 1996). The postlarval stage lasts about a week in the laboratory (Costlow & Bookhout 1959), and postlarvae metamorphose into first stage juvenile crabs soon after settlement (Lipcius *et al.* 1990; Metcalf & Lipcius 1992; Morgan *et al.* 1996).

Juvenile crabs redistribute throughout tributary creeks and rivers and are often a numerically dominant component of the benthic assemblage in shallow areas of estuaries throughout their range. Structured habitats like SAV and emergent salt marsh vegetation have

commonly been accepted as the most important nursery areas for postlarval and small juvenile blue crabs (Heck & Thoman 1984; Williams *et al.* 1990; Perkins-Visser *et al.* 1996; Beck *et al.* 2001; Heck *et al.* 2003; Minello *et al.* 2003; Lipcius *et al.* 2005). However, ontogenetic changes in habitat use for small juvenile blue crabs are not well understood, particularly as they relate to density-dependence and emigration (Orth & van Montfrans 1987; Williams *et al.* 1990; Pile *et al.* 1996; Moksnes *et al.* 1997; Ryer *et al.* 1997; Pardieck *et al.* 1999; Etherington & Eggleston 2000; Heck *et al.* 2001; Etherington & Eggleston 2003; Etherington *et al.* 2003; Spitzer *et al.* 2003; Reyns & Eggleston 2004; Rakocinski & McCall 2005; Lipcius *et al.* 2007). Such habitat changes are likely influenced by numerous interactive factors operating at multiple spatial scales. In general, habitat changes are difficult to detect and measure accurately, and inferences about processes may not transfer among estuaries. In the lower Chesapeake Bay, high variability in the magnitude of recruitment and rapid changes in distribution and abundance may make it impossible to determine such changes in habitat use in all but the most temporally and spatially comprehensive sampling (e.g., Etherington & Eggleston 2000, 2003).

Regardless of the relative importance of various estuarine habitats, structured habitats like SAV provide protection from predators for the smallest blue crabs and also for larger crabs during molting (Ryer *et al.* 1990, 1997). Unfortunately, structured habitats are being degraded throughout Chesapeake Bay and other estuaries (Orth & Moore 1983; Minello & Rozas 2002; Stockhausen & Lipcius 2003; Lipcius *et al.* 2005; Orth *et al.* 2006; Rozas *et al.* 2007). Unstructured habitats, such as the muddy, detrital areas along marshes and the lower reaches of tidal creeks, are also important as molting and foraging areas for juvenile and adult crabs (Tagatz 1968a; Hines *et al.* 1987; Mense & Wenner 1989; Williams *et al.* 1990; Wilson *et al.* 1990; Etherington & Eggleston 2000; Minello *et al.* 2003; Rakocinski *et al.* 2003; Spitzer *et al.* 2003; King *et al.* 2005; Lipcius *et al.* 2005; Rakocinski & McCall 2005; Seitz *et al.* 2005).

Blue crabs are omnivorous (Williams 1965; Tagatz 1968a; Mansour 1992), and although

growth rates of blue crabs are rapid and highly variable (Tagatz 1968a,b; Ju *et al.* 2001), overall growth rates do not appear to be strongly affected by salinity (Tagatz 1968b; Cadman & Weinstein 1988; Guerin & Stickle 1997; Smith & Chang 2007). Once metamorphosis into the first crab stage occurs, individuals may undergo 18 or more molts before reaching maturity (Newcombe *et al.* 1949; Van Engel 1958). Individuals in Chesapeake Bay can develop from hatching to a size that makes them available to the commercial fishery (about 75 mm, or 3 inches) within their first year of life, though on average it takes somewhat longer (Williams 1965; Hines *et al.* 1987; Van Engel 1987; Smith & Chang 2007).

Fisheries and management in Chesapeake Bay

The blue crab is woven into the culture and economy of the Chesapeake Bay region more intimately than perhaps any other aquatic species (Warner 1976). The blue crab has supported an important commercial fishery in the Bay since the late 1800s, but the nature of the fisheries changed considerably in the late 1930s, in large part because of the introduction of the commercial crab pot (Van Engel 1962; Rothschild *et al.* 1981; Cronin 1998; Rugolo *et al.* 1998a; Van Engel 1999). Once consistent records were kept, commercial harvest of blue crab in Chesapeake Bay varied in a periodic fashion from the 1920s through the 1970s (Hurt *et al.* 1979), occasionally leading to disastrous forecasts in the periods of low abundance (Van Engel 1987; Rugolo *et al.* 1998a). Similar to observations for Dungeness crab on the west coast of the US (Higgins *et al.* 1997b), harvest tended to swing up and down over periods of a decade or more, but the factors responsible for the periodicity were elusive (Van Engel 1987). Peak harvests occurred around 1950 and during the mid 1960s, and these peaks remain the largest harvests on record (Miller *et al.* 2005; CBSAC 2007). More recent harvest and abundance monitoring indicate that periodic fluctuations continued through the 1980s.

Unfortunately, the blue crab population has experienced a serious decline in abundance that appears to have begun in the early 1990s, breaking the periodic cycle (Lipcius &

Stockhausen 2002; Jensen & Miller 2005; Miller *et al.* 2005; CBSAC 2007). A zooplankton survey indicated a decline in larval abundance and postlarval recruitment that began around 1991, which may have triggered the overall decline (Lipcius & Stockhausen 2002). Fishery-independent monitoring indicates that recent population size may be as little as 50% of the abundance observed in the early 1990s. Specific indices of spawning stock abundance in Virginia show more dramatic declines than other indices of population size (Lipcius & Stockhausen 2002; Miller *et al.* 2005; CBSAC 2007). Similar discrepancies between indices of overall abundance and spawning stock size have been noted in other blue crab populations (Kahn *et al.* 1998).

Reflecting this low abundance, recent commercial harvests have been the lowest on record since reporting began in 1945 (Figure 1.1; Miller *et al.* 2005; CBSAC 2007). Although the population appears to be stable at its current lowered abundance, high exploitation is probably preventing the population from rebounding to former abundances. Key life history features of the blue crab indicate that the population should rebound, and has rebounded in the past, given appropriate controls of effort in the fisheries (Van Engel 1987; Miller *et al.* 2005; Chapter 3). Despite the reduced recruitment and abundance, the blue crab fishery remains consistently one of the highest value fisheries in the Bay and is the leading contributor to the total U.S. landings of blue crab (Fogarty & Lipcius 2007; NMFS 2007).

A pattern of large fluctuations in abundance followed by a rapid decline, like that observed for the blue crab stock in Chesapeake Bay, has been observed for other fish and crustacean stocks. Prager *et al.* (1990) noted that the blue crab shares many life history features with fish stocks that have undergone similar sharp declines following intense exploitation. Such a pattern was also demonstrated for a number of king crab stocks in the eastern Bering Sea, and Otto (1986) attributed the stock declines to environmental effects on recruitment and increases in natural mortality. Large increases in natural mortality in king crab stocks have at times appeared to be linked to outbreaks of nemertean brood symbionts that cause serious egg mortality (Kuris *et al.* 1991). Disease has been suggested as a major influence
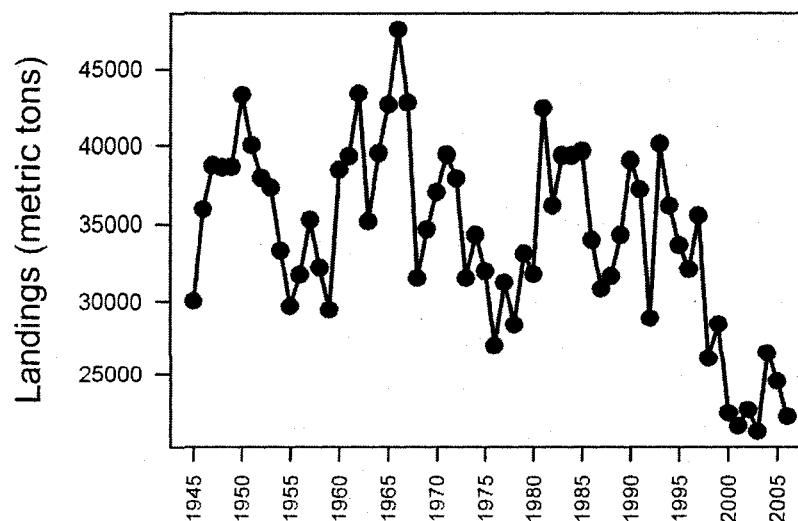
Figure 1.1: History of commercial landings of blue crab in Chesapeake Bay, 1945-2006 (data from CBSAC 2007).

on blue crab mortality (Noga *et al.* 1998), especially given continuing degradation of water quality, but no comprehensive assessment of blue crab diseases in Chesapeake Bay has been undertaken.

More generally, Jamieson (1986) described the history and management of a variety of invertebrate fisheries in British Columbia and made a number of observations that are particularly applicable to blue crab in Chesapeake Bay:

1. Stocks changed rapidly from an apparently stable state to a depleted state, and often the change was not clearly recognized until it was over. He suggested that such rapid changes should be expected when the relationship between stock and recruitment is uncertain and exploitation is intense, and that they would be least detectable when fisheries do not capture juvenile stages (i.e., no early warning system).

2. Initial reactive management struggled because advice and information were needed about species for which little biological information was available, and scientists studying the species were not adequately trained to respond to the needs of management.

The scientists studying these local populations were trained as "pure" ecologists and were not equipped to answer questions about population dynamics and the effects of fishing.

3. Collection of accurate catch and effort data took a low priority and was complicated by widespread and diffuse landings, a consequence of the artisanal nature of the fisheries.

A number of the fisheries for blue crab capture juveniles, such as the scrape fishery in seagrass beds and other collections for soft crab operations. However, no system was in place to officially monitor catches of juvenile crabs and the decline in recruitment that occurred in the early 1990s caught management agencies off guard. Furthermore, the impending decline may have been impossible to detect even with a monitoring program in place due to the rapid nature of the decline. Recruitment fell by more than 50% over a period of only one to two years (Lipcius & Stockhausen 2002; CBSAC 2007).

Management reaction to the decline was complicated by a debate over whether an actual decline had occurred or whether it was merely a low phase in the abundance cycles that had been observed previously. Collection of data on catches was obfuscated by reporting system changes and by the artisanal nature of the fisheries; a complex network of watermen, dealers, and processors collected and distributed blue crab products to market. The development of a comprehensive data collection system for the commercial fisheries remains a goal of management agencies today (Miller *et al.* 2005; CBSAC 2007). As a result, little reliable fishery-dependent data was available to assess population dynamics and the causes of the decline; the first Baywide assessment of the stock was not completed until 1997 (Rugolo *et al.* 1997). Similar struggles to assess and manage blue crab stocks have occurred throughout the Gulf of Mexico (Guillory *et al.* 1998).

The history of management for the blue crab stock in Chesapeake Bay is typical of traditional, inshore invertebrate fisheries. Such fisheries often expand with an increasing human population in coastal areas that favors local and regional seafood products (Rugolo *et al.* 1998a). Management reacts to perceived increases in exploitation with simple,

"untested" regulations that seem appropriate as modest controls (Jamieson 1986; Van Engel 1987; Cronin 1998; Perry *et al.* 1998). As increasing exploitation shows stronger effects on populations, more and more stringent regulations are added as logistics and stakeholder acceptability allow. This reactive style of management was typical of most early commercial fisheries in the United States, and was common for fisheries in the Chesapeake Bay. Unfortunately, this style of management leads to a disjunct web of restrictions and regulations that are difficult to enforce, and the effectiveness of individual management measures is impossible to assess.

The fisheries for blue crab in Chesapeake Bay were regulated to some degree as early as 1900, but the earliest fluctuations in landings appeared to be affected more by environmental factors than regulations (Van Engel 1999). Over time, various regulations were developed in Maryland and Virginia to control effort and conserve the stock in the face of rising exploitation. Current and past regulations for the blue crab fisheries in Chesapeake Bay include:

- effort and gear restrictions, such as seasonal closures, limits on the time of day when crabbing is permitted, limits on the number of pots, and specified configurations for pots, scrapes, trotlines, dredges, and pounds;

- size and catch limits, including minimum sizes and bushel (pot fishery) and barrel (dredge fishery) limits; and

- restrictions specifically designed to protect the female spawning stock, including spawning area closures and limits on possession of sponge crabs (egg-bearing females).

Despite the imposition of so many regulations, and perhaps because of it, management agencies struggle to determine whether specific regulations are having the desired effect and find it difficult to confidently develop stock rebuilding plans.

As an example, the sanctuary implemented to protect the female spawning stock in Virginia (Van Engel 1958; Seitz *et al.* 2001) appears to protect females that make it to

the spawning grounds (Lambert *et al.* 2006a), but estimates of spawning stock abundance have shown no recovery. Lack of recovery indicates that the protection must be extended to females prior to their migration to the spawning grounds. As noted by Orensanz *et al.* (1998) for crustacean stocks in Alaska, "... the loss of reproductive contribution by a given female is the same whether she is harvested before or during the spawning season. While frequently implemented in fisheries worldwide (and often well accepted by fishermen), spawning season closures do not have the intended effect and are unlikely to circumvent the risk of recruitment overfishing."

Meanwhile, the blue crab stock in Chesapeake Bay has not been restored to historically higher abundances. The resilient nature of blue crab populations provides hope that the population can rebound, but management jurisdictions will need to define goals for the fishery and develop a more comprehensive management plan in cooperation with stakeholders (CBSAC 2007). In many ways the situation has changed little since the early 1980s (Rothschild *et al.* 1981). A particular difficulty, given the lack of organization among independent-minded watermen, will be the identification of both ecological and economic objectives that are acceptable to a majority of resource users (Johnson *et al.* 1998).

Once goals and objectives are defined, management will proceed most effectively if scientific advice can be provided in the context of alternative strategies. Ideally, the consequences of alternative management strategies can be evaluated by condensing existing knowledge through modeling (Hilborn & Walters 1992; Holt 1998; Walters & Martell 2004). Similar to many fisheries throughout the world, management strategies for the Chesapeake Bay blue crab will need to focus on reducing fishing capacity and providing appropriate incentives to watermen to maintain healthy stocks (Guillory *et al.* 1998; Rugolo *et al.* 1998a; Paolisso 2002; Pauly *et al.* 2002; Hilborn *et al.* 2005; Hilborn 2007a,b). Rights-based, limited entry systems of management have been highly successful in many fisheries worldwide. A limited entry scheme has been implemented for the winter dredge blue crab fishery in Virginia and should be considered for other blue crab fisheries as well. Such schemes have already been

discussed in Alabama, Georgia, North Carolina, and Delaware (Cole 1998; Evans 1998; Heath 1998; Henry & McKenna 1998; Johnson *et al.* 1998). Assessment models for blue crab have thus far provided traditional stock assessment advice concerning the effects of fisheries on yield, but have not incorporated any form of decision or risk analysis to guide policy development. Such advances will require more detailed definition of objectives and better coordination in data collection among the various Bay jurisdictions and institutions. Progress will also depend on continued investment in stock assessment, which is relatively young for blue crab and other crustaceans (Smith & Addison 2003).

Stock assessment and estimation of natural mortality

In stock assessments, scientists synthesize existing data and develop models to understand the dynamics of gains and losses in the stock or population of interest. The goal of an assessment is to make quantitative predictions about the reaction of the stock to management actions (Hilborn & Walters 1992), which are designed to control the losses from the population that are caused by humans – the exploitation rate, or fishing mortality rate. Essentially, stock assessments are intended to provide guidance about how much biomass or how many individuals can be harvested from a stock, in addition to natural losses, that will be balanced by natural gains through recruitment. Ideally, the harvest is estimated accurately and precisely and can be maintained through management, leading to a sustainable fishery and a stock that remains a relevant, functioning component of its ecosystem. Of course, biological assessment is only one part of the management process and ultimate decisions about harvest levels must incorporate social, political, and economic concerns; these are especially formidable challenges for blue crab management (Johnson *et al.* 1998; Paolisso 2002).

Stock assessment of invertebrate resources is often complicated by a lack of clear priorities and objectives for research that feeds into the assessment process. Research studies are often focused on biological and ecological questions at relatively small scales, and data

collection at scales relevant to stock assessments is lacking (Incze *et al.* 2003). At a minimum, assessments typically require measures of relative stock abundance and estimates of the amount of catch extracted from the stock with known levels of effort. One of the most serious limitations of stock assessment for blue crab in Chesapeake Bay is the lack of coordinated collection of data on the amount of effort expended in the various fisheries (CBSAC 2007), a difficulty shared with other blue crab stocks (Guillory *et al.* 1998).

Assessments account for the gains to populations through births or immigration from outside areas, and losses from the population through deaths or emigration from the area of interest. Immigration and emigration in fish and wildlife populations often occur because of ontogenetic changes in habitat requirements or as a result of the territoriality of conspecifics. However, fishery stock assessments are typically conducted at spatial scales specified to define the population by boundaries across which little migration is anticipated to take place. Genetic analyses are now commonly used for stock delineation, but direct sampling should be used to verify genetic conclusions (Tringali *et al.* 2008). Specification of spatial scales to align with the definition of a unit stock is a common approach to simplify modeling, and such an approach is used for blue crab assessment in Chesapeake Bay (Miller *et al.* 2005).

If immigration and emigration can safely be ignored, assessments need only to account for the gains to the population through births (spawning and subsequent recruitment) and the losses from the population through deaths (mortality). In most fisheries it is ecologically and economically prudent to take animals from the population only after a certain amount of growth has occurred. Assessments usually focus on the population of animals that are larger than the minimum size at which they are taken by the fishery; animals above this size are considered recruits in the context of the fishery and the assessment. Thus, the gains of interest in assessment models are the number of recruits to the exploited population. Dynamics that occur prior to recruitment are ignored except for their effects that are manifested in the number of recruits.

Mortality is modeled as a process of exponential loss from the population (Figure 1.2),
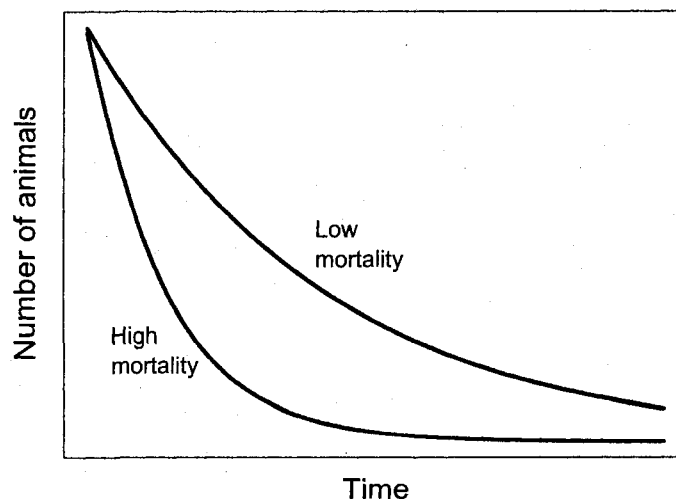
Figure 1.2: Mortality as a process of exponential loss.

and the rate of loss is one of the key parameters to be estimated by an assessment model. In fisheries stock assessments, mortality is accounted for in two components: the rate of natural mortality (M) and the rate of fishing mortality (F). Most models use an instantaneous rates formulation for mortality, wherein instantaneous rates (IM) are directly related to proportional annual mortality (PM) as $PM = 1 - e^{-IM}$ (Figure 1.3). Natural mortality is caused by senescence (old age), predation, disease, and other natural or anthropogenic effects on environmental quality. Fishing mortality is prescribed to include only the mortality caused by the direct removal of animals by the fishery. Unless specifically accounted for, incidental mortality, including direct or indirect mortality associated with bycatch and discarding, is included in natural mortality.

Mortality is modeled as an additive process, such that the total mortality rate for the population (Z) is the sum of M and F. Assessment models are used to estimate the rate at which animals are killed by the fishery, F, and to provide guidance about what amount of fishing mortality the stock can support. Because mortality is an additive process, M has direct effects on model predictions about F. Generally, stocks with higher M are more
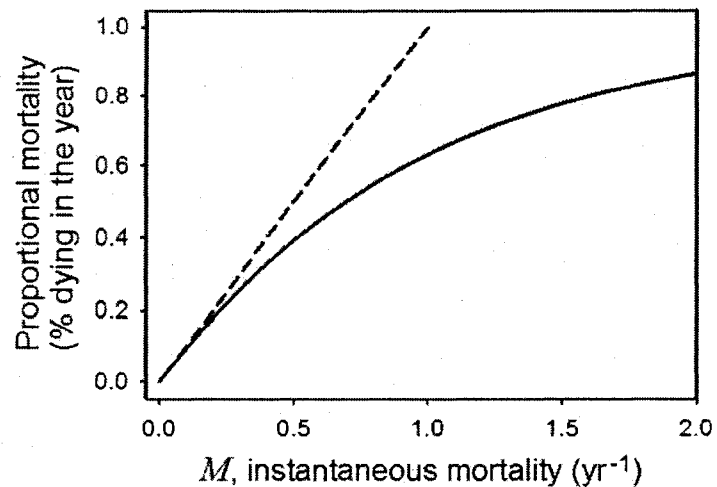
Figure 1.3: Relationship between instantaneous rate of mortality used in assessment models and the proportional annual mortality of animals in the stock. The solid line shows the relationship between the two measures of mortality and the dashed line shows the 1:1 line for reference. For values of M above about 0.4, the instantaneous rate exceeds the proportional mortality.

productive and can support more intense removal rates.

Management targets and strategies for rebuilding depressed stocks are highly dependent on the rate of natural mortality that is assumed in assessment models. Clark (1999) found that for stocks with relatively small M (< 0.3), the fishing mortality target could be double what it should be if M is overestimated by as little as 0.1. Such changes in recommended targets for F can make the difference between continuing depression of the stock and recruitment failure and a successful management scheme that leads to rebuilding. For red king crab in Alaska, Zheng *et al.* (1997a) evaluated strategies to rebuild the stock after a period of overfishing given considerable uncertainty about M. They investigated management scenarios with low and high values of M (low = 0.2-0.3, high = 0.4-0.6), and found that the time it would take for the stock to achieve an abundance considered "rebuilt" nearly doubled with the higher M. Thus, what appear to be small changes in estimates of M can lead to large differences in predictions about stock dynamics.

$$M = \; ?$$
$$M = \; ?$$
$$M = \; .2$$
$$M = \; .2$$
$$M = 0.2$$
$$EUREKA \; ! \; ! \; !$$

Figure 1.4: Pope (1975) suggested that the estimation of M was little better than guesswork.

Review of estimates of M in crustaceans

The estimation of natural mortality has been a major concern for stock assessments for many years. In 1975, recognizing the general difficulty in estimating M, John Pope suggested that the common value for M of 0.2 was a result of little more than guesswork (Pope 1975; Figure 1.4). New and better methods are developed all the time, but the estimation of M remains a substantial challenge to fisheries stock assessment (Quinn & Deriso 1999).

Direct estimates of M for crustaceans are few and far between (Addison 1997; Caddy 1986b; Fogarty & Murawski 1986). In particular, the discontinuous nature of crustacean growth poses two primary difficulties for the estimation of natural mortality:

1. growth through molting eliminates retained hard parts that could be used for ageing and age-based growth analyses; and

2. external tags are lost during molting, which complicates or eliminates the application of tagging studies to estimate mortality rates.

Even in cases where tags can be applied, such as for adult blue crabs, relying on reported

catches of tagged animals from a fishery to estimate the longevity in the absence of fishing is dubious. Due to a lack of guidance from other published studies, estimates of M for crustacean stock assessments are often based on indirect approaches developed for fish stock assessment (see Chapter 3).

Some trends in natural mortality rates across taxa are expected based on simple life history theory that addresses the trade-offs between mortality on the one hand and growth and reproduction on the other. For example, animals that are smaller in size, have higher fecundity, live relatively shorter lives, and grow faster tend to have higher natural mortality rates. Characteristic crustacean species would include shrimp and small crabs. At the other end of the scale are animals that live longer, grow slower, and have larger maximum sizes, like clawed lobsters and large crabs. The idea behind the indirect methods is to make predictions about M for a new stock with certain life history characters based on the empirical relationship between those characters and M for stocks in which M has been estimated.

Some direct estimates of M are available for stocks of commercially important shrimp, crab, and lobster species (Table 1.1). A variety of direct estimation methods have been applied to crustacean stocks, including tagging studies, length-frequency analysis, and estimation of M as a parameter in a population dynamics model. Probably the most reliable direct methods for estimating M are tagging studies, and a great deal of work has been done in developing models to analyze tagging data to estimate mortality rates. Tagging studies have been used to estimate M for some crustaceans for which tag retention is high or can be estimated. Mortality rates for shrimp are usually very high, and large numbers of tags are needed to generate sufficient numbers of tag returns. Xiao & McShane (2000) estimated M to be around 1.2 for western king prawn based on returns from an initial deployment of over 40,000 tags. Siddeek (1991) used a number of smaller experiments, each with about 1,000 tags, and estimated M to be 2.4 for grooved tiger prawn. Xu *et al.* (1995a) were able to estimate M in the absence of a tagging study by taking advantage of a fishery closure. By

Table 1.1: A compilation of direct estimates of M for some exploited crustacean stocks.

Species	M	Number tagged	Study
Western king prawn *Penaeus latisulcatus*	$1.12 - 1.24$	> 40,000	Xiao & McShane (2000)
Grooved tiger prawn *Penaeus semisulcatus*	2.40	ca. 2,000	Siddeek (1991)
Green tiger prawn *Penaeus semisulcatus*	$2.80 - 5.30$	NA	Xu *et al.* (1995a)
Red king crab *Paralithodes camtschaticus*	$0.54 - 0.70$	ca. 10,000	Siddeek *et al.* (2002)
Blue king crab *Paralithodes platypus*	0.19	> 2,700	Siddeek *et al.* (2002)
Golden king crab *Lithodes aequispinus*	$0.38 - 0.57$	ca. 10,000	Siddeek *et al.* (2002)
Southern rock lobster *Jasus edwardsii*	0.12	> 5,000	Frusher & Hoenig (2003)

estimating Z during a period when fishing was not occurring ($Z = M$), they estimated M to be 2.9-5.3 for green tiger prawn.

Natural mortality rates are typically lower for larger species like crabs and lobsters. Siddeek *et al.* (2002) estimated M for three king crab species in Alaska based on tagging experiments. The estimates ranged from 0.2 to 0.7, but they noted that the results were uncertain (95% confidence intervals all included zero). Using tag return data from about 5,000 tagged southern rock lobsters in Australia, Frusher & Hoenig (2003) estimated M to be 0.12, which is similar to other values that are used for lobster assessments for this and other species. Overall, estimates of M for crustaceans vary widely, from as little as 5% mortality per year for some lobster species to 99% per year for shrimp. Estimates for crab species appear to be intermediate between these two extremes, but animal size appears to be a strong determinant of natural mortality rate.

Problem statement and objectives

Natural mortality rates for crustaceans are poorly understood, but are central to population dynamics models used to make predictions about fisheries and stock sustainability. In this dissertation, I examine methods for estimating natural mortality, with specific application to blue crab and the effects of M estimates on fishery assessment and management. In Chapter 2, I demonstrate that a method for estimating M based on lifespan, which has been used often in blue crab assessments, requires an unnecessary but strong assumption and should be replaced by an alternative method when longevity is used to estimate M. This work grew out of the 2005 stock assessment update for Chesapeake Bay blue crab, but has already seen application in assessments of other stocks and species. The approach discussed in Chapter 2 relies on estimates of longevity, and longevity is not well understood for blue crab. In Chapter 3, I present a more comprehensive approach to estimating natural mortality rates for adult blue crabs in Chesapeake Bay, and provide direct and indirect estimates of M that do not rely solely on lifespan. Finally, in Chapter 4 I report on field experiments designed to estimate mortality rates of small juvenile blue crabs in the York River, Virginia, and discuss the implications of size-dependent mortality for stock assessment and management.

Chapter 2

Comparison of Two Approaches for Estimating Natural Mortality Based on Longevity[1]

Introduction

Vetter (1988) noted that her review of the estimation of the instantaneous natural mortality rate (M) was initiated by a discussion among colleagues that identified M as the single most important but least well-estimated parameter in fishery models. Although much has been accomplished in the intervening years, M remains one of the most difficult parameters to estimate in fishery stock assessments. A number of novel approaches using tagging and telemetry data provide promise for making reliable direct estimates of M for a given stock (Hearn *et al.* 1998; Frusher & Hoenig 2001; Hightower *et al.* 2001; Latour *et al.* 2003; Pollock *et al.* 2004). However, such methods are often impracticable and fishery scientists must approximate M by using estimates made for other stocks of the same or similar species or by predicting M from features of the species' life history (Beverton & Holt 1959; Beverton 1963; Alverson & Carney 1975; Pauly 1980; Hoenig 1983; Peterson & Wroblewski 1984; Roff 1984; Gunderson & Dygert 1988; Chen & Watanabe 1989; Charnov 1993; Jensen 1996; Lorenzen 1996).

We are concerned with two approaches for predicting M based solely on the longevity of the members of a stock – an approach that can be used when data are not available to make direct estimates of the parameter. One is a linear regression model (Hoenig 1983) and the other is a simple rule-of-thumb approach. Hoenig (1983) found that M was inversely correlated with longevity across a wide variety of taxa and recommended use of the following predictive equation relating the maximum age observed in the stock (t_{max}) to M:

$$ln\left(\hat{M}\right) = 1.44 - 0.982 * ln\left(t_{max}\right). \tag{2.1}$$

The rule-of-thumb approach consists of determining the value of M such that $100\left(P\right)\%$ of the animals in the stock survive to the age t_{max}; thus,

$$\hat{M} = \frac{-ln\left(P\right)}{t_{max}}. \tag{2.2}$$

The challenge in this approach is determining an appropriate value for the proportion P.

The rule-of-thumb approach has the potential to be used widely because it is presented in Quinn & Deriso (1999) and stock assessment manuals of the Food and Agriculture Organization of the United Nations (FAO; Sparre & Venema 1998; Cadima 2003). The approach has recently been used extensively, in the specific form $M \approx 3/t_{max}$, in work related to stock assessments for blue crab (*Callinectes sapidus*). In this note, we 1) show that the regression model and the rule-of-thumb approach can be compared directly; 2) illustrate the difference in the estimates of M generated by the two approaches; 3) discuss the origins and current use of the rule-of-thumb approach; and 4) recommend that the regression model be used instead of the rule-of-thumb approach.

Methods

With the rule-of-thumb approach, the fraction of a population that survives to a given age is used to estimate M. This approach is equivalent to a quantile estimator (Bury 1975). Suppose the fraction surviving to age t is described by the negative exponential function

$$\frac{N_t}{N_0} = e^{-Zt},$$ (2.3)

where Z is the total instantaneous mortality rate. The quantile estimator is of the form

$$P = e^{-Z\tau_P},$$ (2.4)

where τ_P is the age at which $100\,(P)\,\%$ of the population remains. In the case where $P = 0.05$, the estimator, based on data from a sample of the population, is

$$0.05 = e^{-\hat{Z}t_{0.05}},$$ (2.5)

where 5% of the animals in the sample are older than age $t_{0.05}$.

To estimate M, an empirical approach is usually taken where $t_{0.05}$ is replaced with t_{max}:

$$0.05 = e^{-\hat{M}t_{max}},$$ (2.6)

where t_{max} is either the oldest age observed in the stock or the oldest age found in the literature for the species of interest. When age composition data are used from an exploited stock, Equation 2.6 will provide an estimate of M only if fishing mortality is reasonably close to zero ($M \approx Z$) or if there is a refuge where older animals can accumulate. If exploitation affects all animals in the stock, Equation 2.6 is unlikely to provide a reliable estimate of M.

The rule of thumb for approximating M follows directly from Equation 2.6:

$$
\begin{aligned}
-ln\,(0.05) &= \hat{M} * t_{max} \\
\hat{M} &= \frac{2.996}{t_{max}} \approx \frac{3}{t_{max}}.
\end{aligned}
$$
(2.7)

Most importantly, note that the use of 0.05 or any other proportion in the equations is arbitrary because we have no reason to believe that t_{max} pertains to any particular quantile.

We show in the present study that this arbitrary rule of thumb for approximating M is unnecessary, as an empirical method (Hoenig 1983) provides an analogous estimate based on a substantial data set. Equation 2.1 is based on the same model as that in Equation 2.3 and was developed from a regression of $ln\,(M)$ on $ln\,(t_{max})$ from data on 134 stocks of 79 species of fish, mollusks, and cetaceans. It can be shown to be of the same form as the rule-of-thumb approach as follows:

$$
\begin{aligned}
e^{ln(\hat{M})} &= e^{1.44-0.982*ln(t_{max})} \\
\hat{M} &= \frac{e^{1.44}}{e^{0.982*ln(t_{max})}} \\
&= \frac{4.22}{(t_{max})^{0.982}} \\
&\approx \frac{4.22}{t_{max}}
\end{aligned}
$$
(2.8)

Results

We substituted 1.0 for 0.982 in Equation 2.8 to allow the development of a simple, approximate rule of thumb for direct comparison with $3/t_{max}$. As a result, this rule of thumb strictly applies only to the case where $t_{max} = 1$. Estimates from the regression estimator in Equation 2.1 are always greater than estimates from Equation 2.8 for $t_{max} > 1$, although the difference is usually small (Figure 2.1).
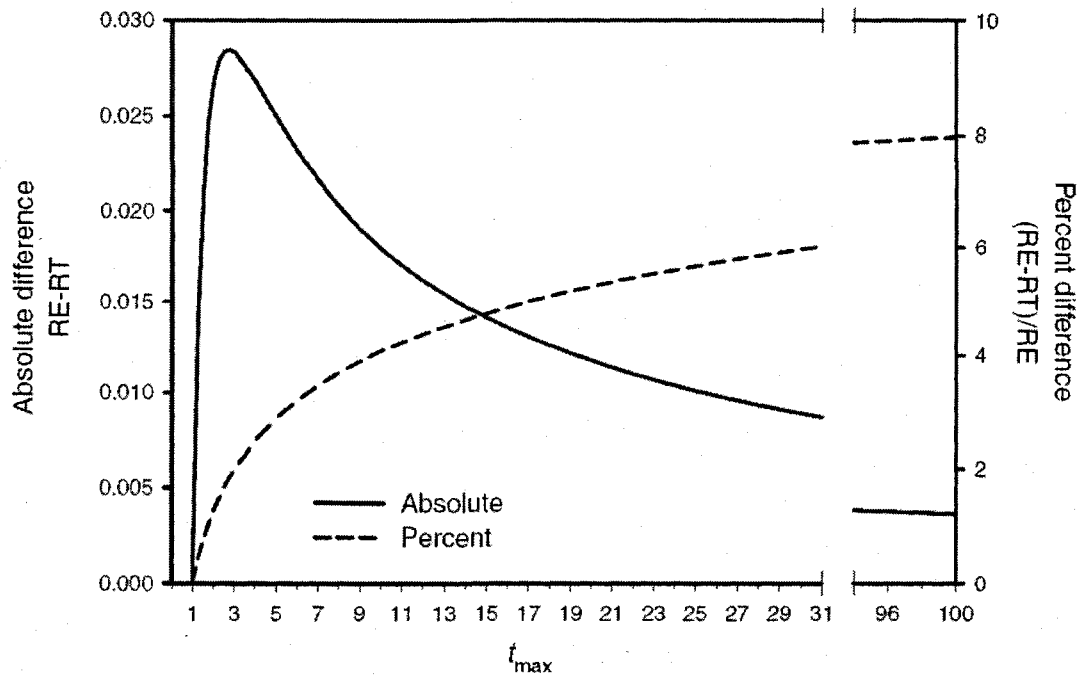
Figure 2.1: The absolute and percent difference between estimates of M from the regression estimator (RE) and the approximate rule of thumb, $4.22/t_{max}$ (RT).
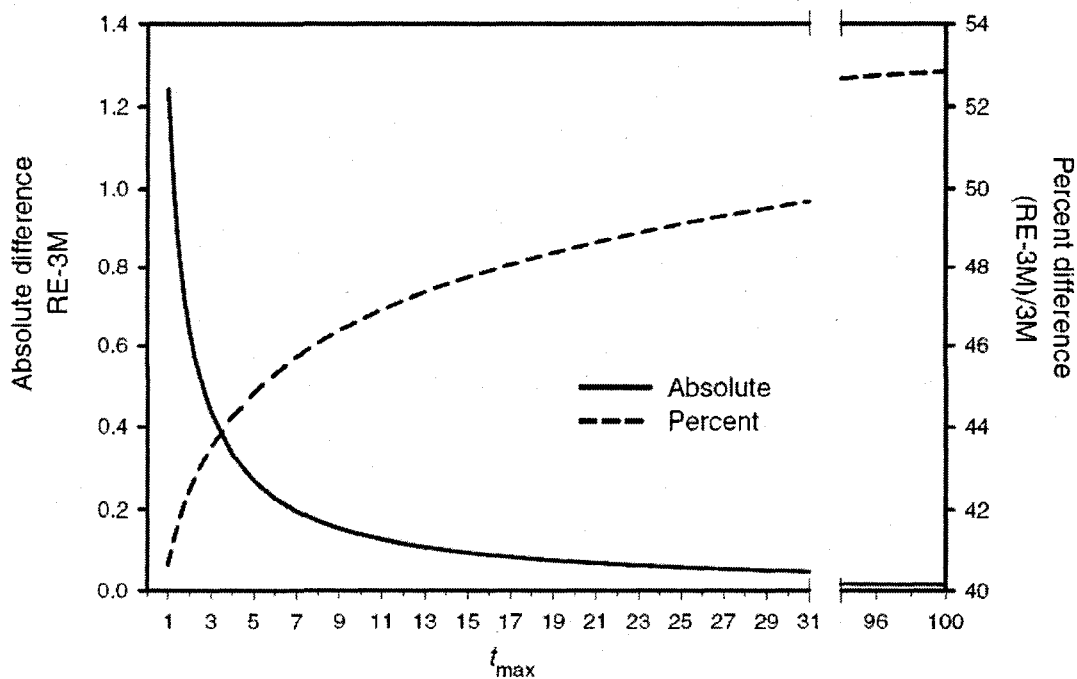
Figure 2.2: The absolute and percent difference between estimates of M from the regression estimator (RE) and $3/t_{max}$ (3M).

Estimates from the regression estimator are typically $40 - 50\%$ greater than estimates from $3/t_{max}$ (Figure 2.2). For example, if a maximum age of eight years is used for blue crab in Chesapeake Bay (Rugolo *et al.* 1998b), $3/t_{max}$ gives an estimate for M of $0.375/yr$ and the regression estimator gives $0.548/yr$.

Perhaps the most significant result is the finding that rearrangement of the regression model yields an estimate of an appropriate value for P in Equation 2.2. The value of 4.22 in Equation 2.8 approximately corresponds to $-ln\,(0.015)$, indicating that the average longevity for stocks in the data set used by Hoenig (1983) is the age at which about 1.5% of the stock remains alive (versus 5% in $3/t_{max}$).

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Discussion

Development of the rule-of-thumb approach

The rule-of-thumb approach appears to have arisen independently in four different places. Cadima (2003) supported the approach by citing the early work of Tanaka (1960). Sparre & Venema (1998) based their presentation on the work of Alagaraja (1984), who provided the mathematics of a method that Sekharan (1975) used without description. Interestingly, Shepherd & Breen (1992) rearranged Equation 2.3 to obtain the rule of thumb based on the results of Hoenig (1983). This latter presentation is provided in Quinn & Deriso (1999). In all of these cases, the proportion of animals surviving to t_{max} is assumed to be some arbitrarily small value, typically 1% or 5%.

The development and use of the specific form $3/t_{max}$ in blue crab work occurred altogether separately. Its use began with an assessment for the Chesapeake Bay stock, in which Rugolo et al. (1998b) used an estimate of M based on "the ICES [International Council for the Exploration of the Sea] convention; that is, 5% survivorship at maximum age following negative exponential depletion." The approach is more explicitly defined in their original document (Rugolo et al.[2]) as $M = (3/maximum\,age)$. The report also states that "this convention ... is widely used for many east coast finfish stocks (NMFS [National Marine Fisheries Service]/NEFSC [Northeast Fisheries Science Center], ASMFC [Atlantic States Marine Fisheries Commission])." Following its introduction by Rugolo et al. (Rugolo et al.[2]; Rugolo et al. 1998b), the $3/t_{max}$ approach has been used in nearly all blue crab stock assessment work conducted on the east coast of the United States (Miller and Houde[3];

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[2]Rugolo, L., K. Knotts, A. Lange, V. Crecco, M. Terceiro, C. Bonzek, C. Stagg, R. O'Reilly, and D. Vaughan. 1997. Stock assessment of Chesapeake Bay blue crab (*Callinectes sapidus*), 267 p. Report of the Technical Subcommittee of the Chesapeake Bay Stock Assessment Committee of the National Marine Fisheries Service, NOAA (National Oceanic and Atmospheric Administration). NOAA Chesapeake Bay Office, 410 Severn Avenue, Suite 107, Annapolis, MD 21403.

[3]Miller, T. J., and E. D. Houde. 1999. Blue crab target setting, 167 p. Final report to the Living Resources Subcommittee of the Chesapeake Bay Program. University of Maryland Center for Environmental Science (UMCES) Technical Series No. TS-177-99. Chesapeake Bay Program, U.S. EPA (Environmental Protection Agency), 410 Severn Avenue, Annapolis, MD 21403.

Miller 2001; Murphy et al.[4]; Helser *et al.* 2002; Kahn[5]).

The references used by Rugolo *et al.* (1998b) in support of what they termed the "ICES convention" (Anthony[6]; Vetter 1988) do not mention the $3/t_{max}$ approach. Rather than advocating a method for determining M, Anthony[6] called for standardization of the range of ages to include in the calculation of yield-per-recruit for a stock; this range of ages was termed the stock's "fishable life span." He proposed that the fishable life span should be defined such that the oldest age would be that at which 5% or less of the initial recruits survived. The use of Anthony's standard to approximate M makes the assumption that the fishable life span of an exploited stock is the same as the longevity of the members of the stock in an unexploited condition. It is unlikely that this assumption will be met unless the fishery is at an early stage in its development because fishing may alter the age structure of the stock (Hilborn & Walters 1992). We note that although a limited number of scientists involved with ICES have used $3/t_{max}$ in a general way, the method has not been adopted as a convention within ICES (O'Brien[7]). Furthermore, we did not find evidence that the approach is currently in common use in stock assessments on the east coast of the United States, with the exception of those for blue crab. Nonetheless, the rule-of-thumb approach certainly has the potential to be used widely, given its repeated presentation in fishery literature and its accumulated momentum in blue crab work.

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[4]Murphy, M. D., C. A. Meyer, and A. L. McMillen-Jackson. 2001. A stock assessment for blue crab, *Callinectes sapidus*, in Florida waters, 56 p. FMRI (Florida Marine Research Institute) Inhouse Report Series IHR 2001-008. Florida Fish and Wildlife Conservation Commission, FMRI, 100 Eighth Avenue SE, St. Petersburg, FL 33701.

[5]Kahn, D. M. 2003. Stock assessment of Delaware Bay blue crab (*Callinectes sapidus*) for 2003, 52 p. Delaware Department of Natural Resources and Environmental Control, Division of Fish and Wildlife, P.O. Box 330, Little Creek, DE 19961.

[6]Anthony, V. C. 1982. The calculation of $F_{0.1}$: a plea for standardization, 16 p. Northwest Atlantic Fisheries Organization (NAFO) Serial Document N557, SCR 82/VI/64. NAFO Secretariat, P.O. Box 638, Dartmouth, Nova Scotia B2Y 3Y9, Canada.

[7]O'Brien, C. M. 2004. Personal communication. Chair of ICES Working Group on Methods of Fish Stock Assessments and ICES Resource Management Committee. CEFAS (Centre for Environment, Fisheries and Aquaculture Science) Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk NR33 0HT, England.

Recommendations

The power of empirical relationships for predicting natural mortality can be rather limited (Vetter 1988; Pascual & Iribarne 1993), and the uncertainty associated with parameter estimates should be taken into account whenever possible (Patterson *et al.* 2001). Furthermore, methods for directly estimating M are likely to be preferable to making predictions based on life history features. Nonetheless, such estimates may be needed when available data are inadequate for making a direct estimate. Given the results of our comparison, we recommend that the regression estimator be used instead of the rule-of-thumb approach when longevity is used to predict M. The regression estimator is based on a least squares fit to an extensive data set and thus matches experience better than a rule-of-thumb approach based on an arbitrary constant.

We recommend that use of the $3/t_{max}$ rule of thumb be abandoned, despite it being entrenched in blue crab literature. For a species like blue crab, for which t_{max} is less than 10 years, the differences in the estimates of M from the regression estimator and $3/t_{max}$ are not trivial ($\sim 45\%$). Although the regression estimator was based on data for fish, mollusks, and cetaceans (Hoenig 1983) and may not be applicable to other exploited taxa, such as crustaceans, the model had a good fit to the data across widely disparate taxa. Finally, estimates of M for blue crab based on longevity are controversial because of continued difficulty in determining an appropriate t_{max}. In the absence of data to directly estimate M for this species, we suggest that the most prudent course of action is a review and comparison of other methods for predicting M.

Acknowledgments

Addendum

In this paper, we stated that the $3/t_{max}$ approach for estimating M was not in common use in assessments on the east coast, save for those of blue crab stocks. Our conclusion was based on our search of the literature and personal communications with stock assessment experts with whom we were familiar. Since the publication of this paper we have been contacted by various individuals that were aware of instances where $3/t_{max}$ was being used. At least three of those individuals referred to assessments on the east coast, and in combination they mentioned the use of $3/t_{max}$ in at least six separate assessments. The $3/t_{max}$ approach may be in wider use than we realized.

Chapter 3

Direct and Indirect Estimates of Natural Mortality for Chesapeake Bay Blue Crab[1]

Abstract

Analyses of the population dynamics of blue crab *Callinectes sapidus* have been complicated by a lack of estimates of the instantaneous natural mortality rate (M). We developed the first direct estimates of M for this species by solving Baranov's catch equation for M given estimates of annual survival rate and exploitation rate. Annual survival rates were estimated from a tagging study on adult female blue crabs in Chesapeake Bay, and female-specific exploitation rates for the same stock were estimated by comparing commercial catches with abundances estimated from a dredge survey. We also used eight published methods based on life history parameters to calculate indirect estimates of M for blue crab. Direct estimates of M for adult females in Chesapeake Bay for the years $2002 - 2004$ ranged from 0.42 to 0.87 per year and averaged 0.71 per year. Indirect estimates of M varied considerably depending on life history parameter inputs and the method used. All eight methods yielded values for M between 0.99 and 1.08 per year, and six of the eight methods yielded values between 0.82 and 1.35 per year. Our results indicate that natural mortality

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of blue crab is higher than previously believed, and we consider M values between 0.7 and 1.1 per year to be reasonable for the exploitable stock in Chesapeake Bay. Remaining uncertainty about M makes it necessary to evaluate a range of estimates in assessment models.

Introduction

The estimation of natural mortality rates is one of the most difficult and most critical elements of many fishery stock assessments. The natural mortality rate is a key determinant of the potential productivity of a stock and thus the amount of exploitation a stock can sustain. In general, assuming that natural mortality and harvest mortality are additive, stocks with higher natural mortality rates are more productive and are able to sustain higher rates of exploitation. Lacking evidence to the contrary, most stock assessments assume that natural mortality is constant through time as well as across the sizes or ages of the exploited animals. Thus, a single estimate of the instantaneous natural mortality rate (M) is presumed to apply to the entire exploitable stock.

The values used for M in assessment models can have substantial effects on model results, biological conclusions, and management recommendations. For a simple age-structured model, Clark (1999) found that stock abundance and target harvest rates could be severely overestimated when M was overestimated by as little as 0.1 per year or less, especially when fishing mortality was low ($F < 0.3$ per year). Similarly, harvest policies for U.S. West Coast groundfish based on a catch-at-age model were sensitive to changes in M of less than 0.05 per year (Williams 2002). Using a length-structured model for red king crab *Paralithodes camtschaticus* in Bristol Bay, Alaska, Zheng *et al.* (1997a,b) found that stock rebuilding and long-term harvest strategies were highly sensitive to changes in M of $0.2 - 0.3$ per year. These and other results indicate that it is desirable to have precise knowledge about M for assessment purposes.

Unfortunately, estimates of M used in stock assessment models are often uncertain, partly

because it is difficult and expensive to estimate the parameter. In practice, values of M for use in stock assessments are obtained by two types of methods, which we refer to as direct and indirect. Direct methods involve estimating M from data pertaining solely to the species or stock of interest. Direct methods include field studies designed to estimate mortality rates as well as studies that estimate M as a parameter within a population dynamics model. Indirect methods involve making an analogy among species or stocks. If a stock of interest has life history traits that are similar to those of another group of species or stocks for which M has been estimated, then it is presumed that M for the stock of interest is close to M for the group. For example, species with similar longevity have similar M values, so longevity can be used to predict M (Hoenig 1983). With direct methods, the reliability of the estimate of M depends only on how reliably the parameters have been estimated for the stock of interest. For indirect methods, the reliability of the estimate of M depends on three things: (1) the variability of M among species or stocks with the same life history traits, (2) how well M and the life history traits have been estimated for the species or stocks used to estimate the relationship between M and the life history traits, and (3) how well the life history traits have been estimated for the stock of interest.

Perhaps the most feasible and reliable direct methods for estimating mortality rates are telemetry and tagging studies that can assign fates to tagged individuals; these methods have been used successfully to estimate M for some fish stocks (Hampton 2000; Hightower *et al.* 2001; Latour *et al.* 2001; Heupel & Simpfendorfer 2002; Pollock *et al.* 2004; Waters *et al.* 2005; Leigh *et al.* 2006). It is more difficult to use tagging or telemetry methods to estimate M for crustaceans, largely because crustaceans grow by molting and may shed external tags along with the old carapace during ecdysis. Tag shedding generally limits the time period and portion of the stock that can be used to estimate mortality rates. Nonetheless, a few studies have used tagging experiments to estimate mortality rates (including M) for exploited stocks of shrimp (Siddeek 1991; Xiao & McShane 2000), crabs (Siddeek *et al.* 2002 and references therein), and lobsters (Frusher & Hoenig 2003). Recently, Lambert

et al. (2006b) took advantage of the fact that female blue crabs *Callinectes sapidus* undergo a terminal molt at maturity to estimate survival rates for adult females in Chesapeake Bay with tag return data.

Natural mortality rates have been estimated directly for exploited crustacean stocks in several other ways. Xu *et al.* (1995a,b) took advantage of fishing season closures to estimate M for the green tiger prawn *Penaeus semisulcatus* in Kuwait based on relative abundance data from research surveys. Wang (1999) and Wang & Ellis (2005) estimated M for *P. semisulcatus* in Australia with catch and effort data from a commercial fishery or length frequency data from research surveys. Fu & Quinn (2000) estimated M as a parameter within a length-based population dynamics model for northern shrimp *Pandalus borealis* in Kachemak Bay, Alaska. Zheng *et al.* (1995a,b) reviewed published estimates of M for red king crab and also estimated it as a parameter within a length-based population model. Similarly, Siddeek *et al.* (2002) estimated M within length-based and age-based population models for red king crab and golden king crab *Lithodes aequispinus*.

Studies of exploited lobster stocks have estimated M by both direct and indirect methods. Morgan (1977) estimated M for western rock lobster *Panulirus cygnus* in Australia by some direct methods with variable success. Annala (1977) presented some direct estimates for southern rock lobster *Jasus edwardsii* in New Zealand, and Thomas (1973) and Anthony (1980) reviewed both direct and indirect estimates of M for American lobster *Homarus americanus*. Additional studies of lobsters (Sheehy *et al.* 1999; French McKay *et al.* 2003) and other exploited crustaceans (Gabche & Hockey 1995) have used indirect methods to predict M based on the correlation between mortality and other life history parameters. This indirect approach is also common to fish stock assessments (Vetter 1988; Quinn & Deriso 1999).

Blue crab natural mortality and stock assessment

The blue crab supports major commercial fisheries along the U.S. East Coast south of Connecticut and in all of the states along the Gulf of Mexico. In 2002, blue crab landings constituted approximately 7% of the global landings of true crabs, and U.S. landings have dominated the global catch of blue crab (Fogarty & Lipcius 2007). The commercial fishery for blue crab in the Chesapeake Bay is the leading contributor to the U.S. landings and is one of the most economically important fisheries in the bay. Landings from Chesapeake Bay peaked in 1966 at over 47,000 metric tons but have fallen to all-time lows in the last decade. Landings have averaged less than 25,000 metric tons since 2000 (Miller *et al.* 2005). The decline in landings coincides with a sustained decline in population abundance, which is partly attributable to overfishing (Lipcius & Stockhausen 2002; Bunnell & Miller 2005; Miller *et al.* 2005).

The estimation of M has been a vexing problem for analyses of blue crab stock dynamics (Hewitt and Hoenig 2005 [Chapter 2]). No direct estimates of M exist for blue crab, and assessments have relied on an indirect approach for estimating M based on longevity. The first formal assessment of the blue crab fishery in Chesapeake Bay (Rugolo *et al.* 1998b) introduced an approach for estimating M based on the presumed longevity of the species in an unexploited condition. Rugolo *et al.* (1998b) used a value for longevity of 8 years and estimated M to be 0.375 per year, noting that the longevity value was selected in part to provide a risk-averse assessment (lower M). The approach that they used to estimate M was subsequently employed in other blue crab stock assessments conducted on the U.S. East Coast. Hewitt and Hoenig (2005) [Chapter 2] discussed the history and mechanics of this method and recommended that it be abandoned.

The use of longevity to estimate M for blue crab has been controversial, primarily because of the uncertainty about longevity for this species. Rugolo *et al.* (1998b) based their use of 8 years on a single tag return from an unpublished tagging study, but there was considerable disagreement among scientists, managers, and commercial fishermen about

whether blue crabs could live to age 8. Longevity values ranging from 3 to 8 years have been proposed for blue crab, but there is little evidence in support of any specific value. Aging of blue crab is difficult because individuals lack retained hard parts that may contain indications of age. Analysis of extractable lipofuscins has provided a means to age blue crabs but with only moderate precision and over a limited age range (Ju *et al.* 1999, 2001). An application of this technique to samples of blue crabs from Chesapeake Bay indicated that crabs older than age 2 were a minor portion of the stock but that several individuals may have been age 3 or older (Ju *et al.* 2003). Other evidence about blue crab longevity has come from fishery-dependent tag returns in tagging studies. Despite the potential for error in the interpretation of individual tag returns, studies from North Carolina, Florida, and Chesapeake Bay have all indicated that blue crabs in exploited stocks may live to age 4 (Fischler 1965; Tagatz 1968a; Lambert *et al.* 2006b). Thus, the best available evidence suggests that blue crabs in exploited stocks can live for at least 4 years.

In support of efforts to improve scientific advice to fishery managers and to resolve some of the uncertainty about blue crab natural mortality rates, we developed and compared direct and indirect estimates of M for the blue crab stock in Chesapeake Bay.

Methods

We used two approaches to estimate M for blue crab: (1) direct estimation based on independent estimates of annual survival rate (S) and exploitation rate (u), and (2) indirect estimation based on life history parameters. Whereas the indirect estimates reflect the entire life history of the animal and thus apply to the entire stock, the direct estimates are based on the results of Lambert *et al.* (2006b) and apply only to the adult female portion of the stock.

Direct estimates

We used Brownie tag return models (Brownie *et al.* 1985) to estimate S of adult female blue crabs for 2002, 2003, and 2004 based on a tagging study in Chesapeake Bay. Complete details of the tagging study and the estimation of S are provided by Lambert *et al.* (2006b); we used S estimates $\left(\hat{S}\right)$ based on tagging conducted in the winter. Model selection criteria indicated that the most parsimonious model was one that included a survival rate that was constant across years. However, the difference between that model and a model with separate annual estimates of survival was small (change in the quasi-likelihood Akaike's information criterion [ΔQAIC] = 3.82); thus, we used separate annual estimates to obtain three estimates of M.

Exploitation rate is calculated as C/N, where C is the total catch during the year and N is the abundance at the start of the year. Female-specific u estimates ($\hat{u}$) for Chesapeake Bay were calculated by methods described in Sharov *et al.* (2003) based on annual estimates of baywide abundance of exploitable female blue crabs $\left(\hat{N}\right)$ and annual baywide commercial landings of female blue crabs $\left(\hat{C}\right)$. Abundance was estimated from a stratified random dredge survey conducted during the winter and timed to coincide with the period in which blue crabs in northern, temperate latitudes cease molting and bury themselves in the sediment (Sharov *et al.* 2003; Smith & Chang 2007). Adult female blue crabs are concentrated in deeper waters in the southern portions of the bay during the winter (Jensen *et al.* 2005), but the dredge survey covers the entire bay. The catch per unit area was estimated for crabs that were of legal size or were going to reach legal size during the year. Absolute abundance of crabs per unit area was calculated by dividing the catch per unit area estimates by an estimate of gear efficiency (Sharov *et al.* 2003). Total baywide abundance was then calculated by expanding the overall mean density to the entire area of the bay (9,812 km^2). Sex-specific estimates of u were calculated by separating abundance estimates and landings by sex. The hard-shell crab sector of the fishery reports the catches of males and females separately, but the soft-shell and peeler crab sectors do not. We assumed a 1:1 sex ratio

for landings reported by the soft-shell and peeler crab sectors based on fishery-dependent monitoring by the Maryland Department of Natural Resources (Fegley *et al.* 2006).

We used the independent estimates of S and u in a rearrangement of Baranov's catch equation (Ricker 1975) to solve for M. The catch equation is applicable to fisheries like the Chesapeake Bay blue crab fishery, in which fishing mortality and natural mortality operate concurrently (Type 2 in Ricker's terminology):

$$C = NFA/Z, \tag{3.1}$$

where C and N are as defined above, F is the instantaneous fishing mortality rate per year, Z is the instantaneous total mortality rate per year, A is the total annual mortality rate $(1 - S;$ S is equal to e^{-Z}, where e is the base of natural logarithms), and Z equals $M + F$. Given that u is equal to C/N, the equation can be rearranged to solve for F as $(uZ)/A$. By subtraction, M is equal to $Z - [(uZ)/A]$.

Annala (1977) used this general approach for the southern rock lobster, and Kahn & Helser (2005) employed it in an assessment of the blue crab stock in Delaware Bay. Similar to Lambert *et al.* (2006b), Annala (1977) estimated Z from tag returns obtained from a commercial fishery. He calculated M by the approach presented here but concluded that the approach substantially overestimated M because of tagging effects, such as tagging-related mortality and tag loss. Lambert *et al.* (2006b) indicated that their study did not violate any of the assumptions of the Brownie models, which include these potential biases; we therefore believe the approach is appropriate for our situation. Kahn & Helser (2005) did not use data from a tagging study; rather, they used relative abundance data from a research survey and a catch-survey model to estimate u and Z.

Indirect estimates

We selected eight published indirect methods that are commonly used in fishery stock assessments to obtain ranges of M estimates for blue crab (Table 3.1). Most of the methods were developed primarily for fish and included little data on invertebrates. We recognize the uncertainty associated with using indirect methods that have been derived from data on many species to predict M for a single species (Vetter 1988; Pascual & Iribarne 1993). The use of multiple methods may reduce the bias imposed by any one method.

The indirect methods rely on parameters that are commonly measured in biological studies, including average age at maturity (t_m), longevity (t_{max}), body size, and the parameters of the von Bertalanffy growth model (Brody growth coefficient $[K]$ and asymptotic maximum size in length $[L_\infty]$ or weight $[W_\infty]$). For blue crabs, the carapace width $(CW; \text{mm})$ between the points of the lateral spines was substituted for length (thus, $CW_\infty = L_\infty$). Although considerable research has been conducted into models that account for the discontinuous nature of crustacean growth (reviewed in Smith & Chang 2007), the simpler von Bertalanffy model has been used in many studies of blue crab stocks and provides a reasonable approximation (Bunnell & Miller 2005). Estimates of blue crab life history parameters drawn from the literature and unpublished data were selected to represent the Chesapeake Bay stock (Table 3.1). Whenever possible, we used empirically derived parameter estimates as opposed to estimates based on model inference. For example, we used a range of published estimates for the von Bertalanffy growth model parameters but only included those derived from field data. Two of the indirect methods required estimates of t_{max}, for which we used a range of $4 - 6$ years.

Table 3.1: Indirect methods used to estimate natural mortality rates (M) for blue crab. Descriptions of the methods and sources of input parameter estimates are discussed in the text.

Method	Source(s)	Equation[a]	Input parameter estimates	M range
1	Charnov & Berrigan (1990), Charnov (1993), Jensen (1996)	$M = X/t_m$	$t_m = 1.00 - 1.67,$ $X = 1.65 - 2.20$	$0.99 - 2.20$
2	Charnov (1993), Jensen (1996)	$M = X * K$	$K = 0.47 - 1.09,$ $X = 1.50 - 1.65$	$0.71 - 1.80$
3	Alverson & Carney (1975)	$M = 3K/\left(e^{0.38Kt_{max}} - 1\right)$	$K = 0.47 - 1.09,$ $t_{max} = 4 - 6$	$0.30 - 1.35$
4	Hoenig (1983)	$M = e^{1.44 - 0.982 log_e(t_{max})}$	$t_{max} = 4 - 6$	$0.73 - 1.08$
5	Pauly (1980)	$log_{10}M = -0.0066 - 0.279 log_{10}\left(CW_\infty\right) + 0.6543 log_{10}K + 0.4634 log_{10}T$	$K = 0.47 - 1.09,$ $CW_\infty = 17.6 - 23.5,$ $T = 16.5$	$0.91 - 1.72$
6	Pauly (1980)	$log_{10}M = -0.2107 - 0.0824 log_{10}\left(W_\infty\right) + 0.6757 log_{10}K + 0.4627 log_{10}T$	$K = 0.47 - 1.09,$ $W_\infty = 231 - 464,$ $T = 16.5$	$0.82 - 1.52$
7	Roff (1984)	$M = 3K/\left(e^{Kt_m} - 1\right)$	$K = 0.47 - 1.09,$ $t_m = 1.00 - 1.67$	$0.63 - 2.35$
8	Lorenzen (1996)	$M = 3.00W^{-0.288}$	$W = 25.0 - 450.0$	$0.52 - 1.19$

[a]t_m = age at maturity (years); X = a constant taken from the given sources; K = von Bertalanffy growth coefficient (per year); t_{max} = longevity (years); CW_∞ = asymptotic maximum carapace width (cm) from the von Bertalanffy growth model; T = grand annual mean of water temperature (°C) recorded at the Virginia Institute of Marine Science (Gloucester Point), 1990 − 2003; W_∞ = asymptotic maximum weight (g) from the von Bertalanffy growth model; W = wet weight (g).

Methods 1 and 2 (Table 3.1), based on simple empirical relationships between M and the parameters t_m and K, are built on the work of Beverton & Holt (1959) and Beverton (1963, 1992). Charnov (1993) extended this work and compiled data showing that certain relationships among life history parameters were generally stable within broad taxonomic boundaries. He reasoned that the relationships probably arose from evolutionary tradeoffs. Jensen (1996) derived the same relationships directly from theory, showing that they resulted from a tradeoff between mortality and reproduction when a species evolved to maximize its lifetime fecundity. Jensen (1996) estimated values for the relationships that were somewhat different than those determined by Charnov (1993). We used a range of $1.00 - 1.67$ years as input parameter estimates for t_m, based on Van Engel (1958) and Lippson (1973). Charnov (1993) used the data compiled by Pauly (1980), which was also used to develop methods 5 and 6 (Table 3.1).

Method 3 is taken from Alverson & Carney (1975), in which a theoretical model was developed to predict the age at which a cohort of fish would maximize its collective biomass if growth followed a von Bertalanffy model. They also included an empirical regression model based on 63 fish species to relate t_{max} to the age at which the cohort would maximize its biomass. The first model includes a term for M, and the two models can be combined and rearranged to solve for M given estimates of K and t_{max}.

Method 4, from Hoenig (1983), is a simple linear regression of $log_e(Z)$ against $log_e(t_{max})$. The data showed that Z was inversely related to t_{max}. Because the 134 stocks in the data set were either unexploited or lightly exploited, Z approximates M. Although this method relies solely on an estimate of t_{max}, we used it because it was based on an extensive data set of diverse taxa, including fish, cetaceans, and mollusks.

Methods 5 and 6, multiple linear regressions developed by Pauly (1980), are two of the most common methods used in stock assessments to predict M. The regressions were based on 175 stocks of freshwater and marine fish species. Each of the regression equations relates M to parameter estimates from the von Bertalanffy growth model and the average

temperature of the water in which the stock lives. Separate equations are used for growth models fit to length and weight data. Charnov (1993) and Jensen (1996) showed that temperature added little to the predictive capability of the regressions, but we used them in their original form. We converted CW_∞ (mm) to W_∞ (g) using the following allometric equation (Miller *et al.* 2005):

$$W = 0.000842 * CW^{2.422}. \tag{3.2}$$

Method 7 is taken from Roff (1984), who explored theoretically the evidence that life history parameters were consistently correlated among teleost fishes. In part of his investigation (elaborated on by Jensen 1996), Roff (1984) assumed that evolution had shaped life history parameters to maximize lifetime fecundity through tradeoffs among growth, reproduction, and survival. He determined that the optimal t_m could be estimated from its relationship with K and M. Similar to method 3, the model can be rearranged to solve for M given estimates of K and t_m. Roff (1984) showed that this model had reasonable predictive capability when tested with data from 30 stocks, most of which were taken from Ni (1978). In addition, the predictive capability was similar to that of the length-based regression of Pauly (1980) when tested with a subset of 17 stocks. Interestingly, the equation Roff (1984) developed was the same as that used by Alverson & Carney (1975) to solve for the age at which a cohort would maximize its biomass, implying that the optimal t_m is the same as the age at which a cohort maximizes its biomass.

Lastly, method 8, taken from Lorenzen (1996), predicts M based on its inverse relationship with body size. This method allows M to vary among individuals; however, we used it with a range of sizes for exploitable blue crabs (> 76 mm CW) to produce a range of M estimates in a way similar to the other methods. Peterson & Wroblewski (1984) concluded that mortality due to predation in pelagic marine ecosystems was a power function of body weight. Lorenzen (1996) related estimates of M to wet body weight for a large and diverse

data set for fishes of all sizes in natural ecosystems (lakes, rivers, marine systems) and also found that M was a power function of body weight. The relationship did not differ statistically among ecosystems or latitudinal zones. We used the Lorenzen (1996) equation estimated for all natural ecosystems combined and provided a range of blue crab weights by converting carapace widths using equation 3.2.

Results

Direct estimates

Survival rates of adult female blue crabs in Chesapeake Bay were exceptionally low but consistent. We estimated S to be 0.091 in 2002, 0.097 in 2003, and 0.069 in 2004 (Table 3.2). The 95% confidence intervals for $\hat{S}$ are wide because a variance inflation factor was used to adjust the standard errors of the estimates. The adjustment was necessary because two long-term recaptures of tagged crabs caused the model to fit poorly; these long-term recaptures are possible but unlikely given the S estimates. The standard errors for $\hat{S}$ were much lower when these recaptures were excluded. For example, the 95% confidence interval for the estimate in 2002 was 0.017 − 0.160 without the two long-term recaptures. However, there was no reason to exclude these recaptures, so they were included in the analysis (Lambert *et al.* 2006b). The adjusted confidence intervals may overstate the uncertainty in $\hat{S}$. Female-specific $\hat{u}$ calculated from the dredge survey abundances and commercial landings of female blue crabs varied from 0.578 to 0.748, reflecting intense fishing pressure. Solving Baranov's catch equation for M with $\hat{S}$ and $\hat{u}$ yielded M estimates ranging from 0.423 per year in 2002 to 0.871 per year in 2004 (mean = 0.711 per year). The estimate for 2002 was about 50% of the 2003 and 2004 estimates.

Table 3.2: Annual estimates of survival rate (S) and exploitation rate (u) and resulting estimates of instantaneous fishing (F) and natural (M) mortality rates (per year) for adult female blue crabs in Chesapeake Bay. The estimates of S are based on the tagging study described by Lambert *et al.* (2006b). The 95% confidence intervals (CIs) for $\hat{S}$ are given in parentheses.

Year	$\hat{S}$ (95% CI)	$\hat{u}$	$\hat{F}$	$\hat{M}$
2002	0.091 (0.011 − 0.475)	0.748	1.974	0.423
2003	0.097 (0.028 − 0.291)	0.578	1.493	0.840
2004	0.069 (0.022 − 0.196)	0.628	1.803	0.871

Indirect estimates

The indirect methods collectively provided a broad range of M estimates ($0.30 - 2.35$ per year; Table 3.1). The lowest estimates were given by method 3 with t_{max} of 6 years and K of 1.09 per year. The range of estimates from this method was wider than that from method 4, which only used t_{max}. Methods 1 and 2 produced similar ranges of values and included among the highest estimates (only method 7 gave higher estimates). Methods 5 and 6 produced similar ranges of estimates, roughly in the middle of the collective range. Estimates from method 8, based on weight, were similar to those from method 3 and were nearly identical to estimates based on the more theoretical approach of Peterson & Wroblewski (1984). Although we did not include their approach in Table 3.1, it would add weight to M estimates in the range of $0.5 - 1.2$ per year. The collective range of the M estimates was extensive, but all eight methods yielded values between 0.99 and 1.08 per year, and six methods gave estimates between 0.82 and 1.35 per year (Figure 3.1).

Discussion

The direct estimates of M for adult female blue crabs in Chesapeake Bay represent the first direct estimates for this species that are applicable at the scale of a stock assessment. The direct estimates for 2003 (0.84 per year) and 2004 (0.87 per year) are close to the region
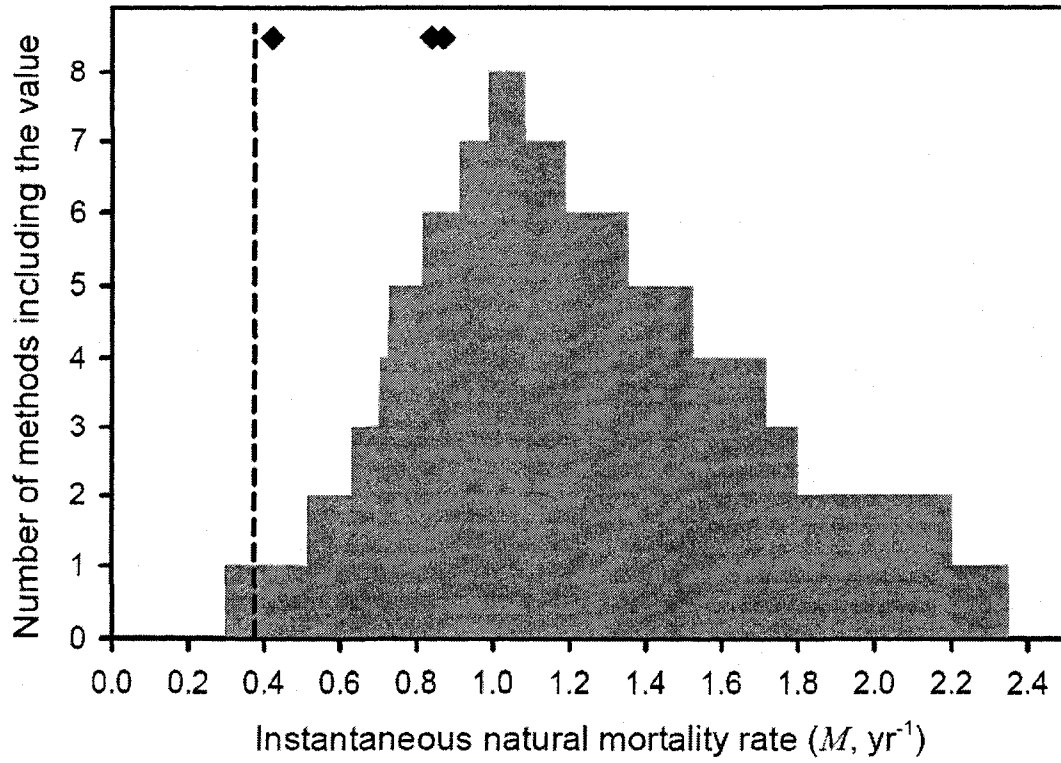
Figure 3.1: Number of indirect estimation methods in Table 3.1 (out of eight possible methods) that yielded given values (x-axis) of instantaneous natural mortality rate (M) for blue crab. The direct estimates of M for adult females in Chesapeake Bay from our study (2002 – 2004) are indicated by diamonds. The vertical dashed line indicates the M value (0.375 per year) used by Rugolo *et al.* (1998b).

of central tendency given by the indirect methods (0.99 − 1.08 per year). Collectively, the direct and indirect estimates indicate that values between 0.7 and 1.1 per year are reasonable estimates of M for the exploitable stock of blue crab in Chesapeake Bay. Estimates at the upper end of this range are further supported by the results from the catch-multiple-survey assessment model of Miller *et al.* (2005), in which process error and the sum of the squared residuals were minimized at M values between 1.00 and 1.25 per year. We suggest that stock assessments for blue crab consider a range of reasonable M values to account for remaining uncertainty about the parameter.

Overall, our results indicate that M for the blue crab in Chesapeake Bay, though still uncertain, is higher than previously assumed. The estimate of 0.375 per year used by Rugolo *et al.* (1998b) does not appear to be credible. Only one indirect method (Alverson & Carney 1975) produced values as low as 0.375 per year and only when extreme values for life history parameters were used (high K, high t_{max}). None of the direct estimates were as low as 0.375 per year. In addition, with an M of 0.375 per year, the catch-multiple-survey assessment model failed to adequately fit the time series of $\hat{u}$ observed in the fishery (Miller *et al.* 2005). From an evolutionary perspective, higher natural mortality rates are consistent with other blue crab life history features, such as fast growth, early maturity, and a relatively short life span (Adams 1980; Gunderson & Dygert 1988).

Changing the estimate of M for blue crab from 0.375 per year to 0.7 − 1.1 per year reflects a significant shift in our understanding of the population dynamics of this species. The higher estimates imply that the exploitable stock is composed primarily of one or two year-classes, which is consistent with the findings of Ju *et al.* (2003). As a result, the age structure of the stock and the ability of the stock to support the fisheries are heavily dependent on the magnitude of annual recruitment.

We recognize several potential concerns with estimating M by using $\hat{S}$ from the tagging study together with the female-specific $\hat{u}$. First, unlike $\hat{S}$, $\hat{u}$ did not account for recreational removals. However, the recreational removals of blue crabs in Chesapeake Bay are believed

to be less than 10% of the commercial harvest (Ashford & Jones 2003). Second, the tagging study included only adult females that had undergone their terminal molt, whereas $\hat{u}$ was calculated for all females that were of legal size or would become legal size during the year. A portion of the exploitable females would not have undergone their terminal molt (Bunnell & Miller 2005). Finally, the periods to which $\hat{S}$ and $\hat{u}$ applied were not exactly matched. The $\hat{S}$ applied to an annual period beginning in October or November (Lambert *et al.* 2006b), whereas $\hat{u}$ applied to calendar years. Overall, we expect that the small difference in timing of the two estimates introduced little error into the estimates of M.

The range of M estimates based on the indirect methods $(0.30 - 2.35$ per year) is considerably wider than ranges generated by similar but smaller sets of indirect methods applied to fish stocks (Gunderson *et al.* 2003; Bacheler *et al.* 2005; Fischer *et al.* 2005). One reason for this is the relatively short life span of blue crab; that is, M varies considerably with small changes in parameters such as t_{max} and t_m for short-lived animals. For example, Simpfendorfer (1999b) applied five indirect methods to a small, short-lived shark species (maximum age $= 6 - 7$ years) and produced a range of M estimates from 0.60 to 1.65 per year. In contrast, Simpfendorfer (1999a) and Heupel & Simpfendorfer (2002) used suites of indirect methods for larger, longer-lived species and found that estimates of M varied among methods by less than 0.25 per year. Another reason for the wide range of M estimates for blue crab is the variability in estimates of the von Bertalanffy growth model parameters, which are used in five of the eight methods. The range of estimates we used for K and CW_∞ accurately reflects the high variability in blue crab growth rates (Ju *et al.* 2001).

Uncertainty appears to be a persistent feature of our understanding of natural mortality in crab stocks. In a study of red king crab, blue king crab *P. platypus*, and golden king crab, Siddeek *et al.* (2002) obtained point estimates of M ranging from 0.19 to 0.70 per year depending on the species and sex. They used a jackknife procedure to determine the precision of the estimates, and all of the 95% confidence intervals included zero. The confidence

intervals spanned ranges of values that were $2.7 - 4.3$ times the point estimates. They also concluded that some of the point estimates were unreasonable considering the life expectancy of the animals. Similarly, Zheng (2003) concluded that a study of M for snow crab *Chionoecetes opilio* in the Bering Sea did little to resolve the large uncertainty about M for this species.

Some of what appears to be uncertainty in our estimates of M for blue crab may actually be true variability in M. Ecological studies of blue crabs offer strong evidence that natural mortality rates vary considerably with respect to a variety of factors such as sex, size, habitat, and season (Heck & Wilson 1987; Lipcius *et al.* 2005). However, it is difficult to apply the findings of such small-scale ecological studies at the scale of stock assessments; a good example is provided by Incze *et al.* (2003) for the American lobster. Nonetheless, the suggestion to specifically include variability in M in assessment models continues to be repeated in the literature, often in connection with evidence demonstrating such variability (Gulland 1987; Vetter 1988; Fu & Quinn 2000; Hampton 2000; Tanasichuk 2000).

Studies of some exploited crustacean stocks have revealed various sources of variability in M and have included such variability in population dynamics models. Xiao & McShane (2000) found that M varied with size or between sexes for the western king prawn *Penaeus latisulcatus*, but size and sex were confounded such that it was unclear which factor was the important one. Year-specific estimates of M for northern shrimp in Kachemak Bay, Alaska, showed an increasing trend through time, which may have resulted from increasing predation pressure from groundfish (Fu & Quinn 2000). Based on a review of previously published estimates, Zheng *et al.* (1995a) concluded that M was lower for intermediate-size red king crabs than it was for smaller and larger crabs and that M varied substantially over time. Thus, they included effects of sex, size, and year on M for red king crab in a population dynamics model. Concerns about over-parameterization of the model led them to develop a more parsimonious version that removed the size dependence in M, but results were similar (Zheng *et al.* 1995b). Siddeek *et al.* (2002) estimated M separately for male

and female king crabs, but attempts to estimate M by year were unsuccessful. Studies that attempt to estimate M within a population dynamics model may be hampered by the common problem of M being confounded with other model parameters (Schnute & Richards 1995; Clark 1999; Wang 1999; Fu & Quinn 2000). Such a problem was at least partly to blame for the inconclusive results of Zheng (2003).

Consistent with a limited understanding of natural mortality, previous assessments of blue crab stocks have not included variability in M. However, M probably varies between sexes, across sizes of crabs in the exploitable stock, or through time. Indeed, one of the indirect methods we considered in this study provided estimates of M that varied by weight, where M was higher for smaller animals (Lorenzen 1996). The general concordance between the direct estimates we obtained for adult females and the indirect estimates suggests that the direct estimates may also apply to males and larger immature crabs that are captured by the fishery. However, values of $\hat{u}$ are higher for females than for males (Miller *et al.* 2005), and more research is needed to determine whether $\hat{S}$ values for adult females are applicable to the rest of the stock. As for variation in M through time, our direct estimates of M for adult females do not have associated measures of precision, so we do not know whether the low value in 2002 reflects a real change in M or simply measurement error.

In the future, blue crab stock assessments will need to use higher estimates of M and will need to evaluate a range of estimates to account for uncertainty about the parameter. Assessments may also need to account for variability in M to be realistic and provide reliable management advice. Given the limited direct evidence about such variability, developments in assessment techniques will need to proceed incrementally and be accompanied by further research.

Acknowledgments

Chapter 4

Mortality and Emigration of Juvenile Blue Crabs

Introduction

The decline in abundance of the blue crab stock in Chesapeake Bay brought together the Virginia and Maryland management authorities and initiated a number of reactions to halt the decline and restore abundance (Cronin 1998; BBCAC 2001; Beem 2006). Among others, three major efforts involving various institutions and collaborations were funded to assist stock restoration: (1) an updated assessment of the stock to guide management decisions about catch, effort, and gear limits and biological reference points (Rugolo *et al.* 1998b; Miller & Houde 1999; Miller *et al.* 2005), (2) the protection of important habitat areas, including the designation of a spawning stock sanctuary in the lower Bay to protect adult female crabs (Lipcius *et al.* 2001; Seitz *et al.* 2001; Lipcius *et al.* 2003), and (3) enhancement of the stock through the release of hatchery-reared crabs into recruitment-limited habitats (Zohar *et al.* 2008).

Stock assessments rely on quantitative models of blue crab stock dynamics, a key element of which is the natural mortality rate that is applied to the individuals in the stock (Chapters 2 and 3). The two other restoration efforts, the spawning stock sanctuary and the stock enhancement program, are focused on increasing the recruitment of juvenile crabs into the adult population. Protection of the spawning stock aims to increase the natural production of larvae, and ultimately recruits, whereas stock enhancement aims to short-

circuit the larval production process and avoid the vagaries of open ocean mortality to increase the abundance of recruited juveniles directly. The spawning stock sanctuary has been studied and its implementation and effectiveness assessed elsewhere (Lipcius *et al.* 2001; Seitz *et al.* 2001; Lipcius *et al.* 2003; Lambert *et al.* 2006a). Here I focus on the role of size-dependent mortality – the change in mortality rates between the juvenile stage and the recruited stage – as it pertains to stock assessment and enhancement.

An important issue for stock assessment, as alluded to in Chapter 3, is whether it is reasonable to apply a constant natural mortality rate (M) to the entire stock for short-lived species like blue crab. A general understanding of the life history of blue crab and the ecology of Chesapeake Bay, as well as field experiments, indicate that natural mortality changes in various ways and that these changes need to be accounted for in population dynamics models. Potential sources of mortality for juvenile crabs (summarized in Van Engel 1987) could include predation, starvation, chronic or acute water quality stress, extreme cold temperatures, disease, and habitat loss. Diseases may be important in connection with degraded water quality in Chesapeake Bay (Kemp *et al.* 2005), but the study of blue crab diseases is relatively young and there is little evidence for a strong effect of diseases in the Bay (Noga *et al.* 1998; Shields 2003; Shields & Overstreet 2007). Habitat loss, including temporary losses caused by poor water quality, could force potential predators and prey into common habitats and increase the effects of predation. Aumann *et al.* (2006) found that, in the absence of prey limitation, hypoxia-induced starvation was low for blue crabs and was far outweighed by the influence of cannibalism (predation).

Predation is probably the major component of natural mortality for blue crabs in Chesapeake Bay. Various fishes prey on juvenile blue crabs (Van Engel 1987; Moody 1994; Guillory & Elliot 2001; Moody 2003), and a more diverse and more abundant suite of fish predators is present in the Chesapeake Bay in summer (Murdy *et al.* 1997). However, the magnitude of predation on juvenile blue crabs by fishes is still poorly understood. In contrast, large blue crabs are important cannibalistic predators on small crabs (Hines *et al.* 1990; Mansour 1992;

Dittel *et al.* 1995; Hines & Ruiz 1995; Ryer *et al.* 1997; Moody 2003; Spitzer *et al.* 2003), and juveniles and adults often occupy the same habitats (e.g., SAV beds and marsh-fringed creeks). Crabs are most vulnerable to predation during and just before and after molting (Ryer *et al.* 1997), and environmental conditions are best for rapid growth and frequent molting in summer. If food is not limited, small crabs (10-30 mm carapace width [CW]) can molt as often as once a week during the summer. Thus, changes in predation pressure in the Chesapeake Bay are likely to cause seasonal changes in mortality, with mortality being highest in summer.

Tethering experiments are commonly used to assess relative survival or predation pressure, and are useful for comparing habitats or evaluating seasonal patterns of mortality. Good examples for blue crabs are provided by Pile *et al.* (1996) and Moody (1994, 2001), in which mortality was found to (1) decline with increasing size, (2) increase in areas without protective structure or cover, and (3) vary by season. Moody (2001) found that the percentage of tethered crabs that died per day dropped from about 50% at the smallest sizes (11-29 mm CW) to about 20% at 50-70 mm CW. Because some crabs in the stock can grow from 10 to 75 mm CW in one season, and crabs can recruit to the fishery at around 75 mm, the substantial change in relative survival with size is relevant to dynamics described in assessment models. Moody (2001) also found that mortality increased during the warmer months of the year, being exceptionally high for juvenile crabs in the summer. Similarly high mortality rates from tethering studies occur in the Gulf of Mexico (Heck *et al.* 2001; Spitzer *et al.* 2003). Tethering studies provide guidance on patterns in mortality rates, but they do not provide absolute rates to be used in population dynamics models applied at the scale of a stock. Among other concerns, tethered crabs suffer higher predation than untethered crabs (Pile *et al.* 1996; Stehlik & Meise 2001).

Mortality rates of juvenile crabs are also important for assessing the effectiveness of stock rebuilding strategies, including stock enhancement via releases of hatchery-reared juveniles. The success or failure of stock enhancement programs depends on whether released juveniles

survive and recruit to the adult population. Furthermore, most stock enhancement programs, such as the one for blue crab in Chesapeake Bay (Zohar *et al.* 2008), are expected to contribute animals to the exploitable stock in order to benefit commercial and recreational fisheries (Bartley & Bell 2008).

Modern rigorous approaches to stock enhancement require the quantification of survival as a function of size-at-release, time of release, and release habitat to optimize release strategies and assess feasibility and cost-effectiveness (Blankenship & Leber 1995; Hilborn 1998; Leber 1999, 2002, 2004; Lorenzen 2005, 2006, 2008). Previous assessments of stock enhancement efforts for blue crab in Chesapeake Bay have included only relative measurements of survival for released crabs, primarily through tethering. Although such experiments provide information that can guide enhancement efforts toward the most appropriate habitats and seasons for release (Hines *et al.* 2008; Johnson *et al.* 2008), they cannot determine the degree to which releases will ultimately contribute to the exploitable stock. Locations and times that are selected as "good" candidates for enhancement releases based on lower relative mortality from tethering trials may not be successful in terms of ultimate survival to the adult stock (Bartley & Bell 2008).

The mortality estimates from Chapter 3 can be viewed as upper bounds on the mortality rates we would expect for juveniles, but we suspect that those estimates will substantially underestimate the mortality rates of small juveniles. To aid the development of modeling approaches and improve predictions about the success of stock enhancement efforts, we estimated mortality rates for juvenile crabs that would serve as recruits to the exploitable population.

Methods

We sought to estimate mortality rates for cohorts of juvenile crabs in selected tidal marsh creeks along the York River, Virginia in 2005 and 2006. Our strategy was to release large cohorts of juvenile crabs that were marked as a single batch and follow the fate of the cohorts

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by repeatedly sampling to recover tagged individuals. Decay in the density of tagged crabs over time following releases was used as a measure of mortality. More direct estimation using wild crabs is possible for larger crabs (> 50 mm) using telemetry (Niezgoda *et al.* 2002) and may be possible for small crabs using PIT tags (Adams *et al.* 2006), but current technological limits prevented us from applying these techniques in the open systems that blue crabs recruit to in the lower Chesapeake Bay.

Previous tagging studies with cohorts of hatchery-reared juveniles (ca. 15-30 mm CW) in lower Chesapeake Bay tributaries indicated that recovery rates of tagged individuals were very low. In creeks and coves along the York River, ranging in size from 10 to 25 hectares (ha), releases of thousands of crabs often resulted in less than 100 recaptures in subsequent sampling with replacement. In addition, we sampled six muddy coves along the middle and lower York River in the spring and summer of 2005 and found rapid decay of the juvenile cohorts in coves with large initial spring densities, not accounting for emigration (Figure 4.1). These results suggested that 10,000 or more juvenile crabs would need to be released in experiments designed to make inferences about mortality based on repeated sampling after release. The sampling effort required to collect such large numbers of juvenile wild crabs for use in experiments is prohibitive, and we chose to use cohorts of hatchery-reared crabs from the Center of Marine Biotechnology (COMB) in Baltimore. The crabs were made available to us through a collaborative effort to assess the feasibility of stock enhancement for blue crabs in Chesapeake Bay (the Blue Crab Advanced Research Consortium; Zohar *et al.* 2008).

Previous work by collaborators at the Smithsonian Environmental Research Center (SERC) has shown that behavior and relative survival of wild and hatchery-reared crabs is not substantially different (summarized in Young *et al.* 2008). Davis *et al.* (2004b) showed that hatchery-reared crabs fed on buried clams and grew similarly to wild crabs in the laboratory. However, a number of other differences were noted in morphology and behavior. Color differences, reduced spine length, and less frequent burying in the sediment were observed
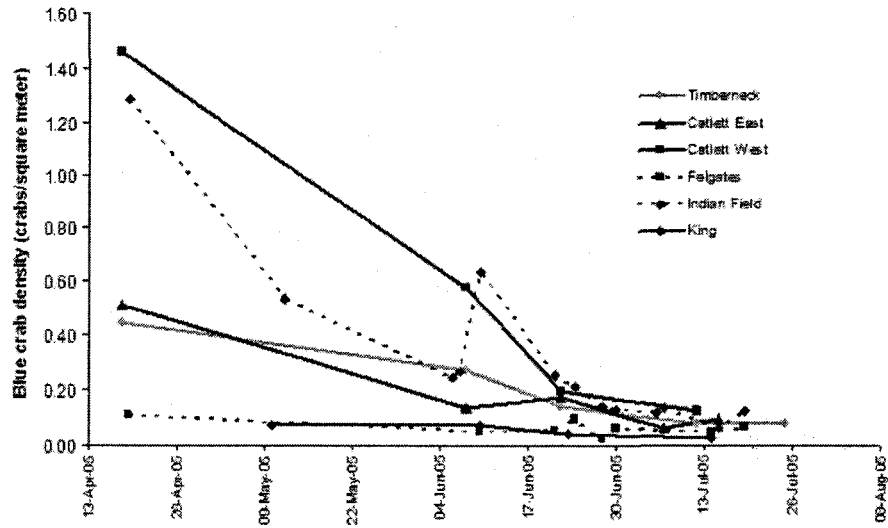
Figure 4.1: Decay rates of juvenile crab densities in selected muddy coves along the York River in 2005.

for hatchery-reared crabs relative to wild crabs (Davis *et al.* 2004b, 2005b). Furthermore, some combination of measured and unmeasured factors resulted in marginally lower survival of hatchery-reared crabs in comparison with wild crabs in tethering trials (Davis *et al.* 2004b, 2005b). A field release experiment also suggested lower survival for hatchery-reared crabs compared to wild crabs, but emigration was not taken into account and could have differentially affected the two groups (Davis *et al.* 2005b). Davis *et al.* (2005b) found that color differences between hatchery and wild crabs disappeared quickly when hatchery crabs were exposed to a natural substrate (within 1-5 days), and that color had little or no effect on survival in lab predation trials. Results from tethering trials in the field were equivocal.

Lateral spines are shorter on hatchery-reared crabs than wild crabs (Davis *et al.* 2004b, 2005b), so the potential exists for elevated short-term mortality in hatchery-reared crabs due to reduced predator defenses. Davis *et al.* (2004b) showed that hatchery crabs released into the wild developed spines as long as wild crabs after one or more molts. Furthermore, Davis *et al.* (2005b) showed that spine length increased in hatchery crabs held in the labo-

ratory after exposure to predators. They suggested that increased spine length provided for higher survival in laboratory predation trials. However, results from laboratory trials were conflicting (crabs exposed to blue crabs had spine lengths equal to controls but survival equal to those exposed to striped bass, with longer spines) and sample sizes were generally small, so it remains unclear what effect spine length has on survival in the wild. In addition, the the effects of conditioning on spine length are probably confounded with large natural variability in spine length, and conditioning of thousands of crabs is not realistic in large releases.

The inclination to bury in the sediment is an important predator avoidance trait for blue crabs. Davis *et al.* (2005b) noted that hatchery crabs buried in the sediment less often than wild control crabs, but Davis *et al.* (2004b) determined that differences in burial rate were small and disappeared after 1-2 days of exposure to natural substrate. However, a 4-day exposure to natural sediment did not offset small differences in tethering or field survival in comparison to wild crab controls (Davis *et al.* 2004b).

Overall, results have been conflicting and equivocal for whether differences in burying tendencies and spine length have important effects on post-release survival of hatchery-reared juvenile blue crabs, but the evidence is not strong that these are serious concerns (Young *et al.* 2008). Thus, to a first approximation, hatchery cohorts provide a means to estimate mortality rates of juvenile crabs that could be expected in wild recruiting cohorts.

Collection, transport, and tagging of crabs

Crabs were hatched and reared to early juvenile stages by the Center of Marine Biotechnology (COMB) in Baltimore, Maryland as part of a collaborative effort to assess the feasibility of stock enhancement for blue crabs in Chesapeake Bay (Zmora *et al.* 2005; Zohar *et al.* 2008). Crabs were reared after hatching in fiberglass indoor tanks at COMB and then transferred for grow-out to concrete ponds at a recently acquired hatchery facility in Piney Point, MD. After the crabs reached release size, the ponds were drawn down and crabs

were collected with dip nets. Crabs were transferred to standard 47-95 liter coolers, which were kept cool by placing two large ice packs under a layer of burlap on the bottom of the coolers. Layers of a few hundred crabs each were placed between burlap sheets on top of the ice packs. The crabs were transported to VIMS by truck and immediately placed in flow-through seawater tanks in the Glucksman Experimental Mesocosm (GEM) Laboratory that were supplied with unfiltered and untreated York River water (23-31.5°C, 18-22 ppt). Whereas unfiltered river water may carry unwanted artifacts from the estuary, Haefner (1971) indicated that "natural" flow-through systems resulted in fewer molt-related complications in soft crab shedding operations than did recirculating systems. Air stones were placed in each tank to maintain acceptable dissolved oxygen levels, and salinity, dissolved oxygen, and temperature were recorded to assess water quality conditions. The day-night cycle in the laboratory was set to match the natural photoperiod.

Crab tagging occurred as soon as possible after transport and followed the procedures described by van Montfrans *et al.* (1986) and Fitz & Wiegert (1991a), except on a much larger scale. Individual half-size microwire tags (0.5 mm long, 0.25 mm in diameter) were injected into the basal muscle of the left or right fifth periopod (swimming leg, backfin) of each crab using MARK IV Automatic Tag Injectors (Northwest Marine Technology, Shaw Island, Washington). The tags are cut from a continuous spool of microwire, magnetized for later detection, and injected through a hollow hypodermic needle. Other tagging methods, such as elastomer injection, have been evaluated for juvenile blue crabs, but are not logistically feasible for tagging numbers as large as those used in our study (Davis *et al.* 2004a).

Groups of 500-1000 crabs were brought to the tagging station and held in aerated coolers. Tagged crabs were retained in the lab until all crabs were tagged and ready for release, which occurred within two or three days. After tagging, crabs were checked with a handheld wand detector to ensure that the tag was properly implanted, and a subsample of crabs was randomly selected from each tagged cohort for size measurements and injury assessment to

characterize the released cohorts. All measurements were made with sliding jaw calipers to the nearest 0.1 mm CW. Once crabs were tagged, checked, and selected crabs measured, the group was returned to the laboratory holding tanks.

We did not measure acute mortality from collection to arrival at the laboratory; i.e., collection and transport mortality. We only tagged crabs that were active and appeared to be in good condition upon arrival at the laboratory tagging station. We discarded dead and moribund crabs, as well as crabs with many missing limbs. Thus, all numbers for experimental releases reflect the number of crabs that were deemed to be in good condition and were tagged for releases.

Tag retention, tagging-related mortality, and growth in the laboratory

A random subset of crabs was retained in the laboratory from each of the three cohorts used in the 2006 field release experiments to examine retention of the microwire tags and to assess mortality resulting from tagging and handling. The person doing the tagging (the tagger) was not aware of which crabs were being selected. To the extent possible, an approximately equal number of crabs was drawn from each tagger. However, the number of taggers varied between four and eight people for the various releases, and we did not have laboratory space to permit a complete assessment of individual tagging proficiency. Past experience indicated little variation among taggers, and all persons that participated as taggers were trained and had prior experience.

Once selected for the lab trials, crabs were transferred to the same flow-through tank system where release crabs were being held. Crabs were held in individual plastic containers (14 cm wide, 14 cm long, 10 cm deep) to prevent cannibalism and injury. The containers had holes along all sides to permit water circulation as they floated in the tanks.

Tagging was necessarily rapid in the large tagging sessions, and we were concerned that tags might not be implanted correctly. If a tag was not injected, but rather was rubbed from the injection needle onto the carapace, it could remain on the crab and the crab would

register as being tagged when checked with the wand. A tag on the carapace could then wash off once the crab was returned to a holding tank. To assess this artifact, we carefully rinsed each of the crabs selected for our experimental trials and checked to be sure that it retained the tag internally rather than on its carapace prior to placing the crab in an individual container.

Experimental controls for the lab trials of mortality and tag retention should include wild crabs, both tagged and untagged, and hatchery crabs that were not tagged. Based on our experience that individually-held juvenile crabs survive well in the laboratory given proper feeding and water quality, as well as similar results in other studies (Tagatz 1968b; van Montfrans *et al.* 1986; Fitz & Wiegert 1991a), our primary concern was tag retention. Tag loss would bias estimates of mortality unless it occurred at a constant rate following tagging and release.

Space limitations in the GEM Lab for the first two releases in 2006 prevented us from running side-by-side controls of all combinations. In the first release (June), we selected 46 tagged hatchery-reared crabs from six taggers to assess tag retention in the laboratory. In the second release (11 July), we selected and monitored 41 tagged hatchery-reared crabs from four taggers to assess tag retention in the laboratory. Unexpected poor survival of laboratory-held crabs in these first two trials caused concern about the water quality conditions in the laboratory tanks. After an increase in available lab space, we began a trial with 14 wild untagged crabs on 28 July to assess survival. This trial ran alongside the remaining portion (17 days) of the 11 July hatchery crab tag retention trial. Wild crabs for this trial were collected from seagrass beds around Allens Island in the lower York River, and sizes were selected to match the sizes of hatchery cohorts. Post-collection treatment was replicated to the extent possible to match the transport and handling of hatchery-reared crabs. Crabs were collected and placed in coolers with burlap for three hours, then transferred to coolers with air stones before finally being selected and placed in individual containers in the laboratory tanks. In the third release (August), we included all controls in the labora-

tory trial: 16 tagged hatchery crabs, 10 tagged wild crabs, 10 untagged wild crabs, and 16 untagged hatchery crabs.

Crabs were checked daily or every other day. At each check, crabs were fed frozen fish (menhaden, mummichogs, anchovies, silversides), and all crabs received the same diet at each feeding. Uneaten food and molted carapaces were removed from the containers and the containers were thoroughly rinsed with water from the tanks. Crabs were measured, checked for a tag, and any molts were noted. Molts were recorded as having occurred on the day prior to finding evidence of a molt. For example, if a crab was checked and found alive and not molted on the second day after tagging, but evidence of a molt was found on the third day, the crab was recorded as having molted on the second day after tagging. Measurements of crabs that had recently molted (post-molt) were replaced by a measurement on the next day once the shell had fully hardened (intermolt). Post-molt crabs may not have fully absorbed water to achieve the full intermolt carapace width (Olmi & Bishop 1983; Cadman & Weinstein 1985).

Mortality, tag retention, intermolt period, and growth per molt of crabs in the lab were examined to determine whether tagged crabs differed from untagged crabs. However, due to the discontinuous nature of the data, intermolt period and growth per molt are used as relative indicators of condition and not as definitive evidence of growth dynamics (Cadman & Weinstein 1985). Furthermore, we did not examine differences in growth and molting by gender because previous work has confirmed that juvenile males and females are similar at sizes less than 50 mm CW (Pullen & Trent 1970; Olmi & Bishop 1983; Cadman & Weinstein 1985, 1988).

For mortality assessment, crabs were assumed to have died immediately after the last inspection at which they were observed alive, similar to recording of molts. For example, if the crab was observed alive on the third day after tagging and was then observed dead on the fourth day after tagging, it was recorded as having lived three days after tagging. Because we could not check the crabs every day following tagging, this procedure was

used to provide consistency. If a crab was checked and alive on the third day, but then checked next on the the fifth day and found dead, a survival time of five days would be an overestimate. Our procedure can only underestimate survival, with the exception of crabs that were found dead the day after tagging. Because we only tagged crabs that appeared to be in good condition, these crabs were assumed to have survived at least one day (i.e., they died immediately prior to the check).

Kaplan-Meier survival functions were computed and plotted to assess survival of animals in the laboratory trials. The Kaplan-Meier estimator was used because of the potential for right-censoring in the data (Williams *et al.* 2002). Some crabs were expected to survive the entire experimental period and their deaths would not be observed. Censoring was also used to handle a single case in the 11 July trial in which the crab escaped from its container after two days. Kaplan-Meier survival functions were estimated and plotted using the functions provided in the *survival* package in R (Venables & Ripley 2002). The estimated probability of surviving until time t is

$$\hat{S}_t = \prod \frac{r_t - d_t}{r_t}, \tag{4.1}$$

where r_t is the number of individuals at risk just before time t (including those censored at that time), d_t is the number of individuals that died at time t, and the product is taken over the times at which deaths occurred before time t. The associated estimate of the variance for the Kaplan-Meier survival function is

$$var\left(\hat{S}_t\right) = \hat{S}_t^2 \sum \frac{d_t}{r_t\left(r_t - d_t\right)}, \tag{4.2}$$

where the sum is over the times at which deaths occurred before time t. In the absence of censoring, the survival function is simply one minus the empirical distribution function, or the observed proportional survival, and the estimated variance is obtained from the binomial distribution:

$$\frac{\hat{S}_t \left(1 - \hat{S}_t\right)}{n} = \frac{r_t \left(n - r_t\right)}{n^3}, \tag{4.3}$$

where n is the number of individuals included in the trial. We plotted survival curves and associated 95% confidence intervals for each trial.

Experimental field releases

We conducted four field release experiments in 2005 and three experiments in 2006. All experiments were conducted in two small tidal marsh coves fringed primarily with salt marsh cordgrass (*Spartina alterniflora*). The coves were embayments off of larger tributaries to the middle York River. In 2005, we conducted experiments in a 10 ha cove near the mouth of Timberneck Creek, approximately 5.6 river kilometers (rkm) upstream of VIMS (Figure 4.2). In 2006, we used a 2.5 ha cove near the mouth of Aberdeen Creek, approximately 7.2 rkm farther upstream of Timberneck Creek (Figure 4.3). The coves are similar in depth and sediment characteristics, and are unvegetated and unstructured except along the margins. The cove in Aberdeen Creek was selected to measure emigration of tagged crabs in 2006. The mouth of the cove is only ca. 15 m across at high tide and is fully wadeable even at high tide (max depth = 1.5 m), permitting sampling with a seine across the mouth of the cove.

In 2005, we used four cohorts of crabs during the summer, fall, and early winter. The cohorts varied in size from 3,700 to 16,000 crabs (Table 4.1), and crabs ranged in size from 10 to ca. 40 mm CW (Figure 4.4). The average size of the crabs in a cohort was determined by operations at the hatchery and grow-out facilities, but all cohorts were similar in size.

Tagged crabs were released into Timberneck cove and spread over an area sized to generate densities that roughly corresponded to wild densities we observed in prior sampling (Seitz *et al.* 2005, 2008; Figure 4.1). Crabs were distributed by hand from a boat as evenly as possible throughout the back area of the cove (Figure 4.5). Similar to Davis *et al.* (2005a), we were concerned about emigration from this relatively open cove, and so we released the
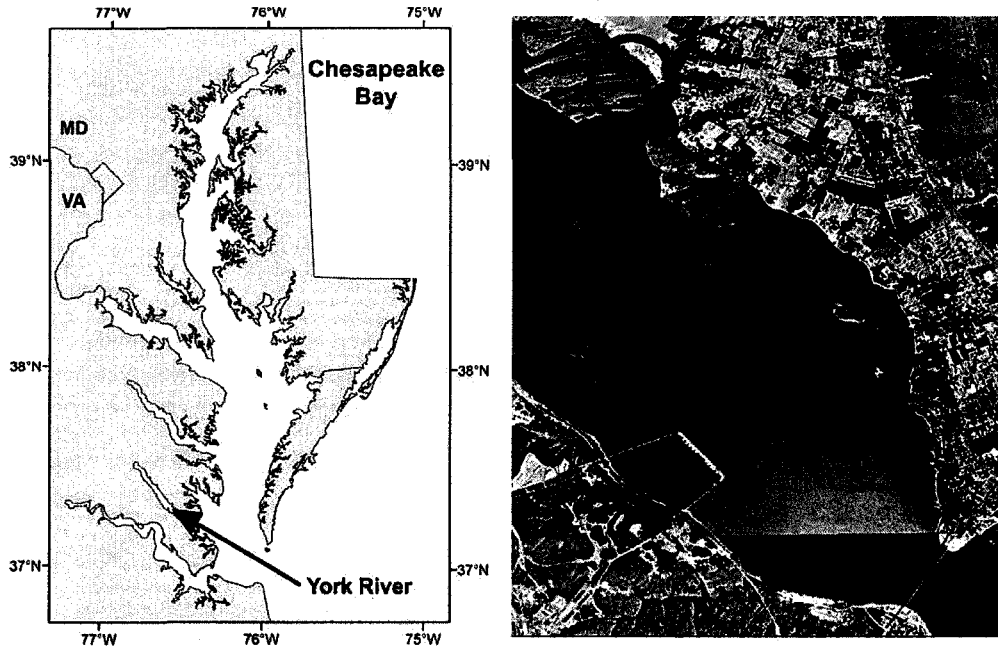
Figure 4.2: [Left] Location of the York River in the Chesapeake Bay. [Right] Location of the cove near the mouth of Timberneck Creek in the middle York River. The cove is approximately 5.6 river kilometers upstream of VIMS, which is located at Gloucester Point (bottom right of the picture).

Table 4.1: Cohorts of hatchery-reared crabs released into Timberneck cove in 2005.

Date released	Number of crabs	Number subsampled	Sex ratio (M:F)
26 July 2005	5,150	534	1.0
9 August 2005	3,678	551	0.9
22 September 2005	6,191	576	1.0
7 December 2005	15,925	328	1.3

Figure 4.3: Location of the cove near the mouth of Aberdeen Creek in the middle York River. The cove is approximately 13 river kilometers upstream of VIMS.
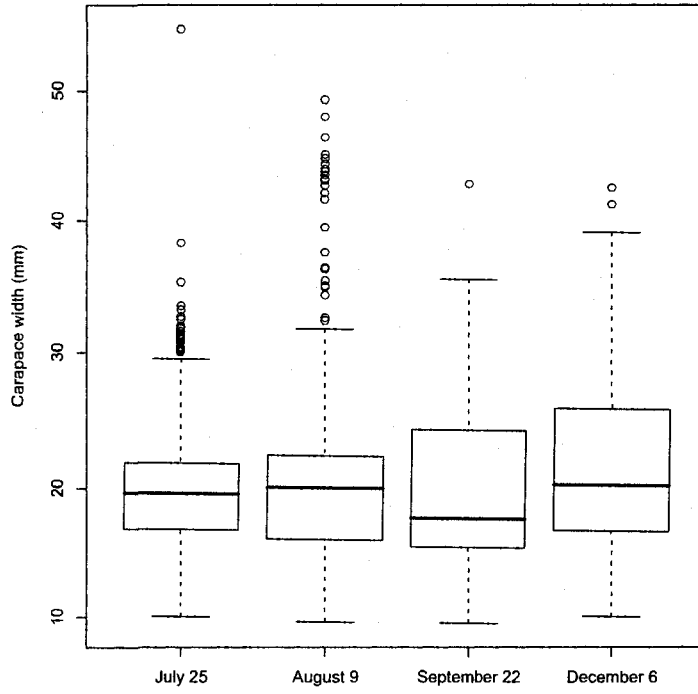
Figure 4.4: Boxplots of length subsamples from the four cohorts of crabs released into Timberneck cove in 2005. The dark center line indicates the median and the edges of the box indicate the first and third quartile.
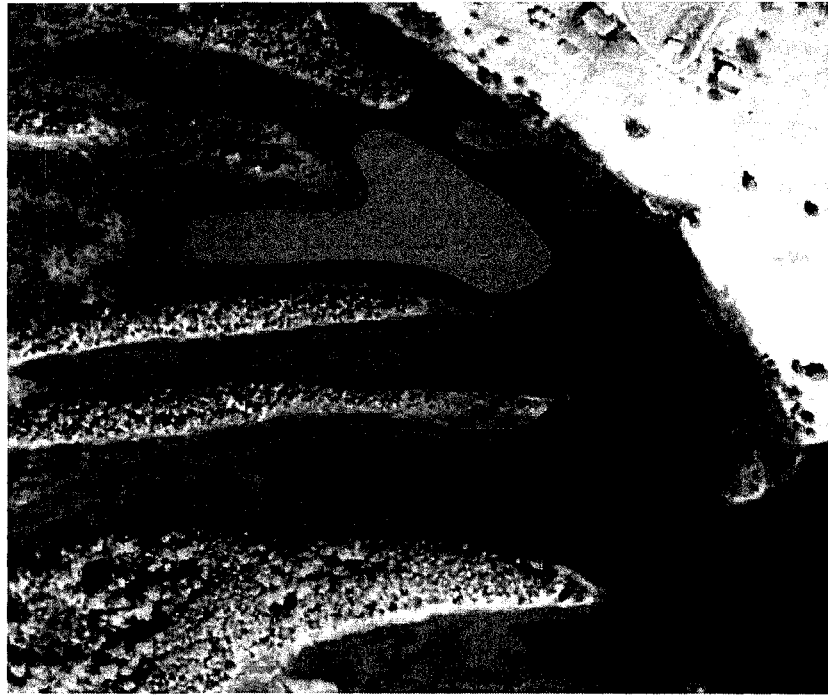
Figure 4.5: Areas where juvenile hatchery-reared crabs were released (orange) and sampled repeatedly in the days and weeks following release (green).

crabs in the back of the cove to reduce emigration rates. Blue crab postlarvae make vertical movements during tidally-mediated up-estuary transport (Olmi 1994; Tankersley & Forward 1994; Forward *et al.* 2003), and juvenile blue crabs use similar behaviors to take advantage of tidal stream transport during secondary dispersal (Etherington & Eggleston 2000; Blackmon & Eggleston 2001; Etherington & Eggleston 2003; Reyns & Eggleston 2004; Forward *et al.* 2004a, 2005). However, these behaviors are best described in association with secondary dispersal of crabs smaller than those used in our experiments (< 10 mm). Nonetheless, we were concerned about the potential for emigration and also a flight response of hatchery crabs released into a novel environment. Our release strategy in Timberneck cove allowed us to sample repeatedly in the front and back ares of the cove to potentially capture crabs as they moved gradually out of the cove away from the release site.

In 2006, we used three cohorts of crabs during summer and early fall. The same collection,

Table 4.2: Cohorts of hatchery-reared crabs released into Aberdeen cove in 2006.

Date released	Number of crabs	Number subsampled	Sex ratio (M:F)
21 June 2006	13,489	519	0.8
13 July 2006	12,004	745	1.0
27 September 2006	11,721	326	1.0

transport, and tagging procedures were used as in 2005 and previous experiments. The cohorts varied in size from 11,721 to 13,489 crabs (Table 4.2), and crabs ranged in size from 10 to ca. 30 mm CW (Figure 4.6). The first cohort was slightly larger than the last two, but size distributions overlapped considerably. The crabs in the 2006 cohorts were slightly smaller than those in the 2005 cohorts.

To assess emigration, we attempted to collect any crabs leaving the cove on ebbing tides following the releases. We used a 30-m bag seine with 6-mm stretch mesh pulled across the entire mouth of the cove. The seine was attached to a seawall on one side and pulled onto the marsh edge on the other. The net was retrieved to the marsh edge at 30-min intervals and all crabs were collected from the net, measured, and checked for a tag. We recorded data for wild crabs to determine "background" levels of emigration against which to compare hatchery crab emigration rates. We continued to reset the net and sample until the tide had fully receded. Given time to sort the catch, we usually obtained 3-5 samples over a tidal period. Sometimes the tides ebbed completely, leaving just a trickle through the mouth of the cove, and other times about 0.5 m of water remained in the channel.

We estimated the decay rates of the cohorts using repeated, simple random sampling inside and outside the release area in the days and weeks following the crab releases. All sampling was conducted using a crab scrape (Figure 4.7), a modified version of a commercial crab scrape used by watermen in seagrass beds. The scrape has an opening 1-m wide and a tickler chain was used to increase capture efficiency, especially for small crabs that were buried shallowly in the muddy sediment. The scrape was deployed and retrieved using an electric winch and was towed for a set distance of 20 m. We continued to revisit the coves
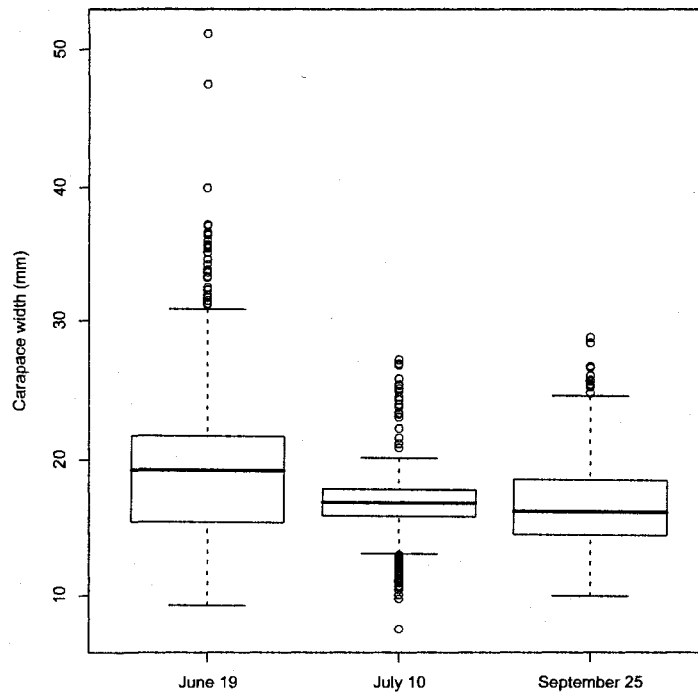
Figure 4.6: Boxplots of length subsamples from the four cohorts of crabs released into Aberdeen Creek in 2006. The dark center line indicates the median and the edges of the box indicate the first and third quartile.
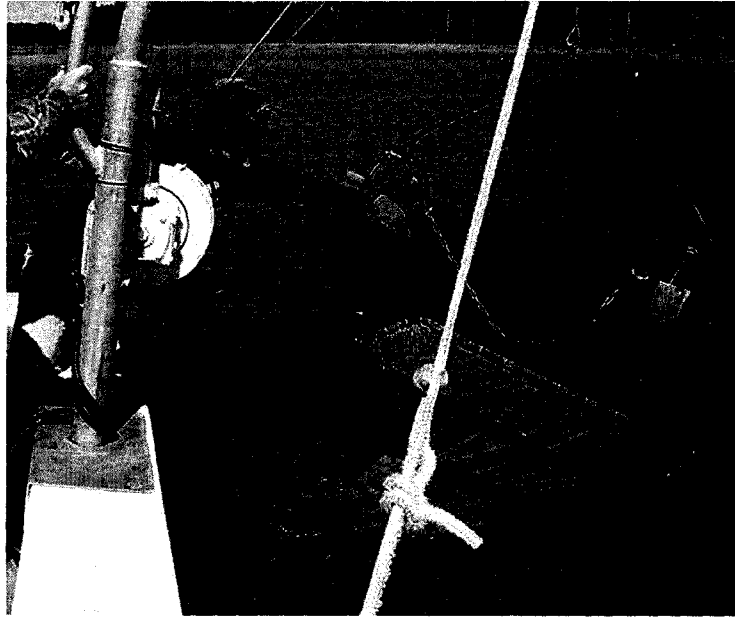
Figure 4.7: Picture of the crab scrape used to sample the coves during field release experiments. Scrape designed by Michael Seebo. Pictured in photo: Alison Smith.

and sample with the scrape until two two consecutive sampling events resulted in fewer than two tagged crabs being captured.

We used USGS DOQQ aerial photos in ArcGIS 9.1 (ArcMap) to digitize areas of the cove that were wetted continuously (except during unusual tides) and could serve as habitat for released juveniles. From that area we digitized a subset that was available to our sampling gear; i.e., had appropriate depth and was free of obstructions (e.g., Figure 4.5). Random points were generated from within the polygons representing the potential sampling area for each sampling event. In the event that two random points fell too close to each other to be considered independent, we discarded the point and used the next one.

In the 2005 experiments in Timberneck cove, sampling outside of the release area was used to detect general movements out of the cove. Sampling inside of the release area was used to estimate densities of tagged crabs and decay rates of the cohort. At each sampling event, we scraped 10-12 random locations in the release area as well as 5-6 locations outside

of the release area.

In 2006, crabs were distributed throughout the entire cove due to the small size of the cove, but we avoided releasing crabs within ca. 100 m of the cove mouth. At each subsequent sampling event, we randomly sampled 10-12 locations within the polygon of potential sampling area in the cove. In seine sampling for emigrating crabs, we attempted to sample each of the first four ebbing tides that followed the releases, but weather prevented us from meeting that goal in all but one experiment (September).

Counts of tagged crabs in scrape samples were used to generate swept-area estimates of crab densities (m^{-2}) for each sampling event, and decay rates were estimated using simple linear regression of $ln(mean\,density)$ against time. We assumed that catch efficiency did not vary among tows or among days during an experiment. We do not have good point estimates of efficiency for the scrape gear, but scrape efficiency has bee shown to be low based on comparisons with suction sampling gear, for which gear efficiency is known to be relatively high. Similarly, Davis *et al.* (2005a) report efficiency for a similar gear used in similar habitats as 5.5%, although no data was presented to support the estimate. Rozas & Minello (1997) point out the necessity of accounting for catch efficiency and the weaknesses of actively towed gears like scrapes and trawls for capturing small blue crabs. However, because catch rates of tagged crabs are typically so low, tows of at least 20 m with an active gear are necessary to obtain recaptures; suction sampling and other similar methods are not feasible alternatives. We chose to compare relative catch rates through time and assumed that changes in the efficiency of the gear were responsible for a negligible amount of variation in the catch rates. Given the short duration of the experiments and the similarity in conditions and tidal stage among sampling events within a release trial, we felt this was reasonable.

Table 4.3: Ranges of water quality variables in the lab tanks during tag retention and mortality trials in June, July, and August 2006.

Trial dates	Dissolved oxygen (mg/L)	Salinity (ppt)	Temperature (C)
19 June - 1 July	5.5 - 6.6	20.2 - 21.0	25.3 - 26.0
11 July - 14 August	4.9 - 7.2	18.4 - 21.4	25.0 - 31.5
28 July - 14 August	4.9 - 7.2	18.4 - 21.4	25.0 - 31.5
15 August - 5 September	4.9 - 6.8	19.6 - 22.3	23.0 - 28.3

Results

Tag retention, tagging-related mortality, and growth in the laboratory

Dissolved oxygen, salinity, and temperature measurements in laboratory tanks reflected ambient York River conditions and were always within acceptable limits for juvenile blue crabs (Table 4.3). In particular, dissolved oxygen levels were adequate; percent saturation readings always exceeded 75%. Crabs do not take up oxygen during molting, so an adequate supply is particularly important at times prior to and after molting (Lewis & Haefner 1976).

In total, we monitored the fates of 113 tagged hatchery and wild crabs over the course of our three tag retention trials (Table 4.4). We never found a tag that had been stuck to the carapace and washed off during an initial check for tag retention, alleviating concerns about immediate tag loss due to tagger error. In addition, although sample size for assessing individual tagger proficiency was small, we did not observe any consistent patterns among taggers for tag loss or post-tagging mortality.

Out of all the tagged crabs, we observed four losses of a tag, but many crabs did not survive through a molt. Tag loss would be expected to occur almost entirely at the first molt (van Montfrans *et al.* 1986; Fitz & Wiegert 1991a). One tag was lost 2-3 days after tagging by apparently working out of the insertion puncture hole; the tag was collected from the inside of the container. Of the 43 crabs that molted successfully at least once, three lost their tag during the first molt (7%). Twenty-two tagged crabs molted a second time (and some as many as four times), and no tags were lost beyond the first molt.

Table 4.4: Summary data on tag retention and mortality for the lab trials in 2006. In the column for the number of crabs, H indicates hatchery crabs and W indicates wild crabs.

Trial dates	Number of crabs	Size of crabs (mean, range; mm CW)	Time to 50% mortality (days)
19 June - 1 July	46 (H)	10.4 - 36.6 (21.2)	4
11 July - 14 August	41 (H)	11.3 - 19.7 (16.4)	7
28 July - 14 August	14 (W)	10.9 - 41.7 (32.4)	> 17 days
15 August - 5 September	52 (32H, 20W)	11.4 - 28.5 (17.5)	> 21 days

In the June trial, all 46 crabs died under supervision in the lab within 10 days of tagging. No censoring was necessary in calculating the survival function and the plot represents proportional survival (Figure 4.8). Sixteen (35%) of the crabs died within one day and 50% had died within four days, suggesting residual negative effects of rearing conditions, collection, transport, and tagging. This suggestion is consistent with anecdotal reports from the Piney Point hatchery that conditions in the ponds were atypically poor during the end of the rearing period. Although temperature and salinity were within typical ranges (ca. 15 ppt and 25°C), dissolved oxygen was well below saturation levels (55 − 58%) and crabs were sluggish upon collection (Paul Flynn, COMB Piney Point hatchery manager, personal communication).

Observations on molting suggested further evidence of residual negative effects. Of the 11 crabs that attempted to molt, five died during or immediately after the molting process; four crabs never shed their old carapace. Because of the overall high mortality and the complications with molting, only seven crabs successfully molted at least once in the lab (including the one that died just after molting), and no crab molted more than once. Crab size did not appear to be the major factor in molting complications or mortality, as crabs between 12.5 and 33.6 mm CW molted successfully.

Although sample size was small for crabs that molted at least once (7), we present data on growth per molt and intermolt period for completeness. The percent increase in size through the first molt relative to initial size ranged from 15 − 30% (median = 17%), but

Figure 4.8: Kaplan-Meier survival function for the 46 crabs retained in the lab from the June 2006 experimental release of hatchery-reared juveniles. Dashed lines are 95% confidence intervals. All of the crabs died during the trial, so no censoring is indicated and the solid line is simply proportional survival.

Figure 4.9: Kaplan-Meier survival function for the 41 crabs retained in the lab from the 11 July 2006 experimental release of hatchery-reared juveniles. Dashed lines are 95% confidence intervals. The censored observation for the escaped crab is indicated with a hatch mark, and three other crabs were censored at 14 days.

there was a weak effect of initial size. The four crabs less than 20 mm initial size all increased about 16% in size, whereas the crabs greater than 21 mm increased 21 − 30% in size.

In the 11 July trial, three crabs survived in the lab far beyond when the other 38 had died. Most crabs perished within two weeks, and 50% of the crabs had died within seven days (Figure 4.9). One crab survived 31 days and two were alive when the trial was ended on the 33rd day. For simplicity of presentation, these three crabs as well as one crab that escaped its container early in the trial were right-censored in the survival function. We right-censored the observations for the three long-lived crabs at 14 days. The poor survival in this trial could not be explained by poor hatchery water quality, as temperature and salinity were normal (13 ppt, 25-29°C) and dissolved oxygen was high (> 5.2 mg/L [median = 6.4] and > 70% saturation [median = 86%]) in the ponds for the week prior to collection.

Thirteen of the crabs molted at least once, including the long-lived crabs censored in the

survival function, and none of the crabs died during molting. Three crabs molted both a second and third time, and one molted a fourth time. Molting occurred among crabs of sizes throughout the initial size distribution. The percent increase in size through the first molt relative to initial size ranged from $11 - 33\%$ (median $= 23\%$), but there was a weak effect of initial size. The two crabs less than 16 mm initial size all increased less than 20% in size, whereas 9 of the 11 crabs greater than 16 mm increased $20 - 33\%$ in size. All three of the second molts increased the size of the crab by about 24%, but the third molt varied from 15 to 36% (median $= 30\%$) increase in size. The fourth molt for the single crab increased its size by 24%.

The small laboratory survival trial that began on 28 July provided confirmatory evidence that the mortality observed for hatchery-reared crabs in the laboratory was due to residual effects from rearing, collection, transport, and tagging. Thirteen of the 14 crabs survived the entire 17 day trial. One crab died on the 15th day, but appeared to have a complication associated with molting; the shell never hardened after more than 32 hours post-molt. The wild crabs were larger on average than the hatchery-reared crabs because smaller juveniles are not present in the lower Chesapeake Bay at this time of year (Table 4.4). Thirteen of the crabs molted at least once during the trial. The percent increase in size through the first molt relative to initial size was similar to the hatchery crabs, ranging from 16 to 30% (median $= 24\%$). Sample size was small, but there did not appear to be an effect of initial size on percent increase in size through the first molt. Six of the crabs molted a second time, and the increase in size ranged from $17 - 30\%$ (median $= 25\%$). Two crabs molted a third time and increased 21 and 30%. The wild crabs in this trial appeared to molt more often than the hatchery-reared crabs in the first two trials.

In the August trial, survival of hatchery-reared crabs was much higher than in the previous trials with tagged hatchery crabs. Nine of the 52 crabs died during the trial, but only one crab died within the first week (on day 6; Figure 4.10). The 43 remaining crabs survived until day 21 and were censored at that time. Of the nine crabs that died, none were untagged
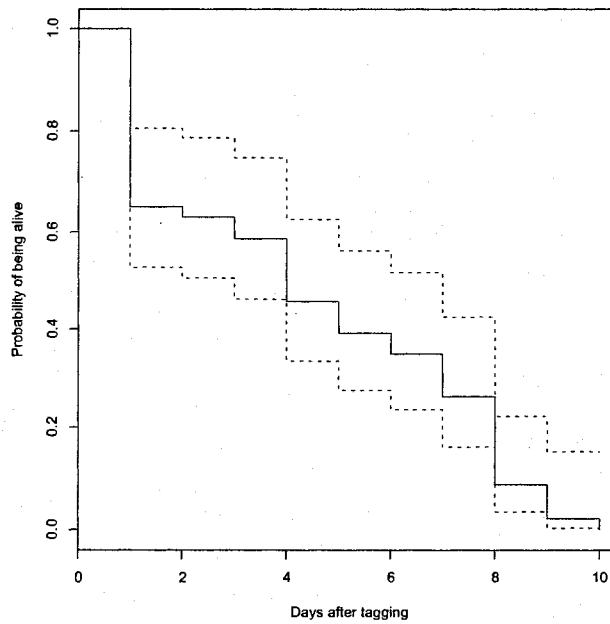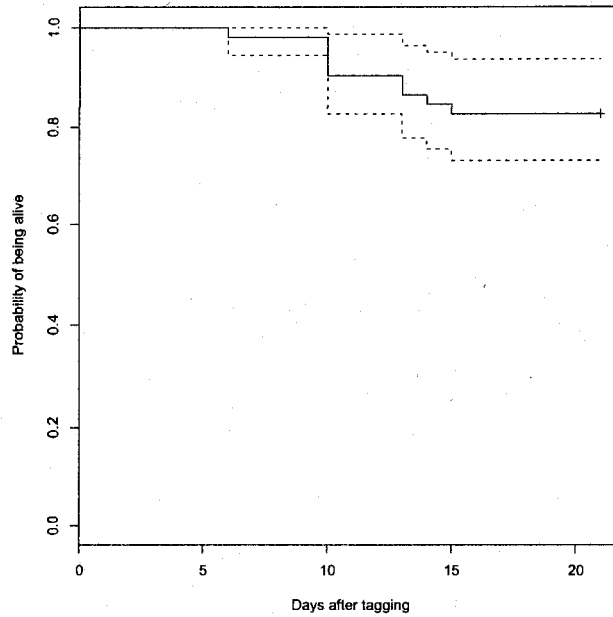
Figure 4.10: Kaplan-Meier survival function for the 52 crabs retained in the lab from the 15 August 2006 experimental release of hatchery-reared juveniles. Dashed lines are 95% confidence intervals. Censored observations are indicated with hatch marks.

wild crabs. Seven hatchery crabs died, three of which were tagged and three of which were not, and two wild tagged crabs died. Because so few wild crabs died, a survival function for hatchery crabs did not differ much from the one for all crabs combined (Figure 4.11). The three tagged hatchery crabs that died perished before their first molt (one died during the molt), whereas the other wild and hatchery crabs that died survived through at least one molt, and three survived through two molts (1 wild, 2 hatchery). No other crabs showed molting complications. Hatchery water quality was similar to conditions for the 11 July cohort during the week prior to collection of this cohort, although dissolved oxygen levels were higher. Temperature and salinity were normal (12-13 ppt, 26-29°C) and dissolved oxygen was high ($>$ 6.8 mg/L [median = 7.3] and $>$ 95% saturation [median = 100%]).

In total, the crabs in this trial molted more than hatchery crabs from previous trials − 49 (94%) of the crabs molted successfully at least once, 43 molted a second time, and six
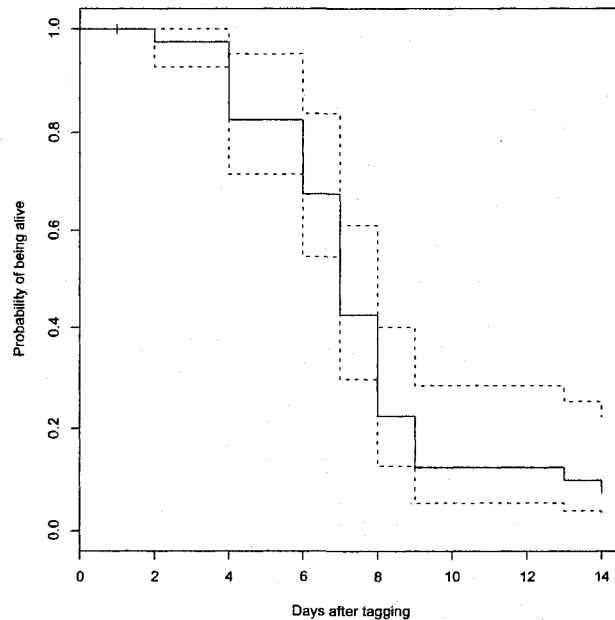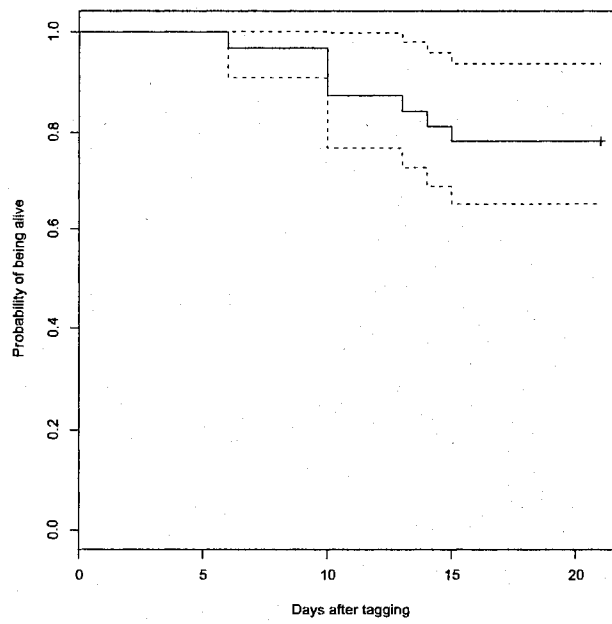
Figure 4.11: Kaplan-Meier survival function for the 32 hatchery crabs retained in the lab from the 15 August 2006 experimental release of hatchery-reared juveniles. Dashed lines are 95% confidence intervals. Censored observations are indicated with hatch marks.

molted a third time. We compared molting and growth between hatchery and wild crabs. For the 29 hatchery crabs that molted at least once, the percent increase in size through the first molt relative to initial size ranged from 5 to 34% (median = 28%), and there was no apparent effect of initial size (Figure 4.12). The only crab that increased in size less than 20% (the 5%) was 15.5 mm CW initially; it molted two more times and did not die during the trial. For the 20 wild crabs that molted at least once, the percent increase in size through the first molt relative to initial size ranged from 18 − 38% (median = 25%), but there appeared to be an effect of initial-size (Figure 4.13). Twenty-five hatchery crabs molted a second time, and the percent increase in size through the second molt ranged from 18 − 29% (median = 23%), and there was no effect of initial size. Eighteen wild crabs molted a second time, and the percent increase in size ranged from 13 − 29% (median = 22%), and there was also no effect of initial size. Two hatchery crabs molted a third time and size increased 19 and 24%. Four wild crabs molted a third time and size increased from 16 − 24% (median = 21%).

Because of the discontinuous data on molting, intermolt period is difficult to interpret for the first molts. In the June trial, all but one of the seven crabs that attempted to molt did so on the first or second day following tagging; the remaining crab attempted to molt on the sixth day. In the 11 July trial, all 13 of the first molts occurred within the first three days of the trial. In the 28 July trial, 6 of 13 wild crabs first molted within 1-2 days of tagging. Lastly, in the August trial, 38 of 49 first molts occurred within 1-3 days of the start of the trial. It appears that molting is accelerated by being placed in a protected container in the laboratory, as it is unlikely that so many crabs were coincidentally ready to molt just before being retained. Especially for hatchery crabs reared in high density amongst other cannibalistic conspecifics, molting may very well be delayed to avoid potential cannibalism. The same may be true for juvenile crabs collected from seagrass beds, where densities are high and cannibalism is an important component of mortality. Intermolt periods of second molts may be more representative of differences between hatchery and wild crabs. The
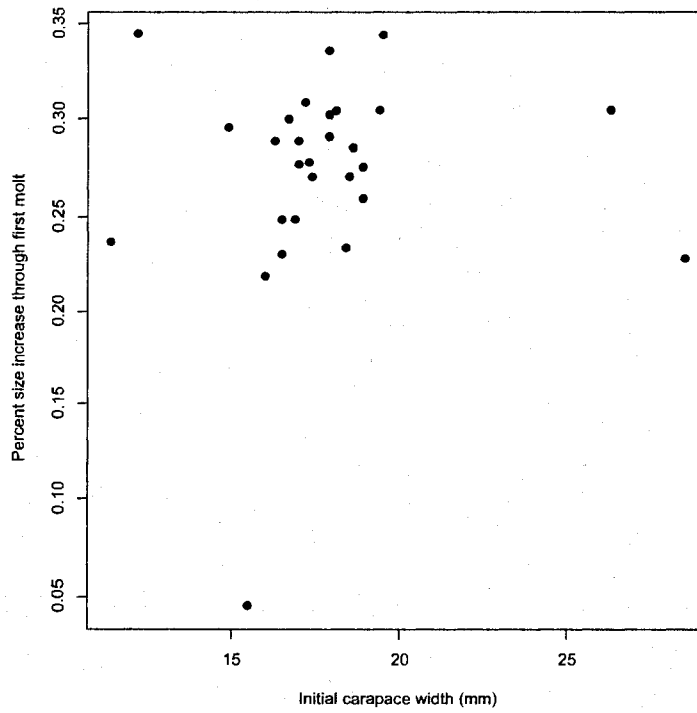
Figure 4.12: Percent increase in size through the first molt relative to initial size for hatchery crabs that molted at least once in the August 15 lab trial.
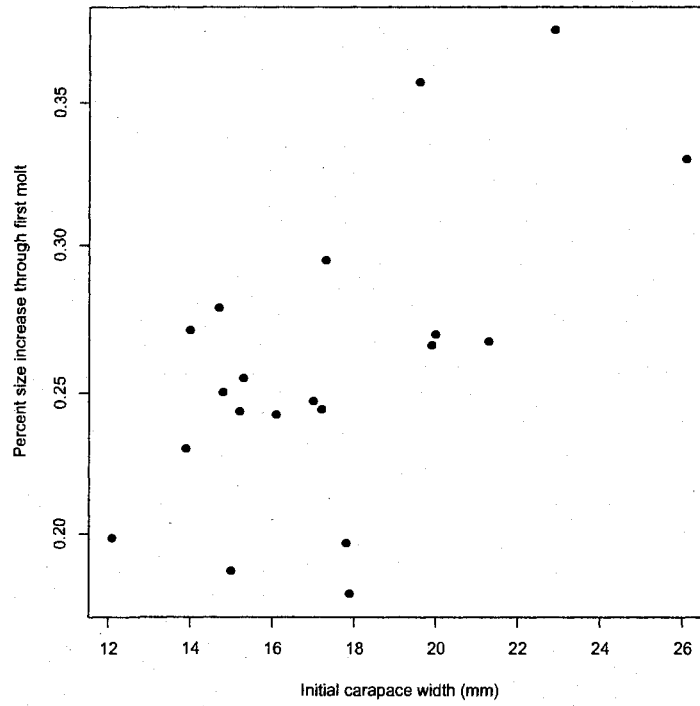
Figure 4.13: Percent increase in size through the first molt relative to initial size for wild crabs that molted at least once in the August 15 lab trial.

three hatchery crabs from the 11 July trial that molted did so in 4-7 days after their first molt, and wild crabs in the 28 July trial molted a second time within 3 to 14 days of the first. Similarly, hatchery crabs from the 15 August trial molted a second time within 4-12 days (median = 7), almost identical to the wild crabs.

The three laboratory trials with hatchery-reared crabs provided conflicting results for survival, but similar results for tag retention and growth. Tag retention was high and growth was similar for hatchery crabs in comparison to wild crabs. Survival of hatchery crabs in the first two trials were considerably lower than for the August trial and were lower in comparison to wild crabs. Whereas mortality through the first week was negligible for wild crabs and hatchery crabs in the August trial, in both earlier trials 50% or more of the hatchery crabs died within the first week.

Experimental field releases

In 2005, we tracked the fate of four cohorts of hatchery-reared juvenile crabs released into Timberneck cove. Crabs did not appear to emigrate from the release area. In the first release in July, we found only three recaptured crabs outside of the release in 75 scrape tows following the release (Figure 4.14). Even fewer crabs were captured outside of the release area in the other three releases. Overall, it was rare to capture a tagged crab outside of the release area, even when crabs persisted for months as during our December release. This generally agrees with sampling from previous years following releases into other coves along the York River, where it was rare to capture a tagged crab anywhere but in the immediate area of release, even in coves that were over 25 ha in size.

Weather conditions prevented sampling on numerous occasions, but five or more sampling events were obtained following each release. Recapture rates of tagged crabs were low in all experiments. Tagged crabs from the cohorts released in summer and early fall persisted for only a few weeks, whereas crabs released in December persisted for over two months (Figure 4.15). Under the assumption that no tagged crabs emigrated from the release area,
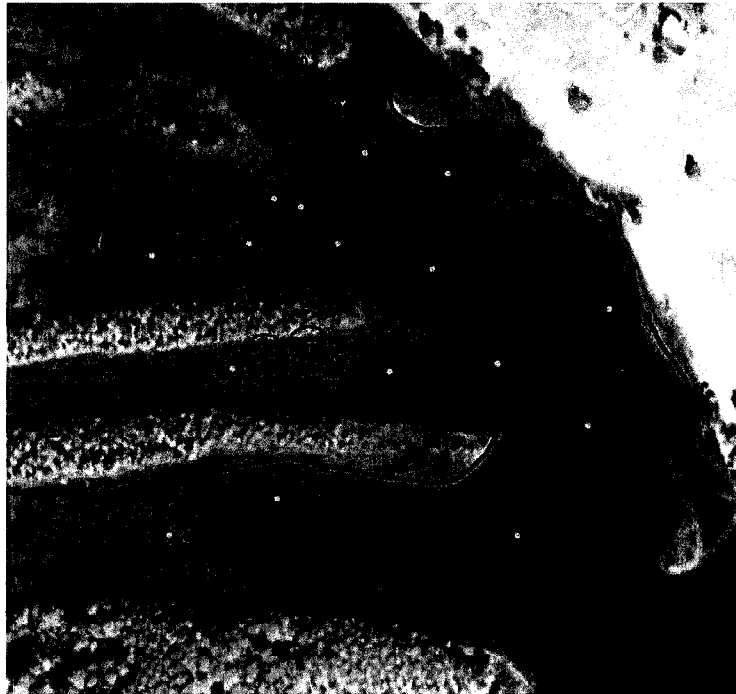
Figure 4.14: Emigration from the cove in Timberneck creek appeared low in the July 2005 release. The number labels are the number of tagged crabs captured in a given scrape tow, and the ones of interest here are the red circles – the ones that left the release area. Recapture numbers are low in this release because only ca. 4,000 crabs were released.
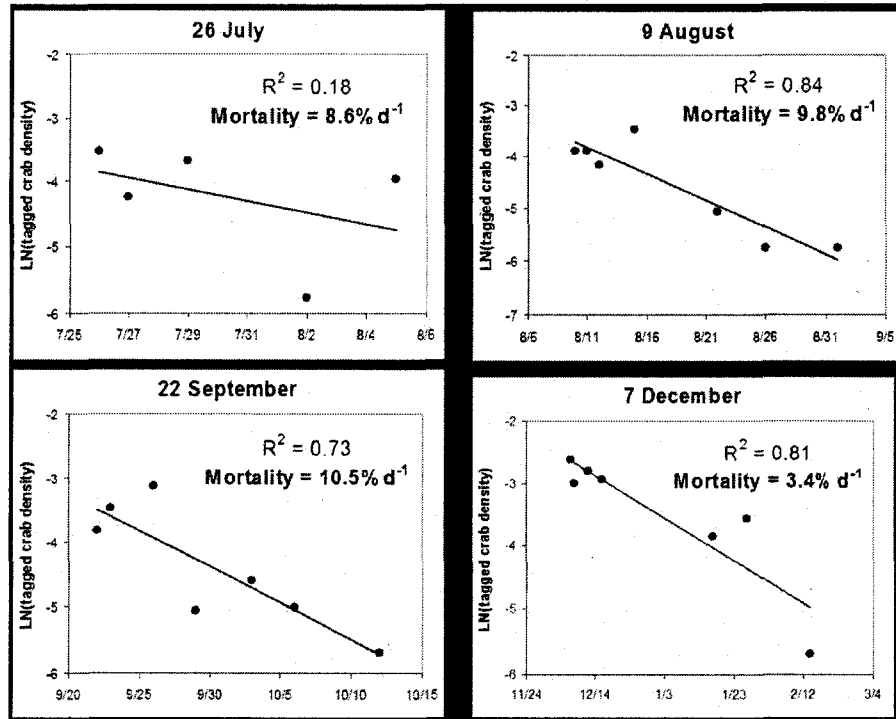
Figure 4.15: Decay rates of juvenile hatchery-reared crabs in Timberneck cove after experimental releases in 2005. Note the change in scales, especially along the x-axis. The time period over which sampling occurred depended on how long we were able to continue detecting tagged crabs, so the appearance of the slopes alone is misleading.

the decay in the densities of tagged crabs can be used as an estimate of mortality. Overall, decay rates were extremely high, on the order of 3 to 10% per day.

Decay rates showed a seasonal pattern, being highest in the summer periods and dropping in December. The December release was unusual in that there was a warm spell in late January, and it appears that lower mortality occurred prior to that rise in temperature. The first six data points appear to describe a different pattern than that suggested after including the mid-February sampling (Figure 4.15). In sampling during the warm spell, crabs were active and aggregated in the deepest channel of the creek. Crabs may have been aggregated in higher densities during the cold period and thus more susceptible to cannibalism once water temperatures and activity of conspecifics increased.
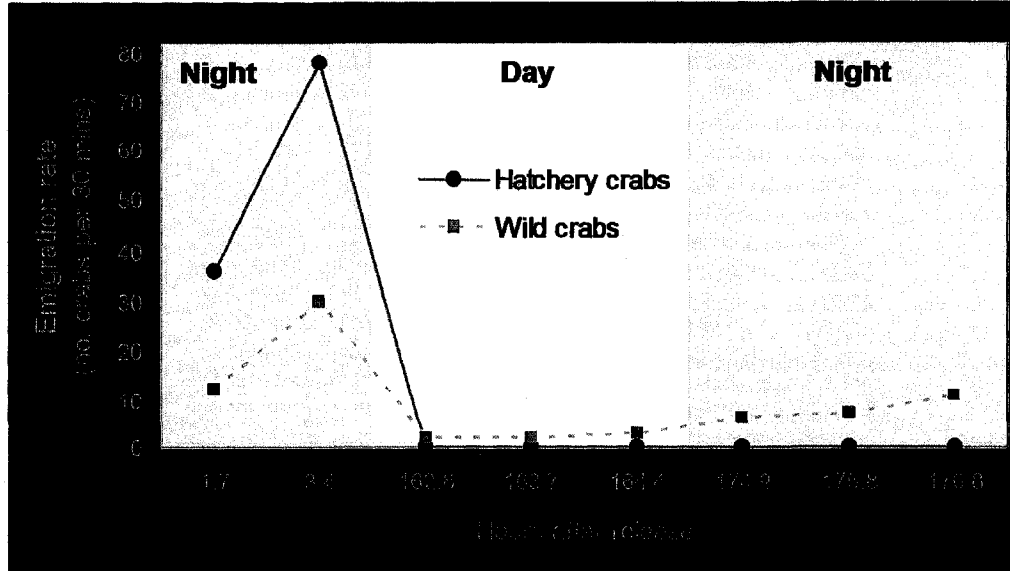
Figure 4.16: Emigration rates of wild and hatchery-reared crabs from Aberdeen cove following the release in June 2006.

We tracked the fate of three cohorts of juvenile crabs released into Aberdeen cove in the summer and fall of 2006. In the two summer experiments (June and July), almost all emigration by hatchery-reared crabs occurred on the first ebb tide following release (Figures 4.16 and 4.17), indicating an initial flight response. The second release was conducted during the day in an attempt to minimize emigration, but a flight response still occurred. Wild crab emigration rates were lower overall and always low during the day, but did appear to increase in association with the releases on the first night after release. The total number of hatchery crabs emigrating from the cove was small relative to the number released.

The first experiment (June) was hampered by frequent storms after the release. As a result, the second sampling was not possible until five days after the release, and substantial loss of tagged crabs had already occurred by that point (Figure 4.18). Only two of the sampling events following this release recovered more than two tagged crabs, indicating that the cohort had been reduced below detectable levels in less than a week. We cannot put much stake in the mortality estimates from this release, but mortality was high.
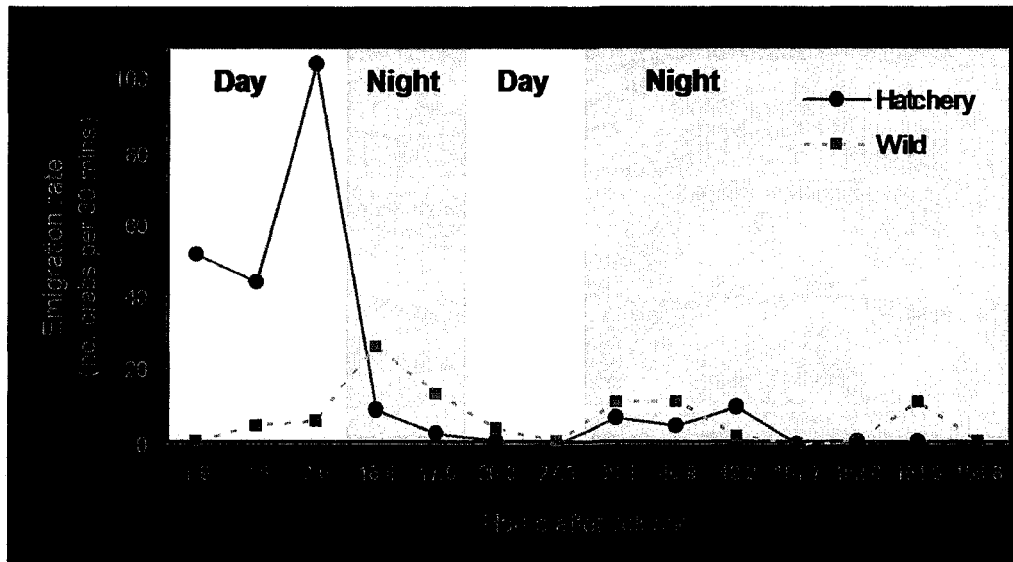
Figure 4.17: Emigration rates of wild and hatchery-reared crabs from Aberdeen cove following the release in July 2006.
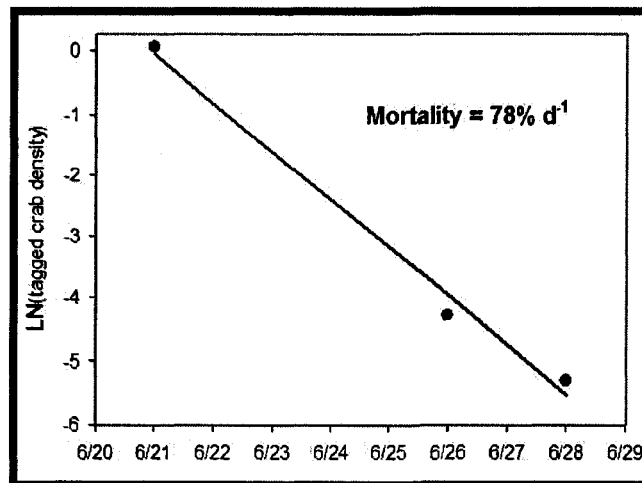
Figure 4.18: Decay rate of a cohort of juvenile hatchery-reared crabs in Aberdeen cove after an experimental release on 21 June 2006.
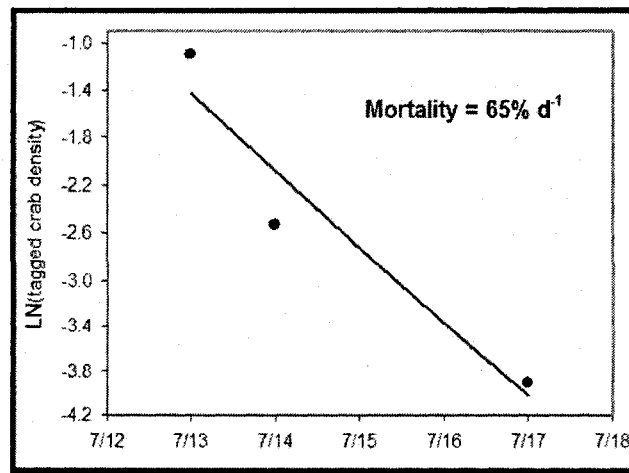
Figure 4.19: Decay rate of a cohort of juvenile hatchery-reared crabs in Aberdeen cove after an experimental release on 13 July 2006.

Sampling was more consistent for the second experiment (July), but the decay of the cohort of tagged crabs was again rapid. Only two sampling events following the release recovered more than two tagged crabs, indicating that mortality was high and the cohort was reduced below detectable levels in only four days (Figure 4.19).

Released crabs did not appear to exhibit a flight response following the fall release (September) and emigrated from the cove in approximately equal numbers to the wild crabs (Figure 4.20). A large pulse of both hatchery and wild crabs emigrated from the cove following a passing storm event on the second night after release. We began sampling as soon as was safe following the storm and recovered nearly as many crabs emigrating from the cove as we recovered in the first sampling following summer releases.

The decay in the numbers of recaptured tagged crabs showed high mortality after the September release (Figure 4.21). Although mortality was lower than in the summer releases, the cohort was reduced below detectable levels within two weeks.
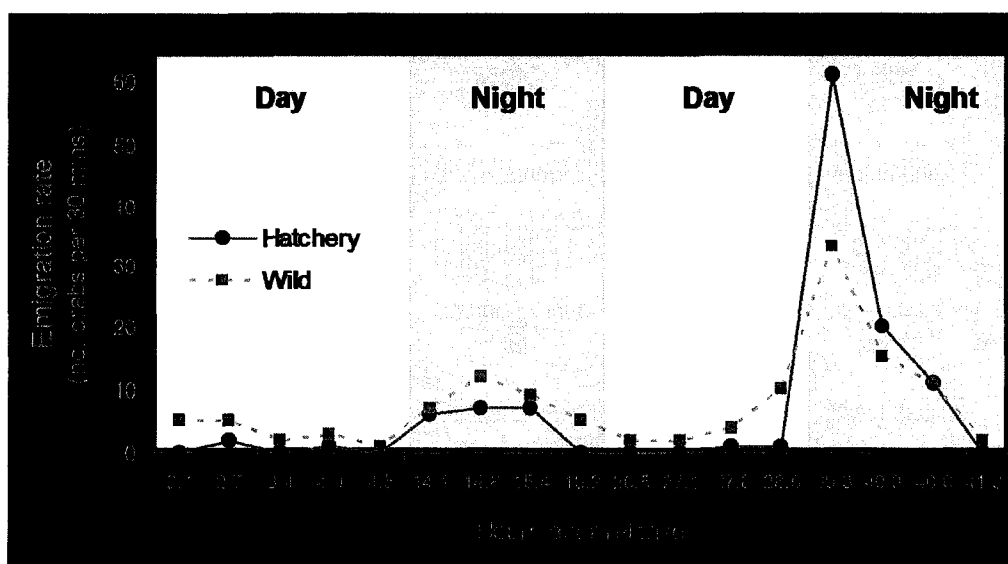
Figure 4.20: Emigration rates of wild and hatchery-reared crabs from Aberdeen cove following the release in September 2006.
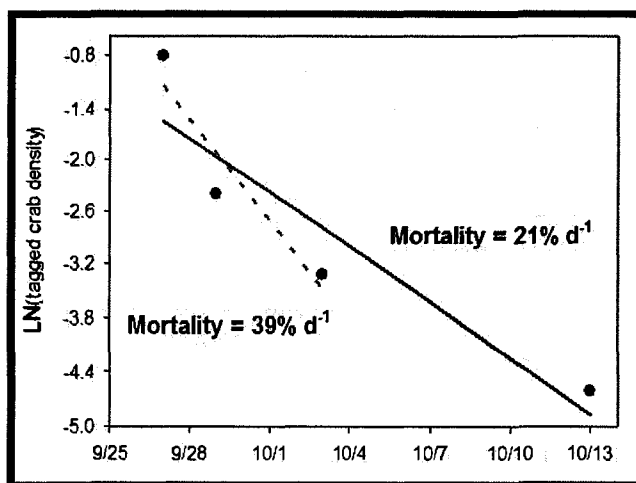
Figure 4.21: Decay rate of a cohort of juvenile hatchery-reared crabs in Aberdeen cove after an experimental release on 27 September 2006.

Discussion

Tag retention, tagging-related mortality, and growth in the laboratory

In the laboratory trials, tag retention was high (> 90%), tag loss occurred only at the first molt, and growth was unaffected by tagging. Our results are essentially identical to previous work using microwire tags with juvenile blue crabs (van Montfrans *et al.* 1986; Fitz & Wiegert 1991a). van Montfrans *et al.* (1986) tagged 27 juvenile crabs between 21 and 39 mm CW and held them in the laboratory individually to assess tag retention, growth, and mortality. Despite their small sample size, tag retention was high. Of the 25 crabs that molted at least once during the 51 day trial, 22 (88%) retained the tag through the first molt. The three crabs that lost their tag had been injected improperly, and the tag had penetrated the endoskeleton and been shed along with the old carapace. All crabs that retained the tag through the first molt and then molted a second time (8) retained the tag through the second molt. In comparison to 30 untagged control crabs, van Montfrans *et al.* (1986) concluded that mortality related to tagging was very low and that growth was mostly unaffected by tagging. More control crabs molted a second time than tagged crabs, but the experiment was terminated before all crabs might have been expected to molt a second time.

In a longer and more substantial trial, Fitz & Wiegert (1991a) tagged 56 juvenile blue crabs that ranged in size from 29 to 67 mm CW as measured between the bases of the lateral spines. Because the sizes do not include spine length, the crabs used in their study were substantially larger than those used by van Montfrans *et al.* (1986) and those used in this study. The crabs were evaluated in the lab for 80 days and 83% of the crabs molted at least twice. They found no effects of tagging on growth in comparison with 56 control untagged crabs. In addition, only one of the 55 crabs (2%) lost its tag during the first molt, and no crabs that molted additional times lost the tag through subsequent molts. In our trials, percent increases in size through molts were similar between hatchery and wild crabs, and

intermolt periods for second and later molts were not different between hatchery and wild crabs. However, growth and survival were lower for the two early cohorts in 2005 (June and July) in comparison to the August cohort when hatchery conditions were improved.

In other laboratory studies, pre-molt size has been an important predictor of the per-molt size increase juvenile blue crabs (Cadman & Weinstein 1988; Guerin & Stickle 1997). However, studies have shown conflicting directions of the effect depending on which measure of size is used. Cadman & Weinstein (1988) found that per-molt increase in volumetric body size increased with pre-molt size, whereas Guerin & Stickle (1997) found that per-molt increase in wet weight and carapace width declined with increasing pre-molt size. Size increases for crabs in our study did not show either of these patterns relative to initial size, except in one case for wild crabs.

Growth rates of hatchery and wild crabs in our study compared well with findings from other studies. Intermolt period and growth rate were not affected by salinity in our study because of the narrow range observed in our tanks (Tagatz 1968b; Cadman & Weinstein 1988; Guerin & Stickle 1997). Tagatz 1968b, Leffler (1972), and Cadman & Weinstein (1988) found that intermolt period decreased and growth rate increased at higher temperatures (23-30°C). Temperature ranges during our trials were similar, which may explain a lack of differences in growth among trials. Crabs in our study tended to have intermolt periods much less than those reported by Cadman & Weinstein (1988) for crabs at 30°C, but were in line with the low ends of ranges reported by Newcombe *et al.* (1949), Van Engel (1958), Tagatz (1968b), and Fitz & Wiegert (1991a).

Survival of hatchery-reared crabs in the first two laboratory trials was considerably lower than for the August trial and lower than survival of wild crabs. Whereas mortality through the first week was negligible for wild crabs and hatchery crabs in the August trial, in both earlier trials 50% or more of the hatchery crabs died within the first week. Because procedures for collection, transport, and tagging of the crabs were essentially identical for all three cohorts, and because of the high survival of wild crabs in the holding tanks, we assume

that survival of the first two cohorts was reduced by some aspect of hatchery operations during the rearing period. Survival of juvenile crabs in the laboratory under salinities like those in our tanks has been shown to be high in other studies (Tagatz 1968b; Fitz & Wiegert 1991a). Water quality conditions at the hatchery for the first cohort were atypically poor and appear to be the cause in that trial. Conditions were much better for the second cohort, but dissolved oxygen was somewhat lower than for the third cohort (minimum = 6.8 mg/L [95% saturation] vs. minimum = 5.2 mg/L [70% saturation]). It seems unlikely that the difference in dissolved oxygen was the culprit in the July cohort, but the collection process may have driven dissolved oxygen to critical levels. Collection of the crabs with dip nets stirs up feces and uneaten food on the bottom of the ponds, which may cause water quality to deteriorate rapidly.

Lacking any other explanation for the difference between the July and August cohorts, it appears that survival of collected crabs is dependent on excellent water quality in ponds prior to collection. Although no controlled trials were run in 2005, we did not observe unusual mortality in crabs that were retained for other laboratory experiments or during the holding process for cohorts in 2005. In all respects, cohorts obtained in 2005 appeared to be similar to cohorts in previous years (2003 and 2004), with high survival and good condition after initial culling for dead and moribund crabs. Grow-out operations for the juvenile crabs were moved from COMB to the Piney Point facility in 2004, so all cohorts we used were reared in similar ways. Pond maintenance and condition during grow-out must be monitored and kept in excellent condition.

Collectively, our study and the studies of van Montfrans *et al.* (1986) and Fitz & Wiegert (1991a) indicate that healthy crabs of initial size between 10 and ca. 70 mm CW can be successfully marked with microwire tags without negative effects on growth, molting, and survival. Our study extends previous findings by demonstrating effectiveness in very small juveniles (< 20 mm CW). Davis *et al.* (2004a) also evaluated microwire tags in small juvenile blue crabs (< 25 mm CW) and found similarly high retention rates over periods of up to 48

days, and little effect on growth and survival from tagging. However, assessments were made by sampling groups of crabs rather than by monitoring individual fates, and small sample sizes and confounding factors (e.g., cannibalism in assessing survival) hampered inferences. Lastly, Okamoto (1999) conducted microwire tagging trials with another portunid, the blue swimming crab, *Portunus trituberculatus*. After 20 days in the laboratory there were no differences in growth or survival between tagged and untagged crabs as small as 10 mm CW. Tag retention was similarly high (usually > 80%), but appeared to be lower for the smallest crabs (ca. 8 mm CW). At sizes greater than 10 mm CW, tag retention rates were similar to those obtained in our and other studies with blue crabs. Sharp *et al.* (2000) found similar results for 96 second stage juvenile spiny lobsters, *Panulirus argus*, tagged with microwire. Tag retention was 96%, with almost all tag loss at the first molt, and no effects on growth or survival compared to control lobsters.

Emigration

The separate measurement of emigration and mortality will remain a difficult task in studies of the dynamics of juvenile crab cohorts. Based on recapture locations of tagged crabs in Timberneck cove in 2005, it appeared that the released crabs were staying mostly within the release area. This was consistent with the results of sampling following release experiments in the initial years of the stock enhancement feasibility investigation, and also sampling from similar studies in upper Chesapeake Bay coves (Davis *et al.* 2005a). In those experiments, the majority of recaptures occurred close to the point of release, even when releases were conducted in larger creeks. However, the substantial emigration from Aberdeen cove during the experiments in 2006 leads us to believe that emigration at this small of a scale may be an all-or-nothing event. Such intrapopulation structuring with regard to dispersal has been noted for other species under threat of predation, splitting the population into "movers" and stayers" (Fraser *et al.* 2001). Crabs that leave the area – the "movers" – may take advantage of ebbing tides and leave quickly and go undetected in subsequent sampling, whereas crabs

that remain – the "stayers" – appear to remain within a relatively small home range.

Our sampling in Timberneck probably underestimated the losses of crabs due to emigration because we did not sample outside of the cove. However, sampling for emigrating crabs at the mouth of Timberneck cove in a way that covers any significant portion of the water column was not possible. Furthermore, recapture rates from our sampling were rather low in an area where it was known that thousands of crabs were released, so recaptures in a wider local region would almost certainly be negligible. We released almost 16,000 crabs in December of 2005, but sampling events sometimes only accounted for a total of 20 tagged crabs. The low number of recaptures also reinforced prior experience that indicating that it would be impossible to collect enough wild crabs to perform these experiments.

An alternative approach to estimating emigration rates would be to use neuston nets at the mouths of coves that sample a known area or volume of the water column. Assuming that crabs are emigrating in a known pattern (e.g., near the surface, in the channel) would allow the correction of numbers to emigration rates for the whole cove. We consider this approach impractical based on supplemental net sampling that we conducted alongside trials in Aberdeen cove in 2006. We sampled with two sets of neuston nets placed at the mouth of the cove inside of the seine on most sampling events. The nets were constructed from 4-mm stretch mesh seine netting and measured 30 cm tall by 100 cm wide. Nets were fished at the surface and anchored to the sediment, and were located in the center of the ebbing flow to the extent possible. Given the small width of the mouth of the cove, we covered a sizeable proportion of the total cross-sectional area of the cove mouth, probably more than could be expected elsewhere without a much greater effort. The nets typically captured very few crabs and the catch rates in the nets were not closely correlated with catches in the seine. Thus, it did not appear that the nets were catching a similarly consistent proportion of the emigrating crabs.

Emigration sampling in Aberdeen cove during 2006 indicated a potential flight response in hatchery-reared juvenile crabs. Strong pulses of emigration occurred on the first ebb

tide following the release in both summer experiments. The notion that this emigration represents a flight response was indicated by the strong emigration during the daytime ebb tide in July; water column transport is typically strongest during the night when visual predators are less effective (Blackmon & Eggleston 2001; Etherington *et al.* 2003; Reyns & Eggleston 2004). Furthermore, emigration of wild crabs, though much smaller in magnitude, was consistently highest at night and essentially negligible during the day. In both summer experiments, wild crab emigration appeared appeared to increase from baseline levels following release. A possible mechanism for this behavior is an avoidance of increased competition for resources, given the similar size ranges of wild and hatchery crabs. However, the relative influence of density-dependence in influencing dispersal in juvenile blue crabs is not clear (Perkins-Visser *et al.* 1996; Pile *et al.* 1996; Moksnes *et al.* 1997; Blackmon & Eggleston 2001; Etherington *et al.* 2003; Reyns & Eggleston 2004). The contribution of emigration to the decay rates we observed was not great, which contrasts strongly with the approximately equal contributions of emigration and mortality to decay rates in very small seagrass patches (Etherington *et al.* 2003).

Hydrodynamic differences between the two coves may play a role in emigration rates of released crabs. Timberneck cove is an open system that rises and falls gradually with the tides, whereas Aberdeen cove has a small inlet and stronger water velocities during tidal exchange. Crustaceans are sensitive to changes in the currents passing over their tactile hairs, such that the stronger pull of water leaving the cove may trigger more small crabs to rise into the water column and emigrate from coves like Aberdeen (Forward *et al.* 2004a, 2005). Etherington & Eggleston (2000, 2003) showed that wind-induced secondary dispersal was common among small juveniles in the North Carolina estuaries, and could occur on very short time scales. Pile *et al.* (1996) also hinted at a role for strong wind events in connection with dispersal of early life stages, and noted a major movement of juveniles from one shore to the other near the mouth of the York River just after a storm event. These observations are in accordance with laboratory and field observations in seagrass by Blackmon & Eggleston

(2001) indicating an important role of active planktonic dispersal in juvenile blue crabs less than 10 mm CW. Rates of dispersal were highest with increased current speeds, providing a link between strong wind events or tides and secondary dispersal. However, Reyns & Eggleston (2004) found that secondary dispersal could be important at night in the absence of strong wind events, but was triggered by strong winds during the day. All previous research on secondary dispersal in blue crabs has focused on individuals smaller than those used in our study. The relatively low background emigration rates of wild crabs that we measured indicate that secondary dispersal is probably relatively unimportant for the sizes of crabs we used.

Temporary emigration from the sampling area could occur if small crabs use the fringing marsh as habitat during high tides. Juvenile and adult blue crabs and other macrofauna commonly use fringing *Spartina alterniflora* stands as cover and foraging habitat in marshes along the Gulf of Mexico (Zimmerman & Minello 1984; Thomas *et al.* 1990; Rozas & Reed 1993; Rozas & Zimmerman 2000; Minello & Rozas 2002; Rozas *et al.* 2007). However, Mense & Wenner (1989) found little evidence for use of the emergent vegetated habitat surrounding marsh creeks in South Carolina by crabs as small as those in our study. Other studies in North Carolina (Rozas & Hackney 1984), Georgia (Fitz & Wiegert 1991b), and Virginia (Varnell & Havens 1995) have documented consistent use of the intertidal marsh area by blue crabs in systems smaller than ours (< ca. 1 ha), but did not directly assess use of the surrounding area covered with emergent vegetation. Fitz & Wiegert (1991b) concluded that crabs may not have been using that portion of the intertidal zone based on comparisons of catches between tidal amplitudes. Yozzo & Smith (1998) reported pit trap catches from within the actual vegetation of two salt marshes on the Eastern Shore of VA near Nassawaddox. Although pit trap catches are dubious as estimates of abundance, in almost 200 pit trap collections in each of two years the two sites yielded only 26 and 57 crabs combined (crab sizes were not reported). Use of the marsh surface appeared to be far less for blue crabs than for daggerblade grass shrimp and mummichogs.

Differences between marshes in the Gulf of Mexico and the mid-Atlantic coast may be due to differences in physiography that limit accessibility (Rozas & Reed 1993). In our coves, the tides rarely inundated the upper marsh and never to any measurable depth, thus limiting accessibility and protection from predators. Based on the general lack of tidal inundation (Thomas *et al.* 1990), the balance of evidence from other studies in similar Atlantic coast systems (partly reviewed in Orth & van Montfrans 1990), and our own experience searching the marsh surface during this study, we consider it unlikely that a large number of crabs were in the marsh itself and unavailable for capture.

Mortality in experimental cohorts of hatchery-reared juveniles

Decay rates of released cohorts in Timberneck Creek were very high, ranging from 3 to 10% per day, and decay rates in Aberdeen Creek were even higher (20 − 75% per day). The field experiments were short (ca. 2 weeks) because of the high decay rates, but showed a seasonal pattern in line with expectations based on predation pressure. Unmeasured emigration from Timberneck cove may bias our estimates of mortality high in 2005. Due to the high laboratory mortality of hatchery-reared crabs in the summer 2006 experiments, those mortality rates are also questionable; as much as 50% of the mortality could have been caused by chronic effects of poor rearing conditions.

To the extent that the decay rates we measured can be considered mortality rates for juvenile crabs, the mortality rates we measured are orders of magnitude higher than current low estimates of adult natural mortality (Chapter 3). The magnitude of mortality rates we measured is striking, but our results differ strongly from results of comparable studies with hatchery-reared blue crabs in similar habitats in upper Chesapeake Bay (Davis *et al.* 2005a; Johnson *et al.* 2008). Released crabs in those habitats can persist in release areas for over a year and recapture rates are far higher than they were in our study. High mortality rates more similar to those measured in our study have been reported from other areas outside of the Chesapeake Bay. Rakocinski *et al.* (2003) determined that mortality and emigration

combined accounted for decay rates of about 15% per day in cohorts of recruiting small (< 15 mm) juvenile blue crabs in soft sediment habitats in Mississippi Sound. Heck *et al.* (2001), and later Spitzer *et al.* (2003), reported that juvenile densities in nursery habitats in Mobile Bay were rarely correlated with postlarval supply and settlement, consistent with strong density-dependence, and that even large settlement events were reduced to "background" juvenile densities within days or weeks. They also reported findings from tethering trials – high, often > 80%, mortality in all habitats – leading them to conclude that predation was decoupling postlarval supply from juvenile abundances. With slightly smaller juveniles (< 10 mm CW) in seagrass, Etherington *et al.* (2003) found that proportional mortality was as high as 65% per six hour period. For mud crabs (*Scylla paramamosain*) 20-60 mm CW, Le Vay *et al.* (2007) found mortality rates on the order of 60% per month.

Lipcius *et al.* 2005, 2007 proposed a revised conceptual model for ontogenetic changes in habitat use by juvenile blue crabs. Their model posits that unstructured habitats such as marsh-fringed creeks and coves serve as secondary nurseries for larger juveniles that have departed the primary nurseries (e.g., seagrass beds) after growing to approximately 25 mm CW. Our results indicate that the value of unstructured habitats may be limited, particularly as primary nurseries, without some form of structure that can provide protection from predators. Habitat enhancement at relatively large spatial scales may increase the value of these unstructured habitats. Although the mortality in these habitats may depend on the availability of alternative prey (Seitz *et al.* 2005), cannibalism is likely a major culprit of the high mortality. In addition, although we did not use the seine collections to estimate predator abundances in Aberdeen cove, predation pressure appears to be high based on the large number of fishes we collected. Moreover, trawl sampling in the middle and upper reaches of the York River indicates that predatory fish abundance is high, which could increase predation substantially on young juveniles in unstructured habitats.

Uncertainty remains a strong feature of field estimates of natural mortality for small juvenile blue crabs. The repeated sampling approach that we used allowed more definitive

measurement of decay rates than in previous studies, but emigration and hatchery-related artifacts confounded inferences about absolute rates of mortality for wild crabs.

Alternative methods for estimating mortality

Despite the short time period involved, our experiments required an enormous amount of field and lab effort. Transport, care, and tagging of the hatchery-reared crabs required the full time efforts of at least six people for three or more days prior to the field releases. During and after release, sampling events required four or five people for about eight hours at a time as often as twice in a 24-hr period. Such experiments are probably not feasible for routine monitoring of the success of releases for stock enhancement efforts. Ideally, experiments to assess stock enhancement efforts need to be carried out in a number of different areas and at different seasons of the year. Both coves that we used for experiments were relatively small (< 10 ha) and thus not representative of the majority of marsh-fringed creeks and coves in the lower Chesapeake Bay. We were forced to restrict our experiments to small areas in order to recover tagged crabs after release. If we had used larger areas, as has been done in the past, the recapture rates would have been far too low to produce meaningful results. The compounded effort required for an approach like ours in multiple places at multiple times would be unrealistic.

Other methods of estimating mortality, such as capture-recapture, may provide more robust estimates of mortality but would suffer some of the same limitations as our approach. For example, studies would need to be restricted to relatively small areas in order to obtain recaptures. If transmitters can be developed for small crabs, telemetry may be the best approach (Niezgoda *et al.* 2002), but current technology limits transmitter application to large juveniles (ca. 60 mm CW or larger). Davis *et al.* (2004b) used ultrasonic telemetry to track seven wild and six hatchery-reared crabs in a creek in the upper Chesapeake Bay. The crabs were ca. 65 mm in CW and only one (a hatchery-reared crab) left the 5.5-ha cove in the first two weeks after release. However, the crab only strayed ca. 100 m from the

cove and remained in the immediate area.

Use of PIT tags in capture-recapture analyses has been tested for fish on small scales similar to our situation in Aberdeen cove (Adams *et al.* 2006). However, the entrance to Aberdeen cove is over twice the width and depth of the location tested by Adams *et al.* (2006), so we would need a considerably larger antenna array. In addition, Aberdeen cove has a unique combination of depth and mouth morphology compared to other tidal creeks in the area, so the applicability of such a system is probably limited by cost and technological limits in most places. An additional problem is that PIT tags and other tags are currently not available in sizes that would permit use with the smaller crabs used in our study. Even for the larger crabs, smaller PIT tags have lower power output and thus reduced detection range, such that a large antenna array would be needed to confidently detect animals moving past the array. Such a system would obviously not be feasible in an area with boat traffic. Regardless of the external tag used, it would be best to hold crabs in the lab until they molt before applying tags, so that inferences about molt-related losses of tags could be based on molt-process growth models.

For crabs in lower Chesapeake Bay habitats, whose mortality rates are extremely high as documented in this study, tagging and repeated subsequent sampling is probably not a realistic option to estimate mortality rates of the smallest crabs (< 30 mm CW). For adult female crabs that have molted to maturity, tag return studies are clearly a good option for estimating mortality rates, including natural mortality when supplemental information on abundance and fishery harvest is available (Chapter 3). For crabs that may continue to shed, internal tags such as microwire may be feasible for small-scale research studies, but large-scale studies that rely on tag returns would need to provide detection equipment to crab packing houses or distributors, and logistical constraints would be substantial. If a probabilistic model of molting (e.g., Smith & Chang 2007) can be incorporated into analyses of tag returns from male crabs or smaller female crabs that will continue to molt, it may be possible to estimate mortality rates for these groups with external tags such as those used by

Lambert *et al.* (2006b) based on tag return data. Telemetry-based approaches and PIT tags could be used for juvenile crabs greater than about 50 mm CW, but estimates from these studies would not apply at the scale of the stock. It may also be possible to design larger-scale, temporally intensive research sampling in ways that provide contrast to estimate mortality rates of recruited cohorts of crabs in subestuaries like the York River (Latour *et al.*, unpublished). Such estimates could ground-truth estimates used in assessment models and those derived from tag returns.

Perspectives on stock restoration efforts

Stock enhancement

Despite the long history of hatchery-based attempts to supplement wild populations in fisheries, a more rigorous, quantitative approach to stock enhancement efforts through the release of hatchery-reared juveniles is relatively new (Blankenship & Leber 1995; Heppell & Crowder 1998; Leber 1999; Lorenzen 2000; Leber 2002, 2004; Lorenzen 2005, 2006). Modern approaches to stock enhancement require quantitative evidence about the various factors that determine the biological value and cost-effectiveness of enhancement programs. Primary considerations focus on the potential impairment of genetic fitness of wild stocks, management of disease and health risks to wild stocks, cost-effectiveness of releasing hatchery-reared animals over natural production, and monitoring survival of released animals (Blankenship & Leber 1995).

The primary goals of enhancement programs intended to supplement natural stocks that are the subject of capture fisheries are the addition of hatchery-reared animals to the commercial catches and supplementation of the spawning stock. Numerous past enhancement efforts, particularly for mobile fish and invertebrates (Caddy & Defeo 2003), have been inconclusive because the survival of released animals was not monitored. When survival is not monitored, programs are not able to quantify the extent to which released animals contribute to populations and fisheries. Based on past experience, it seems clear that the

top priority for research prior to the development of a major enhancement program must be an assessment of the feasibility of contributing animals to the spawning stock or the commercial catch in a cost-effective manner (Lorenzen 2005, 2008). In many cases the required survival rate is beyond biological and technological reality and calls into question the development of a program at all (Heppell & Crowder 1998; Hilborn 1998; Wilson *et al.* 1998; Leber 1999). In such cases, enhancement efforts can become a red herring that stalls progress on more traditional management measures.

Stock enhancement efforts for blue crab in Chesapeake Bay have not yet attempted releases at a scale that would permit tracking the fate of released animals into the exploitable stock. Despite the progress in culture technology (Zmora *et al.* 2005; Zohar *et al.* 2008) and assessments of potential release strategies (Hines *et al.* 2008; Johnson *et al.* 2008), there are not yet robust estimates of survival to the adult stage for hatchery-reared crabs released into Chesapeake Bay. Davis *et al.* (2005a), and later Johnson *et al.* (2008), calculated survival rates for released hatchery-reared crabs in tidal marsh creeks in upper Chesapeake Bay. Their estimates of local survival made a number of strong assumptions about emigration, tag loss, and catch efficiency, but far more crabs survived than in our experiments. In addition, releases of hatchery-reared cohorts the size of those used in our study resulted in greater contribution to the wild population than we can achieve because of lower recruitment to upper Bay habitats. Growth rates of crabs released prior to wild recruitment in upper Bay habitats are exceptionally fast, with crabs growing from ca. 20 mm CW to over 100 mm CW in just 3.5 months. Thus, local enhancement of nursery habitats is feasible, but it remains to be tested whether hatchery-reared crabs can contribute to the spawning stock or fisheries.

Mortality rates like those we observed in nursery habitats in the lower Chesapeake Bay appear to be too high to make simple releases of small hatchery-reared juveniles feasible as a stock restoration tool. Furthermore, natural recruitment would likely swamp any effects of releases of hatchery-reared individuals unless the releases were much larger than currently possible given hatchery and grow-out technology. Whether enhancement efforts are reason-

able at all will depend on whether the stock is limited by poor recruitment and hatchery releases can be expected to replace natural production at a scale that ultimately supplements the spawning stock and fishery. In part, this assessment depends on the differences in mortality between wild and hatchery-reared juveniles (Davis *et al.* 2005a). However, in the context of stock-recruitment relationships, there should be convincing evidence that the stock is limited by recruitment and that recruitment is strongly related to spawning stock abundance. Lacking a strong relationship, particularly when small spawning stock sizes can result in large recruitment events, increases in juvenile abundance through releases can be swamped and ineffective.

Lipcius & Van Engel (1990) found somewhat weak relationships between adult and recruit abundance using collections of crabs at two points in the York River, and later Lipcius & Stockhausen (2002) found relationships between spawning stock and larval and postlarval abundance based on sampling at larger scales. Although the relationships are characteristically noisy, they indicate that recruitment is limited at much reduced stock sizes, as is typical for most marine fish and invertebrate stocks. The questions remains as to whether releases in targeted habitats can be scaled up to a level that contributes to the spawning stock and is not overwhelmed by natural recruitment.

Researchers are now able, and even obligated, to assess the size and timing of releases (Leber 1995), the trade-offs between larger size at release and expense of husbandry, and the value of habitats into which the animals are released. Unfortunately, constraints on hatchery and rearing operations for blue crab do not permit testing of a wide size range of released crabs (Zmora *et al.* 2005; Zohar *et al.* 2008). Smaller size-at-release for blue crabs would eliminate much rearing mortality due to cannibalism and the need to maintain such large numbers of crabs in a flow-through outdoor system potentially subject to episodic poor water quality. However, it is not clear whether the reduction in potential mortality in the hatchery would be offset by the increased mortality on release.

Stock assessment, modeling of natural mortality, and management

Our results reinforce concerns about the realism of estimates of natural mortality rates used in current assessment and population models. Reduced mortality in the December experiment in 2005 and the September experiment in 2006 is consistent with the expectation of reduced mortality in the fall and winter based on predation pressure. However, extrapolation of any of the mortality rates that we measured would lead to virtually 100% mortality on an annual basis.

If mortality rates for wild juveniles are on the order of those measured for hatchery-reared juveniles, stock assessment models that include seasonal dynamics of juvenile growth and mortality will be sensitive to small changes in these parameters. Given that such estimates are likely to remain uncertain and estimation in the field is so impractical for routine application, assessment models may need to include patterns rather than specific estimates. Patterns in mortality can be incorporated and harvest policies set that are robust to reasonable variation in the magnitude of mortality rates.

In developing reference points for the Chesapeake Bay blue crab fishery, Bunnell & Miller (2005) attempted to incorporate an elevated rate of natural mortality for juvenile crabs less than 70 mm CW. The particular equation for M as a function of size was not given, but the results from their individual-based model indicated that so few crabs would survive that essentially no commercial fishery could be supported. In an exploratory matrix model, Miller (2001) used a probability of survival through the entire zoea/newly settled crab period as 0.0000012 given a background instantaneous mortality rate of 0.375 (daily probability of survival = 0.00102) and linear decline from zoeal survival of 0.124 per day for 40 days to background over 142.5 days. Improved estimates of background mortality provided in Chapter 3 would decrease the number of survivors in the model substantially and may lead to different conclusions about the effects of the fishery on population dynamics.

Another important concern for population dynamics models is the time step used in modeling the population. Growth rates are extremely variable for blue crab, but some

crabs can reach exploitable size in one year of life. Such fast growth, coupled with a high population turnover rate for short-lived species like blue crab, may make it necessary to model population dynamics with a time step less than one year. An annual time step implicitly smooths out changes in M that occur during the first year of life, and applies the same M to crabs that are just entering the fishery in the current year and those that have survived from previous years. Although Miller (2003) used a six-month time step in an exploratory spatially-explicit matrix model, current assessment models include an annual time step (Miller *et al.* 2005). Assessment models with shorter time steps may be better able to describe changes in natural mortality rates and capture seasonal dynamics, but data would need to be collected at a finer temporal scale or annual data would need to be partitioned into shorter time periods.

Jamieson (1986) noted a difficulty inherent to management of nearly all invertebrate stocks, that recruitment is highly variable and under little control by fishery regulations.

> "Objectives of management, and any assessment of management performance, should reflect the suggested general inability of man to influence recruitment magnitude for most invertebrates within historic ranges of population abundance."

Invertebrate stocks that meet these criteria represent a classic case of situations in which stock-recruitment relationships are potentially misleading as guides to management. For blue crab, the variability in average fecundity among years could be one source of recruitment variability (Prager *et al.* 1990), although the overall magnitude is probably influenced more by environmental and physical conditions in the open ocean during early development and reinvasion of the estuaries (Provenzano *et al.* 1983; Caddy 1986a; Van Engel 1987; Fogarty *et al.* 1991; Wahle 2003). Although far from a settled issue, current theory for blue crab stock dynamics maintains that recruitment to the fishery may be limited by the magnitude of recruitment in Atlantic coast estuaries, but is more dependent on post-settlement dynamics (density-dependence) in Gulf coast estuaries (van Montfrans *et al.* 1995; Heck

et al. 2001; Spitzer *et al.* 2003; Rakocinski & McCall 2005). Guillory *et al.* (1998) noted that management in the Gulf of Mexico should proceed under the assumption that a stock-recruitment relationship did not exist. It remains unclear whether the adult stock is more tightly coupled to recruitment in the Chesapeake Bay.

Given highly variable recruitment that is under little control by management, Jamieson (1986) suggested that perhaps invertebrate fisheries should focus on extracting appropriate levels of harvest from the recruitment that is available at any one time, rather than aiming for long-term sustainability. Observations that Dungeness crab populations, which share many life history features with blue crab, swing widely in abundance as a result of the complex interactions of density-dependent and density-independent processes leads to caution in attempts to identify large-scale patterns in stock-recruitment relationships (Higgins *et al.* 1997a,b). Van Engel (1987) cautioned against the use of stock-recruitment relationships in management of blue crab stocks, and past periodicity in the blue crab population in Chesapeake Bay and strong environmental control on recruitment indicates that the approach suggested by Jamieson (1986) could be prudent and realistic for this stock. The widespread winter dredge survey provides a strong prediction of annual harvest based on over-winter abundance and may provide the basis for such a strategy (CBSAC 2007). Furthermore, if poor recruitment years can be identified in advance of the upcoming fishing season, as might be accomplished by an addition to or modification of the winter dredge survey sampling, management should cap catches in those years when recruitment is weak.

Literature Cited

ADAMS, A. J., WOLFE, R. K., PINE, III, W. E., & THORNTON, B. L. 2006. Efficacy of PIT tags and an autonomous antenna system to study the juvenile life stage of an estuarine-dependent fish. *Estuaries and Coasts*, **29**, 311–317.

ADAMS, P. B. 1980. Life history patterns in marine fishes and their consequences for fisheries management. *Fishery Bulletin*, **78**, 1–12.

ADDISON, J. T. 1997. Lobster stock assessment: report from a workshop; I. *Marine and Freshwater Research*, **48**, 941–944.

AGUILAR, R., HINES, A. H., WOLCOTT, T. G., WOLCOTT, D. L., KRAMER, M. A., & LIPCIUS, R. N. 2005. The timing and route of movement and migration of post-copulatory female blue crabs, *Callinectes sapidus* Rathbun, from the upper Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology*, **319**, 117–128.

ALAGARAJA, K. 1984. Simple methods for estimation of parameters for assessing exploited fish stocks. *Indian Journal of Fisheries*, **31**, 177–208.

ALVERSON, D. L., & CARNEY, M. J. 1975. A graphic review of the growth and decay of population cohorts. *Journal du Conseil International pour l'Exploration de la Mer*, **36**, 133–143.

ANNALA, J. H. 1977. *Effects of increases in the minimum legal size on the Otaga rock lobster fishery*. New Zealand Fisheries Research Division Occasional Publication 13.

ANTHONY, V. C. 1980. Review of lobster mortality estimates in the United States. *Canadian Technical Report of Fisheries and Aquatic Sciences*, **932**, 17–25.

ARCHAMBAULT, J. A., WENNER, E. L., & WHITAKER, J. D. 1990. Life history and abundance of blue crab, *Callinectes sapidus* Rathbun, at Charleston Harbor, South Carolina. *Bulletin of Marine Science*, **46**, 145–158.

ASHFORD, J. R., & JONES, C. M. 2003. *Survey of the blue crab recreational fishery in Maryland and Virginia, 2002.* Final report from Old Dominion University to the National Oceanic and Atmospheric Administration Chesapeake Bay Office, Annapolis, Maryland.

AUMANN, C. A., EBY, L. A., & FAGAN, W. F. 2006. How transient patches affect population dynamics: the case of hypoxia and blue crabs. *Ecological Monographs*, **76**, 415–438.

BACHELER, N. M., WONG, R. A., & BUCKEL, J. A. 2005. Movements and mortality rates of striped mullet in North Carolina. *North American Journal of Fisheries Management*, **25**, 361–373.

BARTLEY, D. M., & BELL, J. D. 2008. Restocking, stock enhancement, and sea ranching: arenas of progress. *Reviews in Fisheries Science*, **16**, 357–365.

BAUER, L. J. 2006. *Winter mortality of the blue crab (Callinectes sapidus) in Chesapeake Bay.* Master's thesis, University of Maryland, College Park.

BBCAC, (BI-STATE BLUE CRAB ADVISORY COMMITTEE). 2001. *Taking action for the blue crab: managing and protecting the stock and its fisheries.* Tech. rept. Chesapeake Bay Commission.

BECK, M. W., HECK, K. L., ABLE, K. W., & 10 OTHERS. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience*, **51**, 633–641.

BEEM, B. 2006. Planning to learn: blue crab policymaking in the Chesapeake Bay. *Coastal Management*, **34**, 167–182.

BEVERTON, R. J. H. 1963. Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. *Rapports et Proces-Verbaux des Reunions Conseil International pour l'Exploration de la Mer*, **154**, 44–67.

BEVERTON, R. J. H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. *Journal of Fish Biology*, **41 (Supplement B)**, 137–160.

BEVERTON, R. J. H., & HOLT, S. J. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. *Pages 142-177 of:* WESTENHOLME, G. E. W., & O'CONNOR, M. (eds), *The lifespan of animals, CIBA Foundation colloquia on ageing, vol. 5.* Little, Brown and Company, Boston, MA.

BLACKMON, D. C., & EGGLESTON, D. B. 2001. Factors influencing planktonic, post-settlement dispersal of early juvenile blue crabs (*Callinectes sapidus* Rathbun). *Journal of Experimental Marine Biology and Ecology*, **257**, 183–203.

BLANKENSHIP, H. L., & LEBER, K. M. 1995. A responsible approach to marine stock enhancement. *Pages 167-175 of:* SCHRAMM, JR., H. L., & PIPER, R. G. (eds), *Uses and effects of cultured fishes in aquatic ecosystems.* American Fisheries Society, Symposium 15, Bethesda, MD.

BOYLAN, J. M., & WENNER, E. L. 1993. Settlement of brachyuran megalopae in a South Carolina, USA, estuary. *Marine Ecology Progress Series*, **97**, 237–246.

BROWNIE, C., ANDERSON, D. R., BURNHAM, K. P., & ROBSON, D. S. 1985. *Statistical inference from band recovery data: a handbook*, Second edition. U.S. Fish and Wildlife Service Resource Publication 156.

BUNNELL, D. B., & MILLER, T. J. 2005. An individual-based modeling approach to spawning-potential per-recruit models: an application to blue crab (*Callinectes sapidus*) in Chesapeake Bay. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 2560–2572.

BURY, K. V. 1975. *Statistical models in applied science*. John Wiley and Sons, New York.

CADDY, J. F. 1986a. Modelling stock-recruitment processes in Crustacea: some practical and theoretical perspectives. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 2330–2344.

CADDY, J. F. 1986b. Stock assessment in data-limited situations – the experience in tropical fisheries and its possible relevance to evaluation of invertebrate resources. *Pages 379–392 of:* JAMIESON, G. S., & BOURNE, N. (eds), *North Pacific workshop on stock assessment and management of invertebrates*. Canadian Special Publication of Fisheries and Aquatic Sciences 92.

CADDY, J. F., & DEFEO, O. 2003. *Enhancing or restoring the productivity of natural populations of shellfish and other marine invertebrate resources*. FAO Fisheries Technical Paper 448. FAO, Rome.

CADIMA, E. L. 2003. *Fish stock assessment manual*. FAO Fisheries Technical Paper 393. FAO, Rome.

CADMAN, L. R., & WEINSTEIN, M. P. 1985. Size-weight relationships of postecdysial juvenile blue crabs (*Callinectes sapidus* Rathbun) from the lower Chesapeake Bay. *Journal of Crustacean Biology*, **5**, 306–310.

CADMAN, L. R., & WEINSTEIN, M. P. 1988. Effects of temperature and salinity on the growth of laboratory-reared juvenile blue crabs *Callinectes sapidus* Rathbun. *Journal of Experimental Marine Biology and Ecology*, **121**, 193–207.

CBSAC, (CHESAPEAKE BAY STOCK ASSESSMENT COMMITTEE). 2007. *2007 Chesapeake Bay Blue Crab Advisory Report.* National Oceanic and Atmospheric Administration, Chesapeake Bay Office.

CHARNOV, E. L. 1993. *Life history invariants: some explorations of symmetry in evolutionary ecology.* Oxford University Press, New York.

CHARNOV, E. L., & BERRIGAN, D. 1990. Dimensionless numbers and life history evolution: age of maturity versus the adult lifespan. *Evolutionary Ecology,* **4**, 273–275.

CHEN, S., & WATANABE, S. 1989. Age dependence of natural mortality coefficient in fish population dynamics. *Nippon Suisan Gakkaishi,* **55**, 205–208.

CLARK, W. G. 1999. Effects of an erroneous natural mortality rate on a simple age-structured stock assessment. *Canadian Journal of Fisheries and Aquatic Sciences,* **56**, 1721–1731.

COLE, R. W. 1998. Changes in harvest patterns and assessment of possible long-term impacts on yield in the Delaware commercial blue crab fishery. *Journal of Shellfish Research,* **17**, 469–474.

COSTLOW, JR., J. D. 1965. Variability in larval stages of the blue crab, *Callinectes sapidus. Biological Bulletin,* **128**, 58–66.

COSTLOW, JR., J. D. 1967. The effect of salinity and temperature on survival and metamorphosis of megalops of the blue crab *Callinectes sapidus. Helgolander wissenschaftliche Meeresuntersuchungen,* **15**, 84–97.

COSTLOW, JR., J. D., & BOOKHOUT, C. G. 1959. The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. *Biological Bulletin,* **116**, 373–396.

CRONIN, L. E. 1998. Early days of crabbing and a brief history for the Chesapeake Bay. *Journal of Shellfish Research,* **17**, 379–381.

DAVIS, J. L. D., YOUNG-WILLIAMS, A. C., HINES, A. H., & ZMORA, O. 2004a. Comparing two types of internal tags in juvenile blue crabs. *Fisheries Research*, **67**, 265–274.

DAVIS, J. L. D., YOUNG-WILLIAMS, A. C., AGUILAR, R., CARSWELL, B. L., GOODISON, M. R., HINES, A. H., KRAMER, M. A., ZOHAR, Y., & ZMORA, O. 2004b. Differences between hatchery-raised and wild blue crabs: implications for stock enhancement potential. *Transactions of the American Fisheries Society*, **133**, 1–14.

DAVIS, J. L. D., YOUNG-WILLIAMS, A. C., HINES, A. H., & ZOHAR, Y. 2005a. Assessing the potential for stock enhancement in the case of the Chesapeake Bay blue crab (*Callinectes sapidus*). *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 109–122.

DAVIS, J. L. D., ECKERT-MILLS, M. G., YOUNG-WILLIAMS, A. C., HINES, A. H., & ZOHAR, Y. 2005b. Morphological conditioning of a hatchery-raised invertebrate, *Callinectes sapidus*, to improve field survivorship after release. *Aquaculture*, **243**, 147–158.

DITTEL, A. I., HINES, A. H., RUIZ, G. M., & RUFFIN, K. K. 1995. Effects of shallow water refuge on behavior and density-dependent mortality of juvenile blue crabs in Chesapeake Bay. *Bulletin of Marine Science*, **57**, 902–916.

EPIFANIO, C. E. 1995. Transport of blue crab (*Callinectes sapidus*) larvae in the waters off mid-Atlantic states. *Bulletin of Marine Science*, **57**, 713–725.

ETHERINGTON, L. L., & EGGLESTON, D. B. 2000. Large-scale blue crab recruitment: linking postlarval transport, post-settlement planktonic dispersal, and multiple nursery habitats. *Marine Ecology Progress Series*, **204**, 179–198.

ETHERINGTON, L. L., & EGGLESTON, D. B. 2003. Spatial dynamics of large-scale, multistage crab (*Callinectes sapidus*) dispersal: determinants and consequences for recruitment. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 873–887.

ETHERINGTON, L. L., EGGLESTON, D. B., & STOCKHAUSEN, W. T. 2003. Partitioning loss rates of early juvenile blue crabs from seagrass habitats into mortality and emigration. *Bulletin of Marine Science*, **72**, 371–391.

EVANS, C. 1998. Conservation and management of the blue crab fishery in Georgia. *Journal of Shellfish Research*, **17**, 451–458.

FEGLEY, L. W., DAVIS, B. K., DAVIS, G. R., WEBB, K., WALSTRUM, J. C., & BROWN, H. R. 2006. *Harvest and effort characterization of the Maryland Chesapeake Bay blue crab fishery through a cooperative data collection program*. Final report from the Maryland Department of Natural Resources to the National Oceanic and Atmospheric Administration Chesapeake Bay Office, Annapolis, Maryland.

FISCHER, A. J., BAKER, JR., M. S., WILSON, C. A., & NIELAND, D. L. 2005. Age, growth, mortality, and radiometric age validation of gray snapper (*Lutjanus griseus*) from Louisiana. *Fishery Bulletin*, **103**, 307–319.

FISCHLER, K. J. 1965. The use of catch-effort, catch-sampling, and tagging data to estimate a population of blue crabs. *Transactions of the American Fisheries Society*, **94**, 287–310.

FITZ, H. C., & WIEGERT, R. G. 1991a. Tagging juvenile blue crabs, *Callinectes sapidus*, with microwire tags: retention, survival, and growth through multiple molts. *Journal of Crustacean Biology*, **11**, 229–235.

FITZ, H. C., & WIEGERT, R. G. 1991b. Utilization of the intertidal zone of a salt marsh by the blue crab *Callinectes sapidus*: density, return frequency, and feeding habits. *Marine Ecology Progress Series*, **76**, 249–260.

FOGARTY, M. J., & LIPCIUS, R. N. 2007. Population dynamics and fisheries. *Pages 711–755 of:* KENNEDY, V. S., & CRONIN, L. E. (eds), *The blue crab* Callinectes sapidus. University of Maryland Sea Grant College, College Park.

FOGARTY, M. J., & MURAWSKI, S. A. 1986. Population dynamics and assessment of exploited invertebrate stocks. *Pages 228-244 of:* JAMIESON, G. S., & BOURNE, N. (eds), *North Pacific workshop on stock assessment and management of invertebrates.* Canadian Special Publication of Fisheries and Aquatic Sciences 92.

FOGARTY, M. J., SISSENWINE, M. P., & COHEN, E. B. 1991. Recruitment variability and the dynamics of exploited marine populations. *Trends in Ecology and Evolution,* **6,** 241–246.

FORWARD, JR., R. B., TANKERSLEY, R. A., & WELCH, J. M. 2003. Selective tidal-stream transport of the blue crab *Callinectes sapidus*: an overview. *Bulletin of Marine Science,* **72,** 347–365.

FORWARD, JR., R. B., REYNS, N. B., DIAZ, H., COHEN, J. H., & EGGLESTON, D. B. 2004a. Endogenous swimming rhythms of juvenile blue crabs, *Callinectes sapidus,* as related to horizontal transport. *Journal of Experimental Marine Biology and Ecology,* **299,** 63–76.

FORWARD, JR., R. B., COHEN, J. H., IRVINE, R. D., LAX, J. L., MITCHELL, R., SCHICK, A. M., SMITH, M. M., THOMPSON, J. M., & VENEZIA, J. I. 2004b. Settlement of blue crab *Callinectes sapidus* megalopae in a North Carolina estuary. *Marine Ecology Progress Series,* **269,** 237–247.

FORWARD, JR., R. B., REYNS, N. B., DIAZ, H., COHEN, J. H., & EGGLESTON, D. B. 2005. Endogenous swimming rhythms underlying secondary dispersal of early juvenile blue crabs, *Callinectes sapidus. Journal of Experimental Marine Biology and Ecology,* **316,** 91–100.

FRASER, D. F., GILLIAM, J. F., DALEY, M. J., LE, A. N., & SKALSKI, G. T. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *American Naturalist,* **158,** 124–135.

FRENCH MCKAY, D. P., GIBSON, M., & COBB, J. S. 2003. Scaling restoration of American lobsters: combined demographic and discounting model for an exploited species. *Marine Ecology Progress Series*, **264**, 177–196.

FRUSHER, S. D., & HOENIG, J. M. 2001. Estimating natural and fishing mortality and tag reporting rate of southern rock lobster (*Jasus edwardsii*) from a multiyear tagging model. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 2490–2501.

FRUSHER, S. D., & HOENIG, J. M. 2003. Recent developments in estimating fishing and natural mortality and tag reporting rate of lobsters using multi-year tagging models. *Fisheries Research*, **65**, 379–390.

FU, C., & QUINN, II, T. J. 2000. Estimability of natural mortality and other population parameters in a length-based model: *Pandalus borealis* in Kachemak Bay, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 2420–2432.

GABCHE, C. E., & HOCKEY, H.-U. P. 1995. Growth and mortality of the giant African river prawn *Macrobrachium vollenhovenii* (Herklots: Crustacea, Palaemonidae) in the Lobe River, Cameroon: a preliminary evaluation. *Journal of Shellfish Research*, **14**, 185–190.

GARVINE, R. W., EPIFANIO, C. E., EPIFANIO, C. C., & WONG, K-C. 1997. Transport and recruitment of blue crab larvae: a model with advection and mortality. *Estuarine, Coastal and Shelf Science*, **45**, 99–111.

GOODRICH, D. M., VAN MONTFRANS, J., & ORTH, R. J. 1989. Blue crab megalopal influx to Chesapeake Bay: evidence for a wind-driven mechanism. *Estuarine, Coastal and Shelf Science*, **29**, 247–260.

GUERIN, J. L., & STICKLE, W. B. 1992. Effects of salinity gradients on the tolerance and bioenergetics of juvenile blue crabs (*Callinectes sapidus*) from waters of different environmental salinities. *Marine Biology*, **114**, 391–396.

GUERIN, J. L., & 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 moulting. *Journal of Experimental Marine Biology and Ecology*, **218**, 165–186.

GUILLORY, V., & ELLIOT, M. 2001. A review of blue crab predators. *Pages 69-83 of:* GUILLORY, V., PERRY, H., & VANDERKOOY, S. (eds), *Proceedings of the blue crab mortality symposium.* Gulf States Marine Fisheries Commission, Ocean Springs, MS.

GUILLORY, V., PERRY, H., STEELE, P., WAGNER, T., HAMMERSCHMIDT, P., HEATH, S., & MOSS, C. 1998. The Gulf of Mexico blue crab fishery: historical trends, status, management, and recommendations. *Journal of Shellfish Research*, **17**, 395–403.

GULLAND, J. A. 1987. Natural mortality and size. *Marine Ecology Progress Series*, **39**, 197–199.

GUNDERSON, D. R., & DYGERT, P. H. 1988. Reproductive effort as a predictor of natural mortality rate. *Journal du Conseil International pour l'Exploration de la Mer*, **44**, 200–209.

GUNDERSON, D. R., ZIMMERMAN, M., NICHOL, D. G., & PEARSON, K. 2003. Indirect estimates of natural mortality rate for arrowtooth flounder (*Atheresthes stomias*) and darkblotched rockfish (*Sebastes crameri*). *Fishery Bulletin*, **101**, 175–182.

HAEFNER, JR., P. A. 1971. An approach to shedding blue crabs *Callinectes sapidus* in a recirculated seawater system. *American Zoologist*, **11**, 211.

HAMPTON, J. 2000. Natural mortality rates in tropical tunas: size really does matter. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 1002–1010.

HASEK, B. E., & RABALAIS, N. N. 2001. Settlement patterns of brachyuran megalopae in a Louisiana estuary. *Estuaries*, **24**, 796–807.

HEARN, W. S., POLLOCK, K. H., & BROOKS, E. N. 1998. Pre- and post-season tagging models: estimation of reporting rate and fishing and natural mortality rates. *Canadian Journal of Fisheries and Aquatic Sciences,* **55**, 199–205.

HEATH, S. R. 1998. The Alabama blue crab fishery: historical trends, status, management, and future. *Journal of Shellfish Research,* **17**, 435–439.

HECK, JR., K. L., & THOMAN, T. A. 1984. The nursery role of seagrass meadows in the upper and lower reaches of the Chesapeake Bay. *Estuaries,* **7**, 70–92.

HECK, JR., K. L., & WILSON, K. A. 1987. Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. *Journal of Experimental Marine Biology and Ecology,* **107**, 87–100.

HECK, JR., K. L., COEN, L. D., & MORGAN, S. G. 2001. Pre- and post-settlement factors as determinants of juvenile blue crab *Callinectes sapidus* abundance: results from the north-central Gulf of Mexico. *Marine Ecology Progress Series,* **222**, 163–176.

HECK, JR., K. L., HAYS, G., & ORTH, R. J. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series,* **253**, 123–136.

HELSER, T. E., SHAROV, A., & KAHN, D. M. 2002. A stochastic decision-based approach to assessing the status of the Delaware Bay blue crab stock. *Pages 63–82 of:* BERKSON, J. M., KLINE, L. L., & ORTH, D. J. (eds), *Incorporating uncertainty into fishery models.* American Fisheries Society, Symposium 27, Bethesda, MD.

HENRY, L. T., & MCKENNA, S. 1998. Status and management of the blue crab fishery in North Carolina. *Journal of Shellfish Research,* **17**, 465–468.

HEPPELL, S. S., & CROWDER, L. B. 1998. Prognostic evaluation of enhancement programs using population models and life history analysis. *Bulletin of Marine Science,* **62**, 495–507.

HEUPEL, M. R., & SIMPFENDORFER, C. A. 2002. Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 624–632.

HIGGINS, K., HASTINGS, A., & BOTSFORD, L. W. 1997a. Density dependence and age structure: nonlinear dynamics and population behavior. *American Naturalist*, **149**, 247–269.

HIGGINS, K., HASTINGS, A., SARVELA, J. N., & BOTSFORD, L. W. 1997b. Stochastic dynamics and deterministic skeletons: population behavior of Dungeness crab. *Science*, **276**, 1431–1435.

HIGHTOWER, J. E., JACKSON, J. R., & POLLOCK, K. H. 2001. Use of telemetry methods to estimate natural and fishing mortality of striped bass in Lake Gaston, North Carolina. *Transactions of the American Fisheries Society*, **130**, 557–567.

HILBORN, R. 1998. The economic performance of marine stock enhancement projects. *Bulletin of Marine Science*, **62**, 661–674.

HILBORN, R. 2007a. Defining success in fisheries and conflicts in objectives. *Marine Policy*, **31**, 153–158.

HILBORN, R. 2007b. Managing fisheries is managing people: what has been learned? *Fish and Fisheries*, **8**, 285–296.

HILBORN, R., & WALTERS, C. J. 1992. *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. Chapman and Hall, New York.

HILBORN, R., ORENSANZ, J. M., & PARMA, A. M. 2005. Institutions, incentives and the future of fisheries. *Philosophical Transactions of the Royal Society B*, **360**, 47–57.

HINES, A. H. 1982. Allometric constraints and variables of reproductive effort in Brachyuran crabs. *Marine Biology*, **69**, 309–320.

HINES, A. H. 2007. Ecology of juvenile and adult blue crabs. *Pages 565-654 of:* KENNEDY, V. S., & CRONIN, L. E. (eds), *The blue crab* Callinectes sapidus. Maryland Sea Grant College, College Park.

HINES, A. H., & RUIZ, G. M. 1995. Temporal variation in juvenile blue crab mortality: nearshore shallows and cannibalism in Chesapeake Bay. *Bulletin of Marine Science*, **57**, 884-901.

HINES, A. H., LIPCIUS, R. N., & HADDON, A. M. 1987. Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs *Callinectes sapidus* in a subestuary of central Chesapeake Bay. *Marine Ecology Progress Series*, **36**, 55-64.

HINES, A. H., HADDON, A. M., & WIECHERT, L. A. 1990. Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Marine Ecology Progress Series*, **67**, 105-126.

HINES, A. H., JIVOFF, P. R., BUSHMANN, P. J., VAN MONTFRANS, J., REED, S. A., WOLCOTT, D. L., & WOLCOTT, T. G. 2003. Evidence for sperm limitation in the blue crab, *Callinectes sapidus*. *Bulletin of Marine Science*, **72**, 287-310.

HINES, A. H., JOHNSON, E. G., YOUNG, A. C., AGUILAR, R., KRAMER, M. A., GOODISON, M., ZMORA, O., & ZOHAR, Y. 2008. Release strategies for estuarine species with complex migratory life cycles: stock enhancement of Chesapeake blue crabs (*Callinectes sapidus*). *Reviews in Fisheries Science*, **16**, 175-185.

HOENIG, J. M. 1983. Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin*, **82**, 898-903.

HOLT, S. J. 1998. Fifty years on. *Reviews in Fish Biology and Fisheries*, **8**, 357-366.

HURT, P. R., LIBBY, L. M., PANDOLFI, L. J., LEVINE, L. H., & VAN ENGEL, W. A. 1979. Periodicities in blue crab population of Chesapeake Bay. *Climatic Change*, **2**, 75-78.

INCZE, L. S., WOLFF, N., & WAHLE, R. A. 2003. Can scientific observations of early life stages be scaled up to the level of a fished population? A case study using *Homarus americanus*. *Fisheries Research*, **65**, 33–46.

JAMIESON, G. S. 1986. A perspective on invertebrate fisheries management–the British Columbia experience. *Pages 57–74 of:* JAMIESON, G. S., & BOURNE, N. (eds), *North Pacific workshop on stock assessment and management of invertebrates*. Canadian Special Publication of Fisheries and Aquatic Sciences 92.

JENSEN, A. L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 820–822.

JENSEN, O. P., & MILLER, T. J. 2005. Geostatistical analysis of the abundance and winter distribution patterns of the blue crab *Callinectes sapidus* in Chesapeake Bay. *Transactions of the American Fisheries Society*, **134**, 1582–1598.

JENSEN, O. P., SEPPELT, R., MILLER, T. J., & BAUER, L. J. 2005. Winter distribution of blue crab *Callinectes sapidus* in Chesapeake Bay: application and cross-validation of a two-stage generalized additive model. *Marine Ecology Progress Series*, **299**, 239–255.

JIVOFF, P., HINES, A. H., & QUACKENBUSH, L. S. 2007. Reproduction biology and embryonic development. *Pages 255–298 of:* KENNEDY, V. S., & CRONIN, L. E. (eds), *The blue crab* Callinectes sapidus. Maryland Sea Grant College, College Park.

JOHNSON, D. F. 1985. The distribution of brachyuran crustacean megalopae in the waters of the York River, lower Chesapeake Bay and adjacent shelf: implications for recruitment. *Estuarine, Coastal and Shelf Science*, **20**, 693–705.

JOHNSON, D. F., & HESS, K. W. 1990. Numerical simulations of blue crab larval dispersal and recruitment. *Bulletin of Marine Science*, **46**, 195–213.

JOHNSON, D. R. 1995. Wind forced surface currents at the entrance to Chesapeake Bay: their effect on blue crab larval dispersion and post-larval recruitment. *Bulletin of Marine Science*, **57**, 726–738.

JOHNSON, D. R., & HESTER, B. S. 1989. Larval transport and its association with recruitment of blue crabs to Chesapeake Bay. *Estuarine, Coastal and Shelf Science*, **28**, 459–472.

JOHNSON, D. R., HESTER, B. S., & McCONAUGHA, J. R. 1984. Studies of a wind mechanism influencing the recruitment of blue crabs in the Middle Atlantic Bight. *Continental Shelf Research*, **3**, 425–437.

JOHNSON, E. G., HINES, A. H., KRAMER, M. A., & YOUNG, A. C. 2008. Importance of season and size of release to stocking success for the blue crab in Chesapeake Bay. *Reviews in Fisheries Science*, **16**, 243–253.

JOHNSON, JR., J. A., GREEN, D. P., & MARTIN, R. E. 1998. Industry perspectives: the hard blue crab fishery–Atlantic and Gulf. *Journal of Shellfish Research*, **17**, 371–374.

JONES, C. M., McCONAUGHA, J. R., GEER, P. J., & PRAGER, M. H. 1990. Estimates of spawning stock size of blue crab, *Callinectes sapidus*, in Chesapeake Bay, 1986-1987. *Bulletin of Marine Science*, **46**, 159–169.

JU, S.-J., SECOR, D. H., & HARVEY, H. R. 1999. Use of extractable lipofuscin for age determination of blue crab. *Marine Ecology Progress Series*, **185**, 171–179.

JU, S.-J., SECOR, D. H., & HARVEY, H. R. 2001. Growth rate variability and lipofuscin accumulation rates in the blue crab *Callinectes sapidus*. *Marine Ecology Progress Series*, **224**, 197–205.

JU, S.-J., SECOR, D. H., & HARVEY, H. R. 2003. Demographic assessment of the blue crab (*Callinectes sapidus*) in Chesapeake Bay using extractable lipofuscins as age markers. *Fishery Bulletin*, **101**, 312–320.

KAHN, D. M., & HELSER, T. E. 2005. Abundance, dynamics and mortality rates of the Delaware Bay stock of blue crabs, *Callinectes sapidus*. *Journal of Shellfish Research*, **24**, 269–284.

KAHN, D. M., COLE, R. W., MICHELS, S. F., & WHITMORE, W. H. 1998. Development of life-stage-specific indices of relative abundance and stock-recruitment relationships for the Delaware Bay blue crab stock. *Journal of Shellfish Research*, **17**, 529–541.

KEMP, W. M., BOYNTON, W. R., ADOLF, J. E., & 15 OTHERS. 2005. Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Marine Ecology Progress Series*, **303**, 1–29.

KENNEDY, V. S. 2007. External anatomy of blue crab larvae. *Pages 23–54 of:* KENNEDY, V. S., & CRONIN, L. E. (eds), *The blue crab* Callinectes sapidus. Maryland Sea Grant College, College Park.

KING, R. S., HINES, A. H., CRAIGE, F. D., & GRAP, S. 2005. Regional, watershed, and local correlates of blue crab and bivalve abundances in subestuaries of Chesapeake Bay, USA. *Journal of Experimental Marine Biology and Ecology*, **319**, 101–116.

KURIS, A. M., BLAU, S. F., PAUL, A. J., SHIELDS, J. D., & WICKHAM, D. E. 1991. Infestation by brood symbionts and their impact on egg mortality of the red king crab, *Paralithodes camtschatica*, in Alaska: geographic and temporal variation. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 559–568.

LAMBERT, D. M., LIPCIUS, R. N., & HOENIG, J. M. 2006a. Assessing effectiveness of the blue crab spawning stock sanctuary in Chesapeake Bay using tag-return methodology. *Marine Ecology Progress Series*, **321**, 215–225.

LAMBERT, D. M., HOENIG, J. M., & LIPCIUS, R. N. 2006b. Tag return estimation of annual and semiannual survival rates of adult female blue crabs. *Transactions of the American Fisheries Society*, **135**, 1592–1603.

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LATOUR, R. J., POLLOCK, K. H., WENNER, C. A., & HOENIG, J. M. 2001. Estimates of fishing and natural mortality for subadult red drum in South Carolina waters. *North American Journal of Fisheries Management*, **21**, 733–744.

LATOUR, R. J., HOENIG, J. M., HEPWORTH, D. A., & FRUSHER, S. D. 2003. A novel tag-recovery model with two size classes for estimating fishing and natural mortality, with implications for the southern rock lobster (*Jasus edwardsii*) in Tasmania, Australia. *ICES Journal of Marine Science*, **60**, 1075–1085.

LE VAY, L., UT, V. N., & WALTON, M. 2007. Population ecology of the mud crab *Scylla paramamosain* (Estampador) in an estuarine mangrove system; a mark-recapture study. *Marine Biology*, **151**, 1127–1135.

LEBER, K. M. 1995. Significance of fish size-at-release on enhancement of striped mullet fisheries in Hawaii. *Journal of the World Aquaculture Society*, **26**, 143–153.

LEBER, K. M. 1999. Chapter 5: Rationale for an experimental approach to stock enhancement. *Pages 63–75 of:* HOWELL, B. R., MOKSNESS, E., & SVASAND, T. (eds), *Stock enhancement and sea ranching*. Fishing News Books, Blackwell Science Ltd., Oxford.

LEBER, K. M. 2002. Chapter 6: Advances in marine stock enhancement: shifting emphasis to theory and accountability. *Pages 79–90 of:* STICKNEY, R. R., & MCVEY, J. P. (eds), *Responsible marine aquaculture*. CAB International.

LEBER, K. M. 2004. Marine stock enhancement in the USA: status, trends and needs. *Pages 11–24 of:* LEBER, K. M., KITADA, S., BLANKENSHIP, H. L., & SVASAND, T. (eds), *Stock enhancement and sea ranching (second edition): developments, pitfalls and opportunities*. Blackwell Publishing Ltd.

LEFFLER, C. W. 1972. Some effects of temperature on the growth and metabolic rate of juvenile blue crabs, *Callinectes sapidus*, in the laboratory. *Marine Biology*, **14**, 104–110.

LEIGH, G. M., HEARN, W. S., & POLLOCK, K. H. 2006. Time-dependent instantaneous mortality rates from multiple tagging experiments with exact times of release and recovery. *Environmental and Ecological Statistics*, **13**, 89–108.

LEWIS, E. G., & HAEFNER, JR., P. A. 1976. Oxygen consumption of the blue crab, *Callinectes sapidus* Rathbun, from proecdysis to postecdysis. *Comparative Biochemistry and Physiology*, **54A**, 55–60.

LIPCIUS, R. N., & STOCKHAUSEN, W. T. 2002. Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. *Marine Ecology Progress Series*, **226**, 45–61.

LIPCIUS, R. N., & VAN ENGEL, W. A. 1990. Blue crab population dynamics in Chesapeake Bay: variation in abundance (York River, 1972-1988) and stock-recruit functions. *Bulletin of Marine Science*, **46**, 180–194.

LIPCIUS, R. N., OLMI, III, E. J., & VAN MONTFRANS, J. 1990. Planktonic availability, molt stage and settlement of blue crab postlarvae. *Marine Ecology Progress Series*, **58**, 235–242.

LIPCIUS, R. N., SEITZ, R. D., GOLDSBOROUGH, W. J., MONTANE, M. M., & STOCKHAUSEN, W. T. 2001. A deepwater dispersal corridor for adult female blue crabs in Chesapeake Bay. *Pages 643-666 of:* KRUSE, G. H., *et al.* (eds), *Spatial processes and management of marine populations*. University of Alaska Sea Grant College Program, AK-SG-01-02, Fairbanks.

LIPCIUS, R. N., STOCKHAUSEN, W. T., SEITZ, R. D., & GEER, P. J. 2003. Spatial dynamics and value of a marine protected area and corridor for the blue crab spawning stock in Chesapeake Bay. *Bulletin of Marine Science*, **72**, 453–469.

LIPCIUS, R. N., SEITZ, R. D., SEEBO, M. S., & COLON-CARRION, D. 2005. Density, abundance and survival of the blue crab in seagrass and unstructured salt marsh nurseries of Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology*, **319**, 69–80.

LIPCIUS, R. N., EGGLESTON, D. B., HECK, JR., K. L., SEITZ, R. D., & VAN MONT-FRANS, J. 2007. Ecology of postlarval and young juvenile blue crabs. *Pages 535–564 of:* KENNEDY, V. S., & CRONIN, L. E. (eds), *The blue crab* Callinectes sapidus. Maryland Sea Grant College, College Park.

LIPPSON, R. L. 1973. Blue crab. *Pages 26–27 of:* LIPPSON, A. J. (ed), *The Chesapeake Bay in Maryland: an atlas of natural resources*. John Hopkins University Press, Baltimore.

LORENZEN, K. 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. *Journal of Fish Biology*, **49**, 627–647.

LORENZEN, K. 2000. Allometry of natural mortality as a basis for assessing optimal release size in fish-stocking programmes. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 2374–2381.

LORENZEN, K. 2005. Population dynamics and potential of fisheries stock enhancement: practical theory for assessment and policy analysis. *Philosophical Transactions of the Royal Society B*, **360**, 171–189.

LORENZEN, K. 2006. Population management in fisheries enhancement: gaining key information from release experiments through use of a size-dependent mortality model. *Fisheries Research*, **80**, 19–27.

LORENZEN, K. 2008. Understanding and managing enhancement fisheries systems. *Reviews in Fisheries Science*, **16**, 10–23.

MANSOUR, R. A. 1992. *Foraging ecology of the blue crab,* Callinectes sapidus *Rathbun, in lower Chesapeake Bay.* Doctoral dissertation, Virginia Institute of Marine Science, College of William and Mary, Gloucester Point.

McCONAUGHA, J. R., JOHNSON, D. F., PROVENZANO, A. J., & MARIS, R. C. 1983. Seaonsal distribution of larvae of *Callinectes sapidus* (Crustacea: Decapoda) in the waters adjacent to Chesapeake Bay. *Journal of Crustacean Biology,* **3**, 582–591.

MENSE, D. J., & WENNER, E. L. 1989. Distribution and abundance of early life history stages of the blue crab, *Callinectes sapidus,* in tidal marsh creeks near Charleston, South Carolina. *Estuaries,* **12**, 157–168.

METCALF, K. S., & LIPCIUS, R. N. 1992. Relationship of habitat and spatial scale with physiological state and settlement of blue crab postlarvae in Chesapeake Bay. *Marine Ecology Progress Series,* **82**, 143–150.

MILLER, T. J. 2001. Matrix-based modeling of blue crab population dynamics with applications to the Chesapeake Bay. *Estuaries,* **24**, 535–544.

MILLER, T. J. 2003. Incorporating space into models of the Chesapeake Bay blue crab population. *Bulletin of Marine Science,* **72**, 567–588.

MILLER, T. J., & HOUDE, E. D. 1999. *Blue crab target setting.* Final report to the Living Resources Subcommittee of the Chesapeake Bay Program, University of Maryland Center for Environmental Science Technical Series No. TS-177-99. Chesapeake Bay Program, U.S. Environmental Protection Agency, Annapolis, MD.

MILLER, T. J., MARTELL, S. J. D., BUNNELL, D. B., DAVIS, G., FEGLEY, L., SHAROV, A., BONZEK, C., HEWITT, D., HOENIG, J., & LIPCIUS, R. N. 2005. *Stock assessment of the blue crab in Chesapeake Bay, 2005.* Technical Report Series TS-487-05. University of Maryland Center for Environmental Science, Solomons (Available: hjort.cbl.umces.edu/crabs/Assessment05.html).

MILLIKIN, M. R., & WILLIAMS, A. B. 1984. *Synopsis of biological data on the blue crab,* Callinectes sapidus *Rathbun.* NOAA Technical Report NMFS 1/FAO Fisheries Synopsis 138.

MINELLO, T. J., & ROZAS, L. P. 2002. Nekton in Gulf Coast wetlands: fine-scale distributions, landscape patterns, and restoration implications. *Ecological Applications,* **12**, 441–455.

MINELLO, T. J., ABLE, K. W., WEINSTEIN, M. P., & HAYS, C. G. 2003. Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. *Marine Ecology Progress Series,* **246**, 39–59.

MOKSNES, P-O., LIPCIUS, R. N., PIHL, L., & VAN MONTFRANS, J. 1997. Cannibal-prey dynamics in young juveniles and postlarvae of the blue crab. *Journal of Experimental Marine Biology and Ecology,* **215**, 157–187.

MOODY, K. E. 1994. *Predation on juvenile blue crabs,* Callinectes sapidus *Rathbun, in lower Chesapeake Bay: patterns, predators, and potential impacts.* Doctoral dissertation, Virginia Institute of Marine Science, College of William and Mary, Gloucester Point.

MOODY, K. E. 2001. Patterns of predation on juvenile blue crabs in lower Chesapeake Bay: size, habitat and seasonality. *Pages 84–92 of:* GUILLORY, V., PERRY, H., & VANDERKOOY, S. (eds), *Proceedings of the blue crab mortality symposium.* Gulf States Marine Fisheries Commission, Ocean Springs, MS.

MOODY, K. E. 2003. Predators of juvenile blue crabs outside of refuge habitats in lower Chesapeake Bay. *Estuaries,* **26**, 759–764.

MORGAN, G. R. 1977. *Aspects of the population dynamics of the western rock lobster and their role in management.* Doctoral dissertation, University of Western Australia, Nedlands.

MORGAN, S. G., ZIMMER-FAUST, R. K., HECK, JR., K. L., & COEN, L. D. 1996. Population regulation of blue crabs *Callinectes sapidus* in the northern Gulf of Mexico: postlarval supply. *Marine Ecology Progress Series*, **133**, 73–88.

MURDY, E. O., BIRDSONG, R. S., & MUSICK, J. A. 1997. *Fishes of Chesapeake Bay.* Smithsonian Institution Press, Washington D.C.

NEWCOMBE, C. L., SANDOZ, M. D., & ROGERS-TALBERT, R. 1949. Differential growth and moulting characteristics of the blue crab, Callinectes sapidus Rathbun. *Journal of Experimental Zoology*, **110**, 113–152.

NI, I.-H. 1978. *Comparative fish population studies.* Doctoral dissertation, University of British Columbia, Vancouver.

NIEZGODA, G., BENFIELD, M., SISAK, M., & ANSON, P. 2002. Tracking acoustic transmitters by code division multiple access (CDMA)-based telemetry. *Hydrobiologia*, **483**, 275–286.

NMFS, (NATIONAL MARINE FISHERIES SERVICE). 2007. *Commercial fishery landings.* NMFS, Fisheries Statistics Division (Available: http://www.st.nmfs.noaa.gov/st1).

NOGA, E. J., SAWYER, T. K., & RODON-NAVEIRA, M. 1998. Disease processes and health assessment in blue crab fishery management. *Journal of Shellfish Research*, **17**, 567–577.

NORSE, E. A. 1977. Aspects of the zoogeographic distribution of *Callinectes* (Brachyura: Portunidae). *Bulletin of Marine Science*, **27**, 440–447.

OKAMOTO, K. 1999. Tag retention, growth, and survival of the swimming crab, *Portunus trituberculatus* marked with coded wire tags. *Nippon Suisan Gakkaishi*, **65**, 703–708.

OLMI, III, E. J. 1995. Ingress of blue crab megalopae in the York River, Virginia, 1987-1989. *Bulletin of Marine Science*, **57**, 753–780.

OLMI, III, E. J., & BISHOP, J. M. 1983. Variations in total width-weight relationships of blue crabs, *Callinectes sapidus*, in relation to sex, maturity, molt stage, and carapace form. *Journal of Crustacean Biology*, **3**, 575–581.

OLMI, III, E. J., VAN MONTFRANS, J., LIPCIUS, R. N., ORTH, R. J., & SADLER, P. W. 1990. Variation in planktonic availability and settlement of blue crab megalopae in the York River, Virginia. *Bulletin of Marine Science*, **46**, 230–243.

OLMI, III. E. J. 1994. Vertical migration of blue crab *Callinectes sapidus* megalopae: implications for transport in estuaries. *Marine Ecology Progress Series*, **113**, 39–54.

ORENSANZ, J. M., ARMSTRONG, J., ARMSTRONG, D., & HILBORN, R. 1998. Crustacean resources are vulnerable to serial depletion – the multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska. *Reviews in Fish Biology and Fisheries*, **8**, 117–176.

ORTH, R. J., & MOORE, K. A. 1983. Chesapeake Bay: an unprecedented decline in submerged aquatic vegetation. *Science*, **222**, 51–53.

ORTH, R. J., & VAN MONTFRANS, J. 1987. Utilization of a seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Marine Ecology Progress Series*, **41**, 283–294.

ORTH, R. J., & VAN MONTFRANS, J. 1990. Utilization of marsh and seagrass habitats by early stages of *Callinectes sapidus*: a latitudinal perspective. *Bulletin of Marine Science*, **46**, 126–144.

ORTH, R. J., & VAN MONTFRANS, J. 2002. Habitat quality and prey size as determinants of survival in post-larval and early juvenile instars of the blue crab *Callinectes sapidus*. *Marine Ecology Progress Series*, **231**, 205–213.

ORTH, R. J., *et al.* 2006. A global crisis for seagrass ecosystems. *BioScience*, **56**, 987–996.

OTTO, R. S. 1986. Management and assessment of eastern Bering Sea king crab stocks. *Pages 83–106 of:* JAMIESON, G. S., & BOURNE, N. (eds), *North Pacific workshop on stock assessment and management of invertebrates.* Canadian Special Publication of Fisheries and Aquatic Sciences 92.

PAOLISSO, M. 2002. Blue crabs and controversy on the Chesapeake Bay: a cultural model for understanding watermen's reasoning about blue crab management. *Human Organization,* **61,** 226–239.

PARDIECK, R. A., ORTH, R. J., DIAZ, R. J., & LIPCIUS, R. N. 1999. Ontogenetic changes in habitat use by postlarvae and young juveniles of the blue crab. *Marine Ecology Progress Series,* **186,** 227–238.

PASCUAL, M. A., & IRIBARNE, O. O. 1993. How good are empirical predictions of natural mortality? *Fisheries Research,* **16,** 17–24.

PATTERSON, K., COOK, R., DARBY, C., GAVARIS, S., KELL, L., LEWY, P., MESNIL, B., PUNT, A., RESTREPO, V., SKAGEN, D. W., & STEFANSSON, G. 2001. Estimating uncertainty in fish stock assessment and forecasting. *Fish and Fisheries,* **2,** 125–157.

PAULY, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour l'Exploration de la Mer,* **39,** 175–192.

PAULY, D., CHRISTENSEN, V., GUENETTE, S., PITCHER, T. J., SUMAILA, U. R., WALTERS, C. J., WATSON, R., & ZELLER, D. 2002. Towards sustainability in world fisheries. *Nature,* **418,** 689–695.

PERKINS-VISSER, E., WOLCOTT, T. G., & WOLCOTT, D. L. 1996. Nursery role of seagrass beds: enhanced role of juvenile blue crabs (*Callinectes sapidus* Rathbun). *Journal of Experimental Marine Biology and Ecology,* **198,** 155–173.

PERRY, H., JOHNSON, D. R., LARSEN, K., TRIGG, C., & VUKOVICH, F. 2003. Blue crab larval dispersion and retention in the Mississippi Bight: testing the hypothesis. *Bulletin of Marine Science*, **72**, 331–346.

PERRY, H. M., ELEUTERIUS, C. K., TRIGG, C. B., & WARREN, J. R. 1995. Settlement patterns of *Callinectes sapidus* megalopae in Mississippi Sound: 1991, 1992. *Bulletin of Marine Science*, **57**, 821–833.

PERRY, H. M., WARREN, J., TRIGG, C., & VAN DEVENDER, T. 1998. The blue crab fishery of Mississippi. *Journal of Shellfish Research*, **17**, 425–433.

PETERSON, I., & WROBLEWSKI, J. S. 1984. Mortality rate of fishes in the pelagic ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 1117–1120.

PILE, A. J., LIPCIUS, R. N., VAN MONTFRANS, J., & ORTH, R. J. 1996. Density-dependent settler-recruit-juvenile relationships in blue crabs. *Ecological Monographs*, **66**, 277–300.

POLLOCK, K. H., JIANG, H., & HIGHTOWER, J. E. 2004. Combining telemetry and fisheries tagging models to estimate fishing and natural mortality rates. *Transactions of the American Fisheries Society*, **133**, 639–648.

POPE, J. G. 1975. *Estimation of unknown natural mortality*. International Commission for the Northwest Atlantic Fisheries Dumm. Doc. 75/2.

PRAGER, M. H., McCONAUGHA, J. R., JONES, C. M., & GEER, P. J. 1990. Fecundity of blue crab, *Callinectes sapidus*, in Chesapeake Bay: biological, statistical and management considerations. *Bulletin of Marine Science*, **46**, 170–179.

PROVENZANO, JR., A. J., McCONAUGHA, J. R., PHILIPS, K. B., JOHNSON, D. F., & CLARK, J. 1983. Vertical distribution of first stage larvae of the blue crab, *Callinectes sapidus*, at the mouth of Chesapeake Bay. *Estuarine, Coastal and Shelf Science*, **16**, 489–499.

PULLEN, E. J., & TRENT, W. L. 1970. Carapace width-total weight relation of blue crabs from Galveston Bay, Texas. *Transactions of the American Fisheries Society*, **99**, 795–798.

QUINN, II, T. J., & DERISO, R. B. 1999. *Quantitative fish dynamics*. Oxford University Press, New York.

RABALAIS, N. N., BURDITT, JR., F. R., COEN, L. D., COLE, B. E., ELEUTERIUS, C., HECK, JR., K. L., MCTIGUE, T. A., MORGAN, S. G., PERRY, H. M., TRUESDALE, F. M., ZIMMER-FAUST, R. K., & ZIMMERMAN, R. J. 1995. Settlement of *Callinectes sapidus* megalopae on artificial collectors in four Gulf of Mexico estuaries. *Bulletin of Marine Science*, **57**, 855–876.

RAKOCINSKI, C. F., & MCCALL, D. D. 2005. Early blue crab recruitment to alternative nursery habitats in Mississippi, USA. *Journal of Shellfish Research*, **24**, 253–259.

RAKOCINSKI, C. F., PERRY, H. M., ABNEY, M. A., & LARSEN, K. M. 2003. Soft-sediment recruitment dynamics of early blue crab stages in Mississippi Sound. *Bulletin of Marine Science*, **72**, 393–408.

REYNS, N. B., & EGGLESTON, D. B. 2004. Environmentally-controlled, density-dependent secondary dispersal in a local estuarine crab population. *Oecologia*, **140**, 280–288.

RICKER, W. E. 1975. *Computation and interpretation of biological statistics of fish populations*. Bulletin of the Fisheries Research Board of Canada 191. Department of the Environment, Fisheries and Marine Service, Ottawa.

ROFF, D. A. 1984. The evolution of life history parameters in teleosts. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 989–1000.

ROMAN, M. R., & BOICOURT, W. C. 1999. Dispersion and recruitment of crab larvae in the Chesapeake Bay plume: physical and biological controls. *Estuaries*, **22**, 563–574.

ROME, M. S., YOUNG-WILLIAMS, A. C., DAVIS, G. R., & HINES, A. H. 2005. Linking temperature and salinity tolerance to winter mortality of Chesapeake Bay blue crabs (*Callinectes sapidus*). *Journal of Experimental Marine Biology and Ecology*, **319**, 129–145.

ROTHSCHILD, B. J., JONES, P. W., & WILSON, J. S. 1981. Trends in Chesapeake Bay fisheries. *Pages 284–298 of: Improving management of Chesapeake Bay*. Reprinted from *Transactions of the 46th North American Wildlife and Natural Resources Conference*. Wildlife Management Institute, Washington, D.C.

ROZAS, L. P., & HACKNEY, C. T. 1984. Use of oligohaline marshes by fishes and macrofaunal crustaceans in North Carolina. *Estuaries*, **7**, 213–224.

ROZAS, L. P., & MINELLO, T. J. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. *Estuaries*, **20**, 199–213.

ROZAS, L. P., & REED, D. J. 1993. Nekton use of marsh-surface habitats in Louisiana (USA) deltaic salt marshes undergoing submergence. *Marine Ecology Progress Series*, **96**, 147–157.

ROZAS, L. P., & ZIMMERMAN, R. J. 2000. Small-scale patterns of nekton use among marsh and adjacent shallow nonvegetated areas of the Galveston Bay Estuary, Texas (USA). *Marine Ecology Progress Series*, **193**, 217–239.

ROZAS, L. P., MINELLO, T. J., ZIMMERMAN, R. J., & CALDWELL, P. 2007. Nekton populations, long-term wetland loss, and the effect of recent habitat restoration in Galveston Bay, Texas, USA. *Marine Ecology Progress Series*, **344**, 119–130.

RUGOLO, L., KNOTTS, K., LANGE, A., CRECCO, V., TERCEIRO, M., BONZEK, C., STAGG, C., O'REILLY, R., & VAUGHAN, D. 1997. *Stock assessment of Chesapeake Bay blue crab (*Callinectes sapidus*). Report of the Technical Subcommittee of the Chesapeake*

Bay Stock Assessment Committee of the National Marine Fisheries Service, NOAA (National Oceanic and Atmospheric Administration). Tech. rept. NOAA Chesapeake Bay Office, Annapolis, MD.

RUGOLO, L. J., KNOTTS, K. S., & LANGE, A. M. 1998a. Historical profile of the Chesapeake Bay blue crab (*Callinectes sapidus* Rathbun) fishery. *Journal of Shellfish Research*, **17**, 383–394.

RUGOLO, L. J., KNOTTS, K. S., LANGE, A. M., & CRECCO, V. A. 1998b. Stock assessment of Chesapeake Bay blue crab (*Callinectes sapidus* Rathbun). *Journal of Shellfish Research*, **17**, 493–517.

RYER, C. H., VAN MONTFRANS, J., & ORTH, R. J. 1990. Utilization of a seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus*. II. Spatial and temporal patterns of molting. *Bulletin of Marine Science*, **46**, 95–104.

RYER, C. H., VAN MONTFRANS, J., & MOODY, K. E. 1997. Cannibalism, refugia and the molting blue crab. *Marine Ecology Progress Series*, **147**, 77–85.

SANDIFER, P. A. 1973. Distribution and abundance of decapod crustacean larvae in the York River estuary and adjacent lower Chesapeake Bay. *Chesapeake Science*, **14**, 235–257.

SANDOZ, M., & ROGERS, R. 1944. The effect of environmental factors on hatching, moulting, and survival of zoea larvae of the blue crab *Callinectes sapidus* Rathbun. *Ecology*, **25**, 216–228.

SCHNUTE, J. T., & RICHARDS, L. J. 1995. The influence of error on population estimates from catch-age models. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 2063–2077.

SEITZ, R. D., LIPCIUS, R. N., STOCKHAUSEN, W. T., & MONTANE, M. M. 2001. Efficacy of blue crab spawning sanctuaries in Chesapeake Bay. *Pages 607–626 of:* KRUSE, G. H.,

et al. (eds), *Spatial processes and management of marine populations.* University of Alaska Sea Grant College Program, AK-SG-01-02, Fairbanks.

SEITZ, R. D., LIPCIUS, R. N., & SEEBO, M. S. 2005. Food availability and growth of the blue crab in seagrass and unvegetated nurseries of Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology,* **319**, 57–68.

SEITZ, R. D., LIPCIUS, R. N., KNICK, K. E., SEEBO, M. S., LONG, W. C., BRYLAWSKI, B. J., & SMITH, A. 2008. Stock enhancement and carrying capacity of blue crab nursery habitats in Chesapeake Bay. *Reviews in Fisheries Science,* **16**, 329–337.

SEKHARAN, K. V. 1975. Estimates of the stocks of oil sardine and mackerel in the present fishing grounds off the west coast of India. *Indian Journal of Fisheries,* **21**, 177–182.

SHAROV, A. F., VOLSTAD, J. H., DAVIS, G. R., DAVIS, B. K., LIPCIUS, R. N., & MONTANE, M. M. 2003. Abundance and exploitation rate of the blue crab (*Callinectes sapidus*) in Chesapeake Bay. *Bulletin of Marine Science,* **72**, 543–565.

SHARP, W. C., LELLIS, W. A., BUTLER, M. J., HERRNKIND, W. F., HUNT, J. H., PARDEE-WOODRING, M., & MATTHEWS, T. R. 2000. The use of coded microwire tags in mark-recapture studies of juvenile Caribbean spiny lobster, *Panulirus argus. Journal of Crustacean Biology,* **20**, 510–521.

SHEEHY, M. R. J., BANNISTER, R. C. A., WICKINS, J. F., & SHELTON, P. M. J. 1999. New perspectives on the growth and longevity of the European lobster (*Homarus gammarus*). *Canadian Journal of Fisheries and Aquatic Sciences,* **56**, 1904–1915.

SHEPHERD, S. A., & BREEN, P. A. 1992. Mortality in abalone: its estimation, variability and causes. *Pages 276–304 of:* SHEPHERD, S. A., TEGNER, M. J., & GUZMAN DEL PROO, S. A. (eds), *Abalone of the world: biology, fisheries and culture.* Fishing News Books, Cambridge, UK.

SHIELDS, J. D. 2003. Research priorities for diseases of the blue crab *Callinectes sapidus*. *Bulletin of Marine Science*, **72**, 505–517.

SHIELDS, J. D., & OVERSTREET, R. M. 2007. Diseases, parasites, and other symbionts. *Pages 299–417 of:* KENNEDY, V. S., & CRONIN, L. E. (eds), *The blue crab* Callinectes sapidus. University of Maryland Sea Grant College, College Park.

SIDDEEK, M. S. M. 1991. Estimation of natural mortality of Kuwait's grooved tiger prawn *Penaeus semisulcatus* (de Haan) using tag-recapture and commercial fisheries data. *Fisheries Research*, **11**, 109–125.

SIDDEEK, M. S. M., WATSON, L. J., BLAU, S. F., & MOORE, H. 2002. Estimating natural mortality of king crabs from tag recapture data. *Pages 51–75 of: Crabs in cold water regions: biology, management, and economics.* University of Alaska Sea Grant College Program, AK-SG-02-01, Fairbanks.

SIMPFENDORFER, C. A. 1999a. Demographic analysis of the dusky shark fishery in southwestern Australia. *Pages 149–160 of:* MUSICK, J. A. (ed), *Life in the slow lane: ecology and conservation of long-lived marine animals.* American Fisheries Society, Symposium 23, Bethesda, MD.

SIMPFENDORFER, C. A. 1999b. Mortality estimates and demographic analysis for the Australian sharpnose shark, *Rhizoprionodon taylori*, from northern Australia. *Fishery Bulletin*, **97**, 978–986.

SMITH, M. T., & ADDISON, J. T. 2003. Methods for stock assessment of crustacean fisheries. *Fisheries Research*, **65**, 231–256.

SMITH, S. G., & CHANG, E. S. 2007. Molting and growth. *Pages 197–254 of:* KENNEDY, V. S., & CRONIN, L. E. (eds), *The blue crab* Callinectes sapidus. University of Maryland Sea Grant College, College Park.

SPARRE, P., & VENEMA, S. C. 1998. *Introduction to tropical fish stock assessment, Part 1: manual.* FAO Fisheries Technical Paper 306/1, rev. 2. FAO, Rome.

SPITZER, P. M., HECK, JR., K. L., & VALENTINE, J. F. 2003. Then and now: a comparison of patterns in blue crab post-larval abundance and post-settlement mortality during the early and late 1990s in the Mobile Bay system. *Bulletin of Marine Science,* **72**, 435–452.

STEHLIK, L. L., & MEISE, C. J. 2001. Attack and avoidance behavior between large and small blue crabs, *Callinectes sapidus,* in the laboratory. *Page 12 of:* MERCALDO-ALLEN, R., *et al.* (eds), *Collected abstracts of the Northeast Fisheries Science Center's seventh science symposium.* Abstract No. I-4.

STOCKHAUSEN, W. T., & LIPCIUS, R. N. 2003. Simulated effects of seagrass loss and restoration on settlement and recruitment of blue crab postlarvae and juveniles in the York River, Chesapeake Bay. *Bulletin of Marine Science,* **72**, 409–422.

SULKIN, S. D., VAN HEUKELEM, W., KELLY, P., & VAN HEUKELEM, L. 1980. The behavioral basis of larval recruitment in the crab *Callinectes sapidus* Rathbun: a laboratory investigation of ontogenetic changes in geotaxis and barokinesis. *Biological Bulletin,* **159**, 402–417.

TAGATZ, M. E. 1968a. Biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. *Fishery Bulletin,* **67**, 17–33.

TAGATZ, M. E. 1968b. Growth of juvenile blue crabs, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. *Fishery Bulletin,* **67**, 281–288.

TAGATZ, M. E. 1969. Some relations of temperature acclimation and salinity to thermal tolerance of the blue crab, *Callinectes sapidus. Transactions of the American Fisheries Society,* **98**, 713–716.

TAN, E-C., & VAN ENGEL, W. A. 1966. Osmoregulation in the adult blue crab, *Callinectes sapidus* Rathbun. *Chesapeake Science*, **7**, 30–35.

TANAKA, S. 1960. Studies on the dynamics and the management of fish populations. *Bulletin of the Tokai Regional Fisheries Research Laboratory*, **28**, 1–200.

TANASICHUK, R. W. 2000. Age-specific natural mortality rates of adult Pacific herring (*Clupea pallasi*) from southern British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 2258–2266.

TANKERSLEY, R. A., & FORWARD, JR., R. B. 1994. Endogenous swimming rhythms in estuarine crab megalopae: implications for flood-tide transport. *Marine Biology*, **118**, 415–423.

THOMAS, J. C. 1973. *An analysis of the commercial lobster (*Homarus americanus*) fishery along the coast of Maine, August 1966 through December 1970.* NOAA Technical Report NMFS SSRF-667.

THOMAS, J. L., ZIMMERMAN, R. J., & MINELLO, T. J. 1990. Abundance patterns of juvenile blue crabs (*Callinectes sapidus*) in nursery habitats of two Texas bays. *Bulletin of Marine Science*, **46**, 115–125.

TRINGALI, M. D., SEYOUM, S., WALLACE, E. M., HIGHAM, M., TAYLOR, R. G., TROTTER, A. A., & WHITTINGTON, J. A. 2008. Limits to the use of contemporary genetic analyses in delineating biological populations for restocking and stock enhancement. *Reviews in Fisheries Science*, **16**, 111–116.

TURNER, H. V., WOLCOTT, D. L., WOLCOTT, T. G., & 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* Rathbun. *Journal of Experimental Marine Biology and Ecology*, **295**, 107–130.

UPHOFF, JR., J. H. 1998. Stability of the blue crab stock in Maryland's portion of Chesapeake Bay. *Journal of Shellfish Research*, **17**, 519–528.

VAN ENGEL, W. A. 1958. The blue crab and its fishery in Chesapeake Bay: Part 1–Reproduction, early development, growth, and migration. *Commercial Fisheries Review*, **20**, 6–17.

VAN ENGEL, W. A. 1962. The blue crab and its fishery in Chesapeake Bay: Part 2–Types of gear for hard crab fishing. *Commercial Fisheries Review*, **24**, 1–10.

VAN ENGEL, W. A. 1987. Chapter 10: Factors affecting the distribution and abundance of the blue crab in Chesapeake Bay. *Pages 177-209 of:* MAJUMDAR, S. K., HALL, JR., L. W., & AUSTIN, H. M. (eds), *Contaminant problems and management of living Chesapeake Bay resources*. The Pennsylvania Academy of Science.

VAN ENGEL, W. A. 1999. *Laws, regulations, and environmental factors and their potential effects on the stocks and fisheries for the blue crab,* Callinectes sapidus, *in the Chesapeake Bay region, 1880-1940.* Special Report in Applied Marine Science and Ocean Engineering 347 (VIMS SRAMSOE).

VAN HEUKELEM, W. F., & SULKIN, S. D. 1990. Effects of low temperature on activity and survival of juvenile blue crabs. *Bulletin of Marine Science*, **46**, 251.

VAN MONTFRANS, J., CAPELLI, J., ORTH, R. J., & RYER, C. H. 1986. Use of microwire tags for tagging juvenile blue crabs (*Callinectes sapidus* Rathbun). *Journal of Crustacean Biology*, **6**, 370–376.

VAN MONTFRANS, J., PEERY, C. A., & ORTH, R. J. 1990. Daily, monthly, and annual settlement patterns by *Callinectes sapidus* and *Neopanope sayi* megalopae on artificial collectors deployed in the York River, Virginia: 1985-1988. *Bulletin of Marine Science*, **46**, 214–229.

VAN MONTFRANS, J., EPIFANIO, C. E., KNOTT, D. M., LIPCIUS, R. N., MENSE, D. J., METCALF, K. S., OLMI, III, E. J., ORTH, R. J., POSEY, M. H., WENNER, E. L., & WEST, T. L. 1995. Settlement of blue crab postlarvae in western North Atlantic estuaries. *Bulletin of Marine Science*, **57**, 834–854.

VAN MONTFRANS, J., RYER, C. H., & ORTH, R. J. 2003. Substrate selection by blue crab *Callinectes sapidus* megalopae and first juvenile instars. *Marine Ecology Progress Series*, **260**, 209–217.

VARNELL, L. M., & HAVENS, K. J. 1995. A comparison of dimension-adjusted catch data methods for assessment of fish and crab abundance in intertidal salt marshes. *Estuaries*, **18**, 319–325.

VENABLES, W. N., & RIPLEY, B. D. 2002. *Modern applied statistics with S.* Fourth edn. Springer.

VETTER, E. F. 1988. Estimation of natural mortality in fish stocks: a review. *Fishery Bulletin*, **86**, 25–43.

WAHLE, R. A. 2003. Revealing stock-recruitment relationships in lobsters and crabs: is experimental ecology the key? *Fisheries Research*, **65**, 3–32.

WALTERS, C. J., & MARTELL, S. J. D. 2004. *Fisheries ecology and management.* Princeton University Press, New Jersey.

WANG, Y.-G. 1999. A maximum-likelihood method for estimating natural mortality and catchability coefficient from catch-and-effort data. *Marine and Freshwater Research*, **50**, 307–311.

WANG, Y.-G., & ELLIS, N. 2005. Maximum likelihood estimation of mortality and growth with individual variability from multiple length-frequency data. *Fishery Bulletin*, **103**, 380–391.

WARNER, W. W. 1976. *Beautiful swimmers: watermen, crabs, and the Chesapeake Bay.* Little, Brown and Company, Boston.

WATERS, D. S., NOBLE, R. L., & HIGHTOWER, J. E. 2005. Fishing and natural mortality of adult largemouth bass in a tropical reservoir. *Transactions of the American Fisheries Society,* **134**, 563–571.

WILLIAMS, A. B. 1965. Marine Decapod crustaceans of the Carolinas. *Fishery Bulletin,* **65**, 1–292.

WILLIAMS, A. B. 1974. The swimming crabs of the genus *Callinectes* (Decapoda: Portunidae). *Fishery Bulletin,* **72**, 685–798.

WILLIAMS, A. B. 2007. Systematics and evolution. *Pages 1–21 of:* KENNEDY, V. S., & CRONIN, L. E. (eds), *The blue crab* Callinectes sapidus. Maryland Sea Grant College, College Park.

WILLIAMS, A. H., COEN, L. D., & STOELTING, M. S. 1990. Seasonal abundance, distribution, and habitat selection of juvenile *Callinectes sapidus* (Rathbun) in the northern Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology,* **137**, 165–183.

WILLIAMS, B. K., NICHOLS, J. D., & CONROY, M. J. 2002. *Analysis and management of wildlife populations.* Academic Press, San Diego.

WILLIAMS, E. H. 2002. The effects of unaccounted discards and misspecified natural mortality on harvest policies based on estimates of spawners per recruit. *North American Journal of Fisheries Management,* **22**, 311–325.

WILSON, J. A., LANGTON, R. W., & ORSDEL, C. V. 1998. A model for the preliminary analysis of the economic feasibility of Atlantic cod enhancement in the Gulf of Maine (USA). *Bulletin of Marine Science,* **62**, 675–687.

WILSON, K. A., ABLE, K. W., & HECK, JR., K. L. 1990. Habitat use by juvenile blue crabs: a comparison among habitats in southern New Jersey. *Bulletin of Marine Science*, **46**, 105–114.

XIAO, Y., & MCSHANE, P. 2000. Estimation of instantaneous rates of fishing and natural mortalities from mark-recapture data on the western king prawn *Penaeus latisulcatus* in the Gulf St. Vincent, Australia, by conditional likelihood. *Transactions of the American Fisheries Society*, **129**, 1005–1017.

XU, X., BISHOP, J. M., MOHAMMED, H. M. A., & ALSAFFAR, A. H. 1995a. Estimation of the natural mortality rate of green tiger prawns *Penaeus semisulcatus* (de Haan, 1844) in Kuwait waters using relative abundance data. *Journal of Shellfish Research*, **14**, 179–184.

XU, X., MOHAMMED, H. M. A., AL-GHUNAIM, A. Y., & AL-YAMANI, F. 1995b. Temporal variability in natural mortality of green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters. *Journal of Shellfish Research*, **14**, 337–340.

YOUNG, A. C., JOHNSON, E. G., DAVIS, J. L. D., HINES, A. H., ZMORA, O., & ZOHAR, Y. 2008. Do hatchery-reared blue crabs differ from wild crabs, and does it matter? *Reviews in Fisheries Science*, **16**, 254–261.

YOZZO, D. J., & SMITH, D. E. 1998. Composition and abundance of resident marsh-surface nekton: comparison between tidal freshwater and salt marshes in Virginia, USA. *Hydrobiologia*, **362**, 9–19.

ZHENG, J. 2003. Uncertainties of natural mortality estimates for eastern Bering Sea snow crab, *Chionoecetes opilio*. *Fisheries Research*, **65**, 411–425.

ZHENG, J., MURPHY, M. C, & KRUSE, G. H. 1995a. A length-based population model and stock-recruitment relationships for red king crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 1229–1246.

ZHENG, J., MURPHY, M. C., & KRUSE, G. H. 1995b. Updated length-based population model and stock-recruitment relationships for red king crab in Bristol Bay, Alaska. *Alaska Fishery Research Bulletin,* **2**, 114–124.

ZHENG, J., MURPHY, M. C., & KRUSE, G. H. 1997a. Alternative rebuilding strategies for the red king crab *Paralithodes camtschaticus* fishery in Bristol Bay, Alaska. *Journal of Shellfish Research,* **16**, 205–217.

ZHENG, J., MURPHY, M. C., & KRUSE, G. H. 1997b. Analysis of harvest strategies for red king crab, *Paralithodes camtschaticus,* in Bristol Bay, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences,* **54**, 1121–1134.

ZIMMERMAN, R. J., & MINELLO, T. J. 1984. Densities of *Penaeus aztecus, Penaeus setiferus,* and other natant macrofauna in a Texas salt marsh. *Estuaries,* **7**, 421–433.

ZMORA, O., FINDIESEN, A., STUBBLEFIELD, J., FRENKEL, V., & ZOHAR, Y. 2005. Large-scale juvenile production of the blue crab *Callinectes sapidus. Aquaculture,* **244**, 129–139.

ZOHAR, Y., HINES, A. H., ZMORA, O., JOHNSON, E. G., LIPCIUS, R. N., SEITZ, R. D., EGGLESTON, D. B., PLACE, A. R., SCHOTT, E. J., STUBBLEFIELD, J. D., & CHUNG, J. S. 2008. The Chesapeake Bay blue crab (*Callinectes sapidus*): a multidisciplinary approach to responsible stock replenishment. *Reviews in Fisheries Science,* **16**, 24–34.

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