ABSTRACT

JOHNSON, ERIC GORDON. Population dynamics and stock assessment of the blue crab in North Carolina (Under the direction of David B. Eggleston).

The blue crab (*Callinectes sapidus*) is an ecologically important estuarine predator and represents North Carolina's most important commercial fishery. Recent fishery-dependent and –independent data suggest the population is declining. The goal of this study was to increase our understanding of the status and population dynamics of the blue crab in NC by addressing the following objectives: (1) estimate population demographics of blue crabs in salt marsh creeks, (2) construct a discontinuous model of blue crab growth in NC using growth rates estimated from free-ranging blue crabs, and (3) provide a comprehensive stock assessment for the blue crab in NC. A series of complementary laboratory and field studies assessed the nursery role of salt marsh habitats for the blue crab (*Callinectes sapidus*). Population demographics and movement patterns of juvenile and adult blue crabs were quantified in two tidal salt marsh creeks near Beaufort, North Carolina, USA during June – October 2001. While there are many studies that report estimates of population density, mortality rates, or movement rates for blue crabs, this study represents one of the first attempts to estimate all quantities concurrently. Juvenile crabs were mobile within the interstices of the vegetated marsh surface during flood tide, and were equally distributed buried in intertidal marsh and adjacent mud areas during ebb tide. Juvenile crabs may experience a spatial refuge from cannibalism in the marsh surface since adult conspecifics are physically impeded by dense vegetation and rarely move far into marsh habitats. This spatial refuge in the vegetated marsh surface may be significant, since cannibalism represents

a large source of mortality for this species. The relatively high use of the marsh surface by juvenile blue crabs, combined with a general lack of sampling these complex habitats, suggest that crab densities may be even higher in salt marsh systems than previously thought. Growth models commonly used in fisheries and ecological modeling assume growth is a continuous function of age. While this approach is appropriate for finfish, the validity of these models for crustacean species, which grow discontinuously, has been questioned. There is a critical need to compare the predictions of discontinuous and continuous models simultaneously to identify if potential biases are introduced by the assumption of continuous growth for the blue crab. The blue crab stock in North Carolina currently sustains heavy exploitation by the commercial fishery, and information on the recreational fishery is generally lacking. There has been a systematic increase in commercial landings from 1987-1999, followed by a period of reduced landings from 2000-2002. During this period fishery-independent indices of abundance have remained stable, or have shown a significant decline. In no case have any indices of abundance shown an increasing trend. Moreover, adult and spawning stock abundance (SSB) during 2000-2001 were at the lowest levels recorded since 1987, and the mean size of mature females has declined significantly during 1987-2003. Increases in the index of relative SSB in 2002-2003, however, may indicate a recovery. We detected a significant stock-recruit relationship for the blue crab in North Carolina using certain estimates of recruit abundance and recommend an urgent need for conservation of the spawning stock. We encourage decision makers to use the information and recommendations in this dissertation as soon as possible to manage the blue crab fishery in NC in a sustainable manner.

POPULATION DYNAMICS AND STOCK ASSESSMENT OF THE BLUE CRAB IN NORTH CAROLINA

By

ERIC GORDON JOHNSON

A dissertation submitted to the Graduate Faculty of North Carolina State University in partial fulfillment of the requirements for the Degree of Doctor of Philosophy

MARINE SCIENCE

Raleigh
2004

APPROVED BY:

_____	_____
Dr. David B. Eggleston Chair of Advisory Committee	Dr. Joseph E. Hightower
_____	_____
Dr. Kenneth H. Pollock	Dr. Thomas G. Wolcott

This work is dedicated to the memory of my brother,

James Christopher Johnson

BIOGRAPHY

Eric Gordon Johnson was born in Oakland, California on June 11th , 1972 and spent the majority of his childhood in South Bend, Indiana under the shadow of the Golden Dome. He attended DePauw University in Greencastle, Indiana, where he began his undergraduate education as an Economics major. In the spring of 1991, realizing his grievous error, he decided to add Biology as a second major. Following graduation, he spent two years at the Florida Institute of Technology, where he earned a Master of Science degree in Marine Biology. More importantly, while in Melbourne, FL he met his wife, Heather, at a bar. Coincidentally, while also in Melbourne, he met Dr. David Eggleston, near a keg. He then traveled to Raleigh, NC to pursue a Ph.D. at North Carolina State University.

TABLE OF CONTENTS

CHAPTER 3: **Stock assessment of the blue crab in North Carolina**

LIST OF TABLES

LIST OF TABLES (continued)

LIST OF FIGURES

LIST OF FIGURES (continued)

LIST OF FIGURES (continued)

LIST OF FIGURES (continued)

LIST OF FIGURES (continued)

CHAPTER 1

POPULATION DEMOGRAPHICS AND MOVEMENT OF BLUE CRABS IN SALT MARSH CREEKS

ABSTRACT: A series of complimentary laboratory and field studies assessed the nursery role of salt marsh habitats for the blue crab (*Callinectes sapidus*). Population demographics and movement patterns of juvenile and adult blue crabs were quantified in two tidal salt marsh creeks (Prytherch Creek, PC; Haystacks, HS) near Beaufort, North Carolina, USA during June – October 2001. While there are many studies that report estimates of population density, mortality rates, or movement rates for blue crabs, this study represents one of the first attempts to estimate all quantities concurrently. Approximately 1,100 blue crabs were tagged internally with individually coded microwire tags. A Jolly-Seber capture-recapture model was used to estimate population density as well as survival and capture probabilities. Mean crab density in PC was 1.2 crabs/m^2, which was an order of magnitude larger than crab density estimates from HS (0.10 crabs/m^2). Mean daily survival probabilities for crabs residing in PC were 0.98 d $\pm$ 0.08, and 0.96 d $\pm$ 0.03 for crabs in HS. To examine patterns of movement within a salt marsh and to quantify emigration rates from our study areas, crabs were tracked for 24-h using individually numbered floating tags that were affixed to the carapace of juvenile crabs. These independent estimates of emigration allowed us to partition crab loss from salt marsh creeks into mortality and emigration. Juvenile crabs exhibited a high degree of site fidelity to a given marsh creek during summer-fall, suggesting that losses are due more to mortality than emigration and help explain site-specific differences in mean density. Juvenile crabs were mobile within the interstices of the marsh surface during flood tide, and were equally distributed buried in intertidal marsh and adjacent mud areas during ebb tide. Juvenile crabs may experience a spatial refuge from cannibalism in the marsh surface since adult conspecifics are physically impeded by dense vegetation and

rarely move far into marsh habitats. This spatial refuge in the vegetated marsh surface may be significant, since cannibalism represents a large source of mortality for this species. The relatively high use of the marsh surface by juvenile blue crabs, combined with a general lack of sampling these complex habitats, suggest that crab densities may be even higher in salt marsh systems than previously thought.

INTRODUCTION

Estuaries are comprised of a mosaic of habitats that are among the most productive ecosystems on Earth. Within estuaries, salt marshes composed mainly of *Spartina alterniflora* and associated tidal creeks and marsh pools are among the most conspicuous habitats. Due to high densities of fish and crustaceans, salt marsh ecosystems are generally recognized as important nursery areas for many species, and support many lucrative coastal fisheries (Nixon 1980, Boesch & Turner 1984, Zimmerman et al. 2000). The nursery role of estuarine habitats is of special importance to conservation and management issues, and has received increasing attention in light of recent U. S. federal regulations that mandate the identification of Essential Fishery Habitat (EFH) for all federally managed fishery species. Nurseries are those habitats that allow for greater juvenile production as a result of a combination of factors such as increased (1) density, (2) growth, (3) survival, (4) efficient movement to adult habitats (Beck et al. 2001). A comparison of all of these factors across different habitats is ideal, and may aid in determining which habitats serve as key nurseries, as well as the underlying ecological processes responsible.

The blue crab (*Callinectes sapidus*) is a key benthic predator in the ecology of estuarine and nearshore coastal habitats of the Eastern United States and Gulf of Mexico, capable of regulating populations of many benthic and infaunal invertebrate species on which it feeds (Eggleston et al. 1992, Seitz et al. 2001). The blue crab supports some of the most economically important fisheries on the east and gulf coasts of the U.S. Recent declines in blue crab stocks in Chesapeake Bay (Miller & Houde 1998, Lipcius et al.

2002), Delaware Bay (Helser & Kahn 1999) and North Carolina (Eggleston et al. 2004) have been attributed to overfishing and habitat loss. Habitat management plans attempt to protect vital nursery areas for the blue crab and other species from degradation. These plans require information on key nursery habitats for conservation.

Although seagrass beds have generally been considered the primary nursery areas for juvenile blue crabs because of relatively high crab abundances in these habitats (Orth & van Montfrans 1987, Etherington & Eggleston 2000, Etherington & Eggleston 2003), a suite of alternative complex nursery habitats such as salt marsh and shallow detrital habitats have also been identified (Etherington & Eggleston 2000, Minello et al. 2003). The overall objective of this study was to quantify population demographics and movement patterns of juvenile and adult blue crabs in two tidal salt marsh habitats. This study used capture-recapture methodologies that allowed for identification of individually tagged crabs, and included covariates into analyses that traditionally do not include them, which allowed assessment of the relationship between survival, capture probability and crab size. The results are used to assess the nursery role (*sensu* Beck et al. 2001) of tidal salt marshes for blue crabs.

MATERIALS AND METHODS

Study sites

Local population demographics of juvenile blue crabs were studied in two tidal marsh creeks, Prytherch Creek (PC) and Haystacks (HS), located in the Newport River estuary near Beaufort, North Carolina, USA (Fig. 1). Intertidal zones within the study sites were composed mainly of *Spartina alterniflora*, while the subtidal areas consisted of muddy substrate and small patches of oyster, *Crassostrea virginica*. The study sites were

well suited for an intensive capture-recapture study of mobile crabs because of the (1) relatively high densities (0.1 - 1.2 crabs/m^2) of juvenile blue crabs, (2) relatively small size of the study areas (PC = 1,625 m^2, HS = 2,028 m^2), which facilitated intensive sampling, (3) constricted entrance to the study sites, which likely reduced emigration. The upstream boundaries of the study areas were defined by the intertidal marsh, which were generally inaccessible to sampling, and the downstream boundaries were defined by an imaginary line transecting the creek mouth. The estimated total drainage of marsh area into each study area was significantly larger (PC 3,275 m^2, HS 8,270 m^2) than the actual area sampled.

Population sampling

During June-October 2001, PC was sampled on 10 occasions (mean sampling interval 4 days), while HS was sampled on six occasions (mean sampling interval 7.8 days). A 2-m beam trawl (0.76 cm mesh; 0.38 cm mesh cod-end) was used to collect juvenile and adult blue crabs (22 – 153 mm CW). The beam trawl provides an efficient means of sampling blue crabs from shallow water habitats because the width of the net is fixed, allowing for relatively accurate measures of animal densities, and the relatively small size of the net and frame allowed manual towing immediately adjacent to the intertidal marsh in shallow water (<1 m) water. A total of 1,376 individual crabs were captured from PC over 10 sampling intervals and 1,110 individuals from HS over 6 sampling intervals (Appendix Table 1). Of these, 795 individuals were tagged and released in PC, and 347 individuals were tagged and released in HS. Three factors precluded the tag and release of all captured crabs: (1) many crabs were smaller than the lower limit imposed by our tagging gear (22 mm), (2) crabs sustained recent damage

from capture or subsequent interaction with conspecifics, (3) recaptured crabs were necessarily sacrificed to obtain the coded microwire tag (CWT), which coded for the initial date of capture and allowed identification of an individual (see below). Captured crabs were sorted approximately by size (mm CW) and stored in dark holding containers filled with water to minimize agonistic encounters. Additionally, containers were supplied with aeration to minimize physiological stress following capture. Both total and internal CW (ICW; Olmi & Bishop 1983), as well as sex, were recorded for each crab; however, only crabs greater than 22 mm CW were considered in analyses due to limitations of the internal microwire tagging method (see below). ICW is defined as the widest distance across the carapace excluding the lateral spines. Crabs showing obvious recent damage were not tagged and were returned to the population.

Crabs were tagged using stainless steel CWTs (Northwest Marine Technologies, Inc. Shaw Island, WA 98286), which are laser-etched with a sequential numeric code and individually identifiable. CWT's have been used to quantify blue crab demographics such as population size and apparent survival in estuarine systems (van Montfrans et al. 1991, Fitz & Wiegert 1992a,b). Additional laboratory studies (Fitz & Wiegert 1991, van Montfrans et al. 1986, this study) demonstrated that CWT's have negligible effects on mortality and growth. The CWT's were magnetized at the time of injection, which allows for later detection of tags in the field at the time of recapture using a magnetic detection system, and then injected into the basal muscle of the 5^{th} periopod, and were completely internal and retained through molting. To ensure that crabs received a full CWT, a blank tag was cut and saved following each tagging of an individual crab. This procedure was necessary to keep a reference of the numeric sequence to which CWT's recovered from

recaptured crabs could be compared to identify unique individuals. After data collection and tagging, each individual crab was scanned using a magnetic moment detector to check for successful tagging and released into the study site in the approximate area of capture. During recapture efforts, captured crabs were checked for CWT's using a magnetic moment detector (Northwest Marine Technologies). Crabs with CWT's were not released, but were sacrificed to obtain the CWT for individual identification; a procedure that is required to obtain the original date of capture. During each recapture event, untagged crabs were tagged and released to the study site as described above. Individual capture-recapture histories were then used to generate Jolly-Seber (JS) summary statistics for PC and HS (Appendix Tables 1a, b).

Mark-recapture analysis

Population abundance and maximum-likelihood estimates (MLE's) of apparent survival (ϕ) and recapture (p) probabilities were generated from individual capture-recapture histories using the JS model framework (Cormack 1964, Jolly 1965, Seber 1965). The stochastic JS model does not assume population closure (closure = no additions or deletions from the population), and is therefore useful for demographically open populations in which mortality, migration, and recruitment occur (Manly 1984). Following standard JS notation, ϕ_i is the probability of not dying or emigrating from the study site between periods i and $i + 1$, and p_i is the probability of being captured during period i. Estimates of population size ($\hat{N}_i$) for each sampling interval i were calculated as

$$\hat{N}i = n_i / \hat{p}_i,$$

where n_i was the total number of individuals captured in period *i*, and $\hat{p}_i$ the probability of capture from JS modeling as described above. The assumptions of the JS model are: (1) all individuals in the populations at a given sampling time have an equal probability of capture (this value can change over time), (2) every tagged individual in the population has the same probability of survival, (3) tags are neither lost nor overlooked, (4) the duration of the sampling period must be short relative to the time between samples, (5) animals are released immediately after sampling (Lancia et al. 1994). Variation in survival or capture probability among individuals (heterogeneity) can lead to both positive and negative bias in estimates of population size (Pollock et al. 1990). The assumptions of homogeneity of survival and capture probabilities were addressed by goodness of fit (GoF) testing and through the inclusion of covariates, which can account for potential size-specific differences in survival (ϕ) and recapture rates (p). Although often ignored, tag loss can impart significant bias to survival estimates, and reduces the effective recapture rate resulting in a loss of precision. To account for bias due to tag loss and tag induced mortality, estimates of tag retention and mortality due to tagging were generated from a laboratory tagging study and used to correct survival estimates following the procedure of Arnason and Mills (1983). The assumption that sampling is instantaneous was met to the degree possible based on logistical constraints, by relatively short sampling duration (~ 4 hours) and sampling intervals (minimum 4 days).

Goodness-of-fit and model selection

All JS capture-recapture modeling used the computer software program MARK (White and Burnham 1999) for parameter estimation and model selection. GoF tests insured that the JS model provided an adequate fit to the data, and were conducted with

the computer program RELEASE (Burnham et al. 1997). GoF testing is important as a significant lack of fit may indicate that assumptions underlying the model have been violated. Presently, there is no adequate method for assessing GoF with models containing covariates; therefore GoF tests were performed on the most general model of time-varying survival and capture probabilities, with covariates omitted as recommended by Cooch and White (2001). To adjust for lack of fit, overdispersion in the data was quantified using c-hat (χ^2/df) from GoF testing (Lebreton et al. 1992), and, if necessary, used to transform Akaike's Information Criterion (AIC) values to quasi-likelihood adjusted Akaike's Information Criterion ($QAIC_c$). Although the preferred method to estimate c-hat is parametric bootstrapping (Cooch & White 1999), this statistical technique was infeasible due the experimental protocol in which animals were sacrificed at recapture.

Once an adequate fit to the fully time-dependent (ϕ_t,p_t) JS model was established through GoF testing, reduced parameter models (ϕ,p ; ϕ,p_t ; ϕ_t,p ; model notation follows the convention of Lebreton et al. (1992), and uses the subscript t to denote that a parameter can vary over time), holding ϕ and p constant over all sampling intervals, were fitted to capture-recapture histories to determine the most parsimonious model that still provided a good fit to the recapture data. Additionally, since individual crab size may affect the probability of capture and survival, length (CW) was tested as a model covariate. Survival and capture probabilities were constrained to linear and quadratic functions of CW. Individual covariates were converted to standardized values (($x - \bar{x}$)/SD_x), and estimators (ϕ, p) were related to CW using a logit function with beta parameters estimated from MARK. The use of standardized covariates helped insure that

numerical optimization routines arrived at correct parameter estimates (Evan and Cooch 1999).

JS model selection was based on $QAIC_c$, which was adjusted using c-hat values generated from GoF testing. This is generally the preferred method for model selection, as it allows for comparison of a large number of candidate models without an inflation of experimentwise error, and performs well when assumptions may be violated (Burnham et al. 1995). In general, models with $\Delta QAIC_c < 7$ are considered plausible, and models with a $\Delta QAIC_c < 2$ having approximately equal weight (Cooch and White 2001). Maximum likelihood estimates and standard errors of survival and capture probabilities were derived from model averaging of reasonably likely models ($\Delta QAIC_c < 2$) for PC and HS.

Laboratory estimation of tag retention and tag-induced mortality

To determine the extent to which certain model assumptions may have been violated, a 37 d laboratory experiment (August 8 – September 12, 2002) tested the effects of CWT's on blue crab mortality and rates of tag retention (θ). A 2-m trawl was used to collect juvenile blue crabs ranging from 22.7 to 35.1 mm CW from PC. This size range was predominant within both study areas, and was representative of the majority of the study population. Fifteen crabs were randomly selected and subsequently received a CWT using the tagging procedure described above. An equal number of crabs were not tagged and served as a control treatment. Crabs were sexed and measured (mm CW) prior to being randomly assigned to individual plastic containers, which prevented cannibalism and allowed individual crabs to be tracked throughout the duration of the experiment. Crabs in containers were placed into a water table supplied with flow-through seawater and supplemental aeration. Initial size of crabs did not differ

significantly (student's t-test, *df* = 28, p = 0.78) among tagged (27.58 mm CW $\pm$ 1.16 mm) and control (27.99 mm CW $\pm$ 0.88) treatments (Table 1). Crabs were fed to satiation at 1-2 day intervals with snails (*Littorina irrorata*) and fish, principally pinfish (*Lagodon rhomboides*) and killifish (*Fundulus sp.*) collected from local marsh creeks. Crabs were checked daily for mortality and molting. Recently molted crabs were allowed 1 - 2 d to harden prior to being measured and checked for tag retention. A student's t-test was used to test whether or not tagging affected (1) time-to-first-molting (days), (2) molt interval between first and second molts (days), (3) survival, and (4) mean percent increase in CW per molt (%). The mean percent increase in size (i.e., (postmolt CW – premolt-CW)/ premolt-CW) was calculated following each molt event. The assumption that variances were homogeneous was verified using Levene's test of equality of variances. A Chi-square test was used to assess the effects of tagging on mortality.

Field movement rates, emigration and habitat utilization.

One disadvantage of the JS model is the inability to separate the probability of loss (1 - ϕ) into its component processes, mortality and emigration, without additional information (Pollock et al. 1990). To complement the mark-recapture analysis and quantify emigration rates of juvenile crabs within the marsh creeks, as well as provide information on daily patterns of movement and distribution, individual crabs were tagged and tracked within PC and HS. Juvenile crabs (35 - 62 mm CW) were collected from the study sites and fitted with individually numbered floats attached to the lateral spines by a short metal leader and 1 m of monofilament line. Due to the small size of these juvenile crabs, it was not feasible to use ultrasonic telemetry as a study technique (e.g., Bell et al. 2003) because of the large size of the transmitters relative to the crabs.

Crabs were observed to be quite mobile in pilot trials in the tidal creek systems suggesting that the float did not significantly hamper movement. While movement was not hampered in unvegetated habitats, crabs occasionally became tangled within the interstices of the marsh and the tagging method likely limited the distance to which crabs could enter the marsh. The experiment was conducted in four batch releases (two each at PC and HS). Each release consisted of 24 individually tagged crabs, and the interval between trials at each site was no more than 4 days. Tagged crabs were released at flood tide and at random starting locations within the study site boundaries, and allowed a period of four hours to acclimate prior to tracking. Crabs were relocated visually every 1 – 2 h for a period of 24 h. Nighttime tracking was accomplished using a combination of ambient moonlight and a flashlight, and was aided by the reflective surface of the floats. To track movement distance and direction over time, the location of each crab was plotted onto site maps relative to natural landmarks and PVC stakes that were placed at 10 m distances apart. Two metrics were used to quantify movement distance within tidal creeks: (1) the total distance traveled, defined as the sum of the linear distances between all relocation observations, and (2) the net distance traveled, defined as the linear distance between the initial and final relocation observations. An index of meander was also calculated using the ratio of the net distance to the total distance traveled. This value can range between 0 and 1, with 0 indicating random movement and 1 indicating directed movement. Estimates of emigration rates were calculated as the proportion of crabs leaving the study area over 24 h. To determine microhabitat utilization, the habitat type (marsh vs. mud) was recorded for each individual at each resighting, and observations were stratified into two subsets defined by tidal height relative to the marsh surface

(flooded vs. exposed). The proportion of time spent in each microhabitat for individual crabs was then calculated separately for periods when the marsh was flooded and when the marsh was exposed at low tide. We tested separately whether or not the mean proportion of time spent in mud versus intertidal marsh varied for periods when the marsh was flooded or exposed using student's t-tests.

RESULTS

Population structure

The population of crabs within replicate tidal marsh creeks consisted mainly of small individuals ranging from 6 - 79 mm CW, and contained few crabs greater than 120 mm CW (Fig. 2). The size structure of crabs was similar between study sites, with small (0-39 mm CW) to medium (40 –79 mm CW) sized crabs dominating both populations throughout the study duration, composing 95% (range: 88 – 98%) of the total population in PC, and 93% (range: 88 – 97%) in HS. Sex ratios (M:F) were 0.94 at PC and 1.03 at HS, and did not differ significantly from 1:1 at either PC ($\chi^2 = 0.859$, $df = 1$, $p = 0.35$) or HS ($\chi^2 = 0.16$, $df = 1$, $p = 0.69$).

Goodness of fit and capture-recapture model selection

No significant lack of fit to the fully time-dependent JS model was observed for crab recapture data at either PC ($\chi^2 = 18.37$, $df = 11$, $p = 0.07$) or HS ($\chi^2 = 0.86$, $df = 3$, $p = 0.83$), indicating that model assumptions were probably met, and that the JS model framework was appropriate for both populations. Estimates of c-hat generated from GoF testing were 1.39 for PC and 0.34 for HS, and were used to calculate the $QAIC_c$. Since correcting for underdispersion (c-hat < 1) is not suggested, a c-hat of 1.0 was used for HS.

The full JS model allowing varying survival and capture probabilities over time, as well as reduced parameter models, were fitted to the capture-recapture histories of crabs for PC and HS separately. $QAIC_c$ values for PC and HS were then used to rank the models from the candidate model set (Appendix Table 2a, b). More complex models including covariates were then fitted to the capture-recapture data. The smallest $QAIC_c$ for PC was for a model with constant survival and time-specific probability of capture, where p was modeled as a quadratic function of length (CW) for the PC population (Appendix table 2a). Despite the lower $QAIC_c$ values for the models with covariates included, we chose to use the best fitting base model (ϕ, p_t) for the following reasons: (1) estimates of ϕ and p were similar in models with and without covariates (Appendix Table 3), (2) the relationships between size (CW) and model parameter estimates (ϕ, p) differed by study site (Appendix Fig. 1) and the predicted relationships could not be explained biologically, (3) limitations of the data set in which sufficient recapture data for a relatively large size range of crabs was lacking. For example, the majority of captured crabs (88-98%) were within a size range of 22 and 80 mm CW, resulting in a lack of data for both very small (crabs < 22 mm CW) and larger individuals (crabs > 80 mm CW). Thus, the relationships between estimated model parameters (ϕ, p) and size (CW) were poorly defined over a large range of sizes and did not justify using complex models including covariates. Because no single model clearly fitted the data better than another (Appendix table 3), model averaging was used to generate apparent survival and capture probabilities. For the HS population, the model with the best $QAIC_c$ assumed constant survival and time-specific capture probability, where survival was modeled as a linear function of CW, and probability of capture was modeled as a quadratic function of length

(CW; Appendix Table 2b, Appendix Fig. 1). As with PC, models with and without covariates generated similar estimates of survival and capture probability (Appendix Table 4) and the base model with the lowest $QAIC_c$ assumed constant survival and time-specific capture probability. Because the base model (ϕ, p_t) was strongly supported by the data (ΔQAICc values > 2 for all other models; Appendix table 2), model averaging was not required for HS.

Population size and demographic rates

Mean population size in PC ranged from 1,085 – 5,096 crabs over the course of the study (Table 2a) which was an order of magnitude larger than population estimates from HS (range: 102 – 270 crabs). Mean crab density at PC was 1.2 crabs/m^2 and ranged from 0.7 to 3.3 crabs/m^2 over time. Mean crab density at PC was an order of magnitude higher than HS (mean = 0.10 crabs/m^2 and ranged from a minimum of 0.05 to a maximum of 0.13 crabs/m^2).

Mean apparent survival probabilities (ϕ) for crabs residing in PC were 0.80 $\pm$ 0.06 (Table 2a), and 0.74 $\pm$ 0.03 (Table 2b) for crabs in HS. Estimates of tag retention (?) were used to correct estimates of survival (ϕ^c) and SEs for bias due to tag loss, and calculate unbiased estimates of survival probabilities ($\phi^c = \phi / \theta$). After correction, survival probabilities increased to 0.91 $\pm$ 0.08 for crabs at PC (Table 2a) and 0.84 $\pm$ 0.03 for crabs at HS (Table 2b). For comparison with estimated emigration rates (see below), which were daily probabilities, daily crab survival (ϕ_d) was calculated as $\phi_i = (\phi_d)^d$, where d is the time between sampling events in days. Mean daily survival probabilities corrected for tag loss were 0.98 d^{-1} $\pm$ 0.08 ($0.91 = 0.98^4$) for crabs at PC and 0.96 d^{-1} $\pm$ 0.03 ($0.84 = 0.96^4$) for crabs at HS. Coefficients of variation (CV = SE/estimate), which

describe the precision of survival estimates, were 0.09 for PC and 0.04 for HS, indicating relatively precise parameter estimates despite a low capture probability for PC (see below). Following correction for tag loss, apparent survival (ϕ^c = 1 – (mortality + emigration)) was partitioned using estimates of emigration from free-ranging blue crabs (see below) to calculate mortality.

The estimated emigration rate from PC was 0 individuals d^{-1}, and was 0.02 individuals d^{-1} in HS, resulting in roughly equal estimated survival rates for both creeks (PC = 0.98 + 0.0 = 0.98; HS = 0.96 + 0.02 = 0.98), since the probability of loss includes mortality and emigration. Estimates of capture probabilities were ~ 8 fold larger in HS, and were more precise at HS (CV range: 0.09 – 0.19) than at PC (CV range: 0.30 – 0.75). For example, mean recapture probability in PC was 0.06 $\pm$ 0.02 per sampling period, and was time-specific, ranging from 0.02 to 0.17 among sampling intervals for PC (Table 2a). Mean recapture probability in HS was 0.46 $\pm$ 0.10 per sampling period (Table 2b), and ranged from 0.15 to 0.73.

Tag retention and tag-induced mortality

Proportional mortality of juvenile blue crabs in the laboratory was low in both tagged (7%) and control (13%) treatments, and was not significantly different between treatments (χ^2 = 0.28, *df* = 1, p = 0.60). Of the 15 tagged individuals, 13 retained the tag through the entire experiment (37 d) for an overall tag retention of 88% (Table 1). In both cases in which tags were shed, tag loss occurred during the first molt following tagging. All crabs that retained the tag through the first molt retained the tag through all subsequent molts. Mean time to first molt was not significantly different (student's t-test, t = 0.08, *df* = 28, p = 0.77) between tagged (5.9 d $\pm$ 0.5) and control (6.1 d $\pm$ 0.5)

treatments. The intermolt period between first and second molts was also not significantly different (student's t-test, t = 1.41, *df* = 1,17, p = 0.25) between tagged (12.7 d $\pm$ 0.8) and control (14.3 d $\pm$ 1.1) treatments. Proportional size increases were not significantly different between tagged and control treatments after the first molt (student's t-test, t = 0.35, *df* = 1,28, p = 0.56), but marginally significant after the second molt (student's t-test, t =3.61, *df* = 1,17, p = 0.08; Table 1), with size increases in the tagged treatment being higher than in the control. This result is likely spurious since tagging would likely have a negative impact on growth.

Movement in the field

Emigration rates of crabs from tidal creeks were extremely low (0.02 crabs d^{-1}, for HS, and 0 crabs d^{-1} for PC), indicating high site fidelity of juvenile crabs to individual tidal marsh creeks during summer. The mean total distance that crabs moved in tidal marsh creeks was 19 m for PC (range: 6 – 48 m) and 25 m for HS (range 4 – 50 m). Mean net movement was 12 m for PC (range: 6 – 23 m) and 18 m for HS (range: 4 – 37 m). The index of meander was 0.68 for PC, and 0.73 for HS, indicating juvenile crabs exhibited relatively directed movement over a period of one day. Movement speeds were slow, and averaged 0.77 m h^{-1} and 1.09 m h^{-1} for PC and HS, respectively, and reflected the tendency of crabs to bury into the mud during ebb tide.

Relocation observations were also used to calculate the proportion of time individual crabs spent in either the *Spartina alterniflora* marsh surface or unvegetated muddy creek during flood vs. ebb tidal stages. When the marsh was flooded at high tide, crabs utilized the vegetated marsh surface significantly more often than the adjacent muddy creek habitats in both PC (student's t-test, t = 5.09, *df* = 29, p < 0.001) and HS

(student's t-test, t = 3.862, *df* = 34, p < 0.001; Fig. 3). When the marsh was exposed at low tide, there was no significant difference in the proportion of time crabs spent in the marsh versus muddy creek bottom (Fig 3), indicating that ~50% of the tagged crabs remained buried in mud within the vegetated marsh surface at low tide.

DISCUSSION

Capture-recapture techniques using microwire tags are a powerful tool for estimating demographic rates and habitat use of mobile animals, information that is key to identifying the nursery role of a given estuarine habitat. The key findings from these complementary field and laboratory experiments were: (1) mean density of juvenile blue crabs was an order of magnitude higher at Prytherch Creek than the Haystacks salt marsh creek, (2) survival was similar between sites, and subtle differences in daily probabilities of loss only partially explained the order of magnitude differences in mean crab density (see below), (3) microwire tagging had negligible effects on crab growth and mortality, (4) juvenile crabs displayed very little emigration from a given salt marsh creek, (5) crabs took refuge in the vegetated marsh surface during flood tide and often buried in mud during exposure of the marsh at during ebb tide. The results from this study indicate relatively high survival of juvenile blue crabs in salt marsh creeks, but it appears that the same habitat type can harbor strikingly different densities of crabs. This might be due to differences in proximity to sources of postlarval and early juvenile recruits ingressing through nearby Beaufort Inlet (Fig. 1), as well as to tidal creek morphology, which provided more marsh edge at PC than HS (see below). The extent of potential differences in crab density in similar marsh habitats is still not clear since inferences from

this study are based on only two replicate creeks. While there are many studies that report estimates of population density, mortality rates, or movement rates for blue crabs, this study represents one of the first attempts to estimate all quantities concurrently. Concurrent estimates of the probability of and loss and emigration allowed for survival to be explicitly estimated. It is also one of several studies to apply capture-recapture techniques to juvenile blue crabs, and the first to allow for the identification of individual crabs, as well as attempting to account for size-specific variation in capture and loss probabilities. Identification of individuals if necessary for incorporating covariates into capture-recapture models.

Assumptions of the Jolly-Seber model

Meeting the assumptions of capture-recapture models is critical to ensuring unbiased parameter estimates, and is requisite to designing capture-recapture experiments (Pollock & Mann 1983). Below, we consider the assumptions of the JS capture-recapture model (see Methods) employed in this study, and the degree to which these assumptions may have been violated. If tagged individuals are more likely to be captured than untagged individuals, these individuals will be more likely to be subsequently recaptured, which will lead to an underestimation of population size since tagged individuals constitute a greater proportion of recaptured individuals than in the overall population under study. Conversely, if tagged individuals are less likely to be recaptured than untagged individuals, then population size will be overestimated. In the present study, we used a beam trawl to capture crabs within each study site. It is unlikely that the capture probabilities of tagged and untagged individuals differed because the efficiency of capture by actively trawling should be independent of tag status. Additionally, the

shortest interval between sampling periods was 4 d, which should have been sufficient to allow for mixing of tagged and untagged individuals. A previous tagging study using blue crabs reported adequate mixing after only several days (Fitz & Wiegert 1992).

Although the presence or absence of a tag is unlikely to affect capture rates, aspects of the ecology of blue crab and the large variations in size likely generated heterogeneous capture probabilities. Larger blue crabs are capable of faster movement rates, and may be more likely to evade sampling by the beam trawl than smaller crabs. This assertion was supported by field observations in which net avoidance by larger individuals was observed. Similarly, the smallest crab sizes are not sampled as effectively as larger crabs by trawl gear (Orth and van Montfrans 1987), leading to reduced capture probabilities for the smallest crabs. We attempted to address differences in capture probabilities directly by the inclusion of length as a covariate, which would allow explicit estimation of capture probabilities as a function of length. The relationship of length and capture probability was best described by a quadratic function in both study populations (Appendix fig. 1), but was generally an increasing function of size (CW) at PC and generally decreasing with size (CW) at HS (Appendix Fig. 1). We could find no biological justification for the different observed patterns between capture probability and size at PC and HS, and lacked sufficient data for both small (<22 mm CW) and large (>80 mm CW) to adequately model this complex relationship. Although our data did not justify the inclusion of covariates, factors such as body size may affect capture probabilities, and we encourage the use of covariates to investigate this potential relationship in future studies whenever feasible.

Survival rates are assumed constant for each tagged animal in the population. If

tagging causes reduced survival of tagged animals, then survival rates will be underestimated. Laboratory studies (van Montfrans et al. 1986, Fitz & Wiegert 1991, this study) demonstrated that microwire tagging has negligible effects on survival. Mortality rates are likely to vary as a function of body size since larger individuals attain a relative refuge from predation with size (Hines & Ruiz 1995). Smaller individuals also molt more frequently than larger crabs, and are particularly vulnerable to increased predation immediately following molting while in a soft-shell state (Ryer et al. 1997). Conversely, survival of large crabs may be underestimated since large crabs are capable of relatively large daily movements (e.g. mean 131 m d^{-1}; range: 0 – 569 m d^{-1} ; Wolcott & Hines 1990), and are more likely to emigrate from study populations than smaller crabs. While we used body size as a covariate to assess size-specific differences in survival, a decrease in mortality with size may be balanced by an increase in emigration with size. The loss rates estimated in this study likely represent mainly mortality, however, since smaller crabs composed 88 – 98% of the study populations, and emigration rates for these sizes were extremely low. As with capture probabilities, our data did not justify the inclusion of covariates to explain the relationship between size (CW) and survival.

The effects of tag loss include both direct and indirect consequences on parameter estimation. Most important is that tag loss will result in fewer recaptures, and consequently survival will be underestimated. Our estimate of tag retention (88%) was similar to rates reported by van Montfrans (1986), but lower than those (96 - 98%) obtained by Fitz & Wiegert (1991). High tag retention (Fitz & Wiegert 1991) was likely a factor of the larger size of crabs used in their experiment (46.4 mm CW) versus this study (27.6 mm CW). Both cases of tag loss in the present study were associated with

the first molt following tagging, and occurred in the smallest individuals. In this study, most tagged crabs were less than 40 mm CW and therefore survival estimates were corrected for tag loss (Arnason and Mills 1981).

Population size and demographic rates

Mean densities of blue crabs in this study (0.7 – 3.3 crabs m^{-2} for PC and 0.04 – 0.10 crabs m^{-2} for HS) were generally similar to available estimates from other salt marsh systems along the U.S. east coast during summer-fall: 0.4 – 4.8 crabs m^{-2} (Orth & van Montfrans 1987), 0.08 – 0.15 crabs m^{-2} (van Montfrans et al. 1991), and 0.2 crabs m^{-2} (Fitz & Wiegert 1992). Estimates of population densities are often difficult to obtain because they require that the sampling efficiency and selectivity of the sampling gear be known for a given species. Assuming catch efficiencies less than 100% (i.e., not all animals present are captured), densities will be underestimates of true abundance. Catch efficiency for the blue crab has been estimated for dredges (Voelstad et al. 2000), trawls (Orth & van Montfrans 1987) and suction sampling (Orth and van Montfrans 1987), but interactions between gear type (Kneib 1997, Rozas and Minello 1997), habitat (Rozas and Minello 1997), and tidal stage (Kneib & Wagner 1994) make direct comparisons difficult. JS models allow for estimation of capture efficiency and provide an alternative method for estimating density.

The populations in both PC and HS were consistently dominated by smaller size classes (0-39 mm CW). This is in contrast to patterns of relative abundance reported for blue crab populations elsewhere, in which larger crabs were most common. In salt marsh habitats in Georgia, crab sizes ranging from 51 - 125 mm CW predominated (Fitz & Wiegert 1992a,b) and in Chesapeake Bay, crab sizes ranging from 50 - 99 mm CW were

most abundant (van Montfrans et al. 1991). Differences in sampling regimes likely explain the differences in relative abundance observed in the present study versus the previous studies (van Montfrans et al. 1991, Fitz & Wiegert 1992b). In contrast to Fitz & Wiegert (1992b), who sampled exclusively in subtidal habitats (minimum depth 1.5 m), and van Montfrans (1991), who used block nets to capture crabs before they buried at low tide and uncovered buried crabs by hand at low tide, we sampled areas immediately adjacent to the marsh edge, and continuously sampled shallow habitats (<0.1 m) until the study sites had completely drained at low tide. This method of sampling appeared to preferentially catch smaller crabs found in these shallow areas. For example, our continuous tracking of individual crabs found smaller crab size classes utilized intertidal habitats almost exclusively, and rarely moved into subtidal areas. Furthermore, an inverse relationship between crab size and distance from unvegetated habitats was reported by Arnold & Kneib (1983), with smaller individuals concentrated on the marsh surface relative to large crabs that were restricted mainly to the marsh edge at high tide (Kneib 1995).

One striking feature of our blue crab density estimates was that those in HS were an order of magnitude lower than those in PC. This pattern of abundance may be explained by several factors affecting additions and losses to the local population. The most parsimonious explanation was the higher probability of loss for HS relative to PC. Overall, daily probabilities of loss between sites were similar (PC = 0.98 vs HS = 0.96), but could lead to differences in local population size over relatively short time scales. For instance, assuming no recruitment, a cohort at PC would be reduced to 55% of initial abundance after one month (0.98^{30}), whereas an identical cohort at HS would be reduced

to 29% (0.96^{30}) over 30 days. This roughly two-fold expected difference in crab abundance between PC and HS after 30 days, however, is not sufficient to explain the order of magnitude difference in crab density observed between PC and HS. Differential recruitment between sites may also explain the observed differences in density between PC and HS. PC is located closer to Beaufort Inlet (Fig.1), the likely source of emigrating megalopae to both study areas, and in close proximity to a high flow channel (Hettler and Chester 1990). Differences in the spatial scale and morphology of the tidal creeks may also have led to increased densities at PC relative to HS. The PC site was smaller, composed of many pools and rivulets, and had a greater percentage of edge microhabitat relative to HS. Survival of blue crabs is higher along marsh edge microhabitats than the central channel of tidal creeks, and higher in a small tidal creek compared to a large one (Ryer et al. 1997).

The probability of crab loss (mortality + emigration) observed in our study (2 – 4% crabs d^{-1}) was similar to previous reported estimates for blue crabs using mark-recapture techniques in Chesapeake Bay during summer (van Montfrans et al. 1991; 5.7 – 8.2% d^{-1}), and to the highest loss rates observed in Georgia (Fitz & Wiegert 1992b; 40% biweekly ≈ 3% daily). Loss probabilities for blue crabs in tidal marsh creeks in this study indicate that loss is relatively constant over summer and early fall (June – October), as seems to be the case in Chesapeake Bay tidal creeks (van Montfrans et al. 1991, Ryer et al. 1997). Juvenile crabs in this study displayed a high degree of site fidelity to individual tidal creek systems during summer. Although movement rates of crabs in this study were lower than those reported previously (Wolcott & Hines 1990, Hines et al.1995), it was not surprising given the relatively small size of individuals in this study.

The low rates of emigration for juvenile crabs (35 – 67 mm CW) were in contrast to previous studies on early post-settlement blue crabs (2.1 – 9.1 mm CW) in NC, which reported high rates of emigration (Etherington et al. 2003). While ontogenetic changes in blue crab behavior may explain the lower rates of emigration in this study, the different emigration rates may also be explained by differences in the spatial and temporal scale of the experiments. The earlier study (Etherington et al. 2003) was conducted at a spatial scale of 1 m^2 for a period of 24 h, while this study was conducted at a scale of 2,000 – 3,000 m^2 for a period of months. Further, density-dependent emigration of early juvenile benthic instars (J1-J2; Reyns and Eggleston *In prep*) may also explain the reduced emigration rates in our study since our densities (0.1 – 1.2 crabs m^2) were an order of magnitude smaller than those in the earlier study (16 and 64 crabs m^2; Etherington et al. 2003).

Utilization of marsh habitats

Juvenile crabs moved onto the marsh surface at high tide, a pattern consistent with earlier observations of habitat utilization in this species (Kneib & Arnold 1983, Fitz & Wiegert 1991, Kneib 1995). Crabs in this study were found in association with the marsh edge, and rarely traveled more than 3 m into the marsh. While the method of tagging crabs using floats attached to the dorsal carapace likely impeded travel through the heavily vegetated marsh, Kneib (1995) found that crabs rarely migrated far onto the marsh surface. Additional evidence that blue crabs migrate only partially into the marsh vegetation during high tide comes from data on predation rates by blue crabs on ribbed mussels (*Geukensia dismissa*; Stiven & Gardner 1992) and periwinkle snails (*Littorina irrorata*; Lewis & Eby 2002), which decreased with intertidal elevation. Several authors

have recognized the value of salt marshes as a refuge for juvenile fishes and crustaceans from predators (Boesch & Turner 1983, Zimmerman & Minello 1984, Rozas & Zimmerman 2000, Minello et al. 2003). Juvenile crabs may experience a spatial refuge from cannibalism in the vegetated marsh since adult conspecifics are physically impeded by dense vegetation and rarely move far into marsh habitats (Arnold & Kneib 1983, Kneib 1995, Kneib 1997). This spatial refuge in the vegetated marsh surface from larger conspecifics may be significant, since a majority of blue crab mortality in previous studies has been attributed to cannibalism (Dittel et al. 1995, Hines & Ruiz 1995, Ryer et al. 1997). The marsh surface may also provide refuge to juvenile crabs by the exclusion of transient finfish predators that are known to invade inundated marsh creeks at high tide (Helfman et al. 1983, Rountree & Able 1992, Szedlmayer & Able 1993).

As the marsh became exposed at low tide, crabs buried within the marsh and unvegetated creek bottom. Burying behavior has been described for various life stages of the blue crab (Wilson et al. 1987, van Montfrans 1991, Tankersley & Forward 1994). This behavior may represent a trade-off between predation risk and foraging behavior (Gilliam & Fraser 1987, Dahlgren & Eggleston 2000). Risk of predation in subtidal areas is likely increased, since greater densities of crabs are concentrated in subtidal habitats at low tide. Since crabs cannot actively forage while buried, the decreased risk of predation associated with burial may outweigh the benefits of continuous feeding. The ecological processes underlying size- and tide-specific habitat use of the marsh surface by juvenile crabs is unknown.

The patterns of high survival and densities of blue crabs within tidal salt marsh creeks reported here are consistent with the conclusions of Minello et al. (2003), who

found salt marshes to be important nursery areas for decapod crustaceans, and this study provides additional information on the demographic processes underlying the importance of salt marshes as nurseries for estuarine-dependent species. Moreover, relatively high use of the vegetated marsh surface by juvenile blue crabs, combined with a general lack of sampling these complex habitats, suggest that crab densities may be even higher in salt marsh systems than previously thought.

ACKNOWLEDGMENTS

We thank the many graduate and undergraduate students and technicians for assistance in field and laboratory experiments. Special thanks are required to J. Buckel, H. Johnson, G. T. Kellison, N. Reyns and S. Searcy for their assistance in the field. We thank J. van Montfrans and the Virginia Institute of Marine Science for access to the microwire tagging equipment, and for providing technical training. We thank K. Pollock for statistical advice on capture-recapture modelling, and J. Hightower for comments on earlier drafts of this manuscript. We thank G.T. Kellison and C. Taylor for generating the map of the study sites. Funding for this research was provided by the North Carolina Sea Grant Fishery Resource Grant Program (99-FEG-10 and 00-FEG-11), NSF grant (OCE-97-34472) to D. E., and the PADI foundation to E. J.

LITERATURE CITED

Akaike H (1973) 2nd International Symposium on Information Theory, Chapter Information theory and an extension of maximum likelihood principle, pp. 267-281. Budapest: Akademia Kiado.

Arnason AN, Mills KH. (1981) Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark-recapture experiments. Can J Fish Aquat Sci 381:1077-1095

Arnold WS, Kneib RT (1983) The size distribution of blue crabs (*Callinectes sapidus* Rathbun) along a tidal gradient in a Georgia salt marsh. Georgia J Sci 41:93-94

Beck MW, Heck KL, Able K, Childers D, and 9 others (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51:633-641

Bell GW, Eggleston EG, Wolcott, TG (2003) Behavioral responses of free-ranging blue crabs to episodic hypoxia: I. Movement. Mar Ecol Prog Ser 259:215-225

Boesch DF, Turner RE (1984) Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7:460-468

Burnham KP, Anderson DR, White GC, Brownie C, Pollock KH (1987). Design and analysis methods for fish survival experiments based on release-recapture. Am Fish Soc Monogr 5

Cooch E, White G (2001) Using MARK – a gentle introduction (2^{nd} edition)

Cormack RM (1964) Estimates of survival from the sighting of marked animals. Biometrika 51:429-438

Dahlgren CP, Eggleston DB (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology 81(8):2227-2240

Eggleston DB, Lipcius RN, Hines AH (1992) Variation in density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. Mar Ecol Prog Ser 85:55-68

Etherington LL, Eggleston DB (2000) Large-scale blue crab recruitment: Linking postlarval transport, post-settlement planktonic dispersal, and multiple nursery habitats. Mar Ecol Prog Ser 204:179-198

Etherington LL, Eggleston DB (2003) Spatial dynamics of large-scale, multi-stage crab (Callinectes sapidus) dispersal: determinants and consequences for recruitment. Can J Fish Aquat Sci 60(7):873-887

Etherington, LL, Eggleston DB, Stockhausen, WT (2003) Partitioning rates of early juvenile blue crabs from seagrass habitats into mortality and emigration components. Bull Mar Sci 72(2):371-391

Fitz HC, Wiegert RG (1991) Tagging juvenile blue crabs, *Callinectes sapidus*, with microwire tags: retention, survival, and growth through multiple molts. Bull Mar Sci 11:229-235

Fitz HC, Wiegert RG. (1992a) Utilization of the intertidal zone of a salt marsh by the blue crab *Callinectes sapidus*: density, return frequency, and feeding habits. Mar Ecol Prog Ser 86:249-260

Fitz HC, Wiegert RG. (1992b) Local population dynamics of estuarine crabs: abundance, recruitment and loss. Mar Ecol Prog Ser 87:23-40

Gilliam JF, Fraser DF (1987) Habitat selection under predation hazard: Test of a model with foraging minnows. Ecology 68(6)1856-1862

Helfman GS, Stoneburner DL, Bozeman EL, Christian PA, Whalen R (1983) Ultrasonic telemetry of American eel movements in a tidal creek. Trans Amer Fish Soc 112:105-110

Horvitz, DG, Thompson, DJ (1952) A generalization of sampling without replacement from a finite universe. J. Amer. Stastist. Assoc., 47, 663-685

Helser TE, Kahn.DM (1999) Stock assessment of Delaware Bay blue crab (*Callinectes sapidus*) for 1999. Dept. of Natural Resources, Delaware Division of Fish and Wildlife, 89 Kings Highway, Dover DE 19901

Hettler WF, Chester AJ (1990) Temporal distribution of ichthyoplankton near Beaufort, Inlet, North Carolina. Mar Ecol Prog Ser 68:157-168

Hines AH, and Ruiz GM (1995) Temporal variation in juvenile blue crab mortality: nearshore shallows and cannibalism is Chesapeake Bay. Bull Mar Sci 57:884-901

Jolly GM (1965) Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52:225-247

Kneib RT (1997) The role of tidal marshes in the ecology of estuarine nekton. Ansell AD, Gibson RN, Barnes M (eds) Oceanography and Marine Biology: an Annual Review 35:163-220, UCL Press

Kneib RT (1995) Behavior separates potential and realized effects of decapod crustaceans in salt marsh communities. J Exp Mar Biol Ecol 193:239-256

Kneib RT, Wagner SL (1994) Nekton use of vegetated marsh at different stages of tidal inundation. Mar Ecol Prog Ser 106(3):227-238

Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: case studies and recent advances. Ecol Monogr 62:67-118

Lewis DB, Eby LA (2002) Spatially heterogeneous refugia and predation risk in intertidal salt marshes. Oikos 96(1):119-129

Lipcius RN, Stockhausen W (2002) Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay Mar Ecol Prog Ser 226:45-61

Manly BFJ (1984) Obtaining confidence limits on parameters of the Jolly-Seber model for capture-recapture data. Biometrics 40:749-758

Miller TJ, Houde ED (1998) Blue crab target setting. Final Report for Living Resources Subcommittee, Chesapeake Bay Program, U.S. EPA, 410 Severn Ave., Annapolis, MD 21403

Minello TJ, Able KW, Weinstein MP, Hays CG (2003) Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. Mar Ecol Prog Ser 246:39-59

Nixon SW (1980) Between coastal marshes and coastal waters – a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. In:Hamilton P, MacDonald KB (eds) Estuarine and wetland processes. Plenum, New York

Olmi III EJ, Bishop JM (1983) Variations in total width-weight relationships of blue crabs, *Callinectes sapidus*, in relation to sex, maturity, molt-stage, and carapace form. J Crust Biol 3(4):575-581

Orth RJ, 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*. Mar Ecol Prog Ser 231:205-213

Orth RJ, 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. Mar Ecol Prog Ser 41:283-294

Pollock KH (1981) Capture-recapture models allowing for age-dependent survival and capture rates. Biometrics 37:521-529

Pollock KH, Mann HK (1983) Use of an age-dependent mark-recapture model in fisheries research. Can J Fish Aquat Sci 40:1449-1455

Pollock KH, Nichols JD, Brownie C, Hines JE (1990) Statistical inference for capture-recapture experiments. Wildlife Monographs 107

Rountree RA and Able KW (1992) Foraging habits, growth, and temporal patterns of salt-marsh creek habitat use by young-of-the-year summer flounder in New Jersey. Trans Amer Fish Soc 121:765-776

Rozas LP, McIvor CC, Odum WE (1988) Intertidal rivulets and creekbanks: corridors between tidal creeks and marshes. Mar Ecol Prog Ser 47:303-307

Rozas LP, Minello TJ (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 LP, Zimmerman RJ (2000) Small-scale patterns of nekton use among marsh and adjacent shallow nonvegetated areas of the Galveston Bay estuary, Texas (USA). Mar Ecol Prog Ser 193:217-239

Ryer CH. (1987) Temporal patterns of feeding by blue crabs (*Callinectes sapidus*) in a tidal marsh creek and adjacent seagrass meadow in the lower Chesapeake Bay. Estuaries 10:136-140

Ryer CH, van Montfrans J, Moody KE (1997) Cannibalism, refugia and the molting blue crab. Mar Ecol Prog Ser 147:77-85

Seber GA (1965) A note on the multiple recapture census. Biometrika 52:249-259

Seitz RD, Lipcius RN, Hines AH, Eggleston DB (2001) Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. Ecology 82(9):2435–2451

Stiven AE, Gardner SA (1992) Population processes in the ribbed mussel *Geukensia dismissa* (Dillwyn) in a North Carolina salt marsh tidal gradient: spatial pattern, growth and mortality. J Exp Mar Biol Ecol 160:81-102

Szedlmayer ST, Able KW (1993) Ultrasonic telemetry of age-0 summer flounder, *Paralichthys dentatus*, movements in a southern New Jersey estuary. Copeia 1993:728-736

Tankersly RA, Forward, Jr RB (1994) Endogenous swimming rhythms in estuarine crab megalopae: Implications for flood-tide transport. Mar Biol 118(3):415-423

van Montfrans J, Capelli J, Orth RJ, Ryer CH (1986) Use of microwire tags for tagging juvenile blue crabs (*Callinectes sapidus* Rathbun). J Crust Biol 6(3):370-376

van Montfrans J, Ryer CH, Orth RJ (1991) Population dynamics of the blue crab *Callinectes sapidus* Rathbun in a lower Chesapeake Bay tidal marsh creek. J Exp Mar Bio Ecol 153:1-14.

Voelstad JH, Sharov AF, Davis G, Davis B (2000) A method for estimating dredge catching efficiency for blue crabs, *Callinectes sapidus*, in Chesapeake Bay. Fish Bull 98(2):410-420

Werner EE, Mittlebach GG, Hall DJ, Gilliam JF (1983) Experimental tests of optimal habitat use in fish: The role of relative habitat profitability. Ecology 64(6):1525-1539

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46[Suppl]:120-138

Weisberg SB, Whalen R, Lotrich VA (1981) Tidal and diurnal influence on food consumption of a salt marsh killifish *Fundulus heteroclitus*. Mar Biol 61:243-246

Wilson KA, Heck KL, Able, Jr. KW (1987) Juvenile blue crab, Callinectes sapidus, survival: An evaluation of eelgrass, *Zostera marina*, as refuge. Fish Bull 85(1):53-58

Wolcott TG, Hines AH (1990) Ultrasonic telemetry of small-scale movements and microhabitat selection by molting blue crabs (*Callinectes sapidus*). Bull Mar Sci 46(1):83-94

Zimmerman RJ, Minello TJ (1984) Densities of *Penaeus aztecus*, *Penaeus setiferus*, and other natant macrofauna in a Texas salt marsh. Estuaries 7:421-433

Table 1. Mean (± SE) initial and final juvenile blue crab carapace width, mortality, tag retention estimates, and first and second molt increments for tagged and untagged (control) crabs using coded microwire tags in a laboratory experiment. N = 15 crabs tagged and 15 crabs untagged (control). Overall tag retention was not applicable (N/A) to control groups since they did not receive a microwire tag.

	Tagged	Control
Initial CW (mm)	27.58 ± 1.16	27.99 ± 0.88
Final CW (mm)	41.28 ± 1.64	39.86 ± 1.95
Mortality (%)	7	13
Time to first molt (d)	5.93 ± 0.53	6.13 ± 0.46
(Overall tag retention (%))	88	N/A
Time between first and second molts (d)	12.70 ± 0.84	14.33 ± 1.11
(Tag retention between first and second molts (%))	100.00	N/A
Size increase at first molt (%)	26.7 ± 0.9	25.8 ± 1.2
Size increase at second molt (%)	28.9 ± 0.9	26.4 ± 1.0

Table 2. Estimates and approximate standard errors of juvenile blue crab population size (N), survival (ϕ), and capture probabilities (p) for populations in Prytherch Creek (A) and Haystacks (B) using Jolly-Seber capture-recapture models. Estimates of tag retention (?) were used to correct estimates of survival and SEs for bias due to tag loss, and calculate unbiased estimates ($\phi_i^c = \phi_i / \theta$).

A.) Prytherch Creek

Date	Period	N_i	SE	ϕ_i	SE	ϕ_i^c	SE	p_i	SE
June 11	1								
June 15	2	1,085						0.17	0.05
June 19	3	1,968						0.05	0.02
June 23	4	1,447						0.10	0.03
June 27	5	1,216		0.80	0.06	0.91	0.08	0.05	0.02
July 1	6	1,866						0.04	0.02
July 5	7	1,402						0.03	0.02
July 9	8	1,548						0.03	0.02
July 13	9	5,096						0.02	0.01
July 17	10	2,265						0.03	0.02
	$\bar{x}$			0.80	0.06	0.91	0.08	0.06	0.02

B.) Haystacks

Date	Period	N_i	SE	ϕ_i	SE	ϕ_i^c	SE	p_i	SE
August 22	1								
August 28	2	270						0.54	0.10
August 31	3	260		0.74	0.03	0.84	0.03	0.32	0.05
September 7	4	228						0.15	0.05
September 18	5	152						0.55	0.14
October 1	6	102						0.73	0.20
	$\bar{x}$			0.74	0.03	0.84	0.03	0.50	0.05

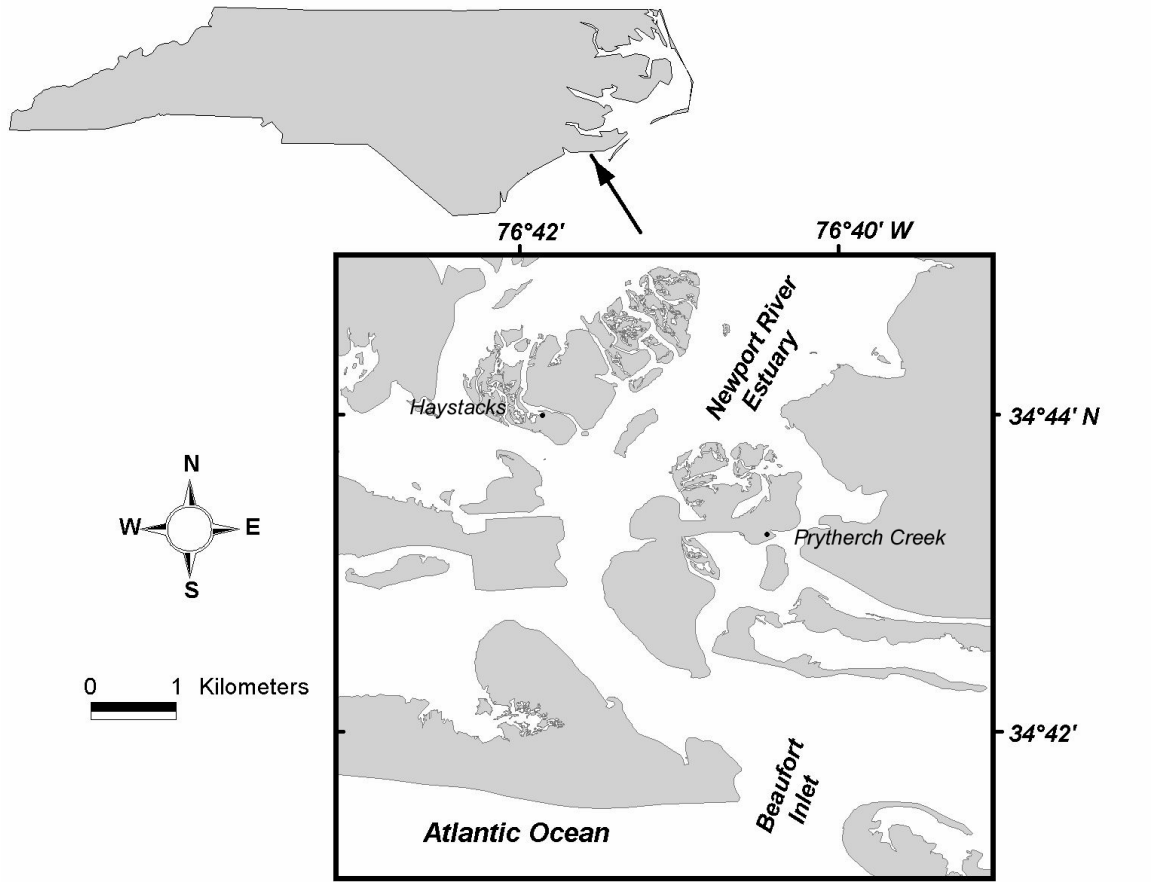


Figure 1. Locations of salt marsh creek study sites at Prytherch Creek (PC) and Haystacks (HS) near Beaufort Inlet, North Carolina, USA.

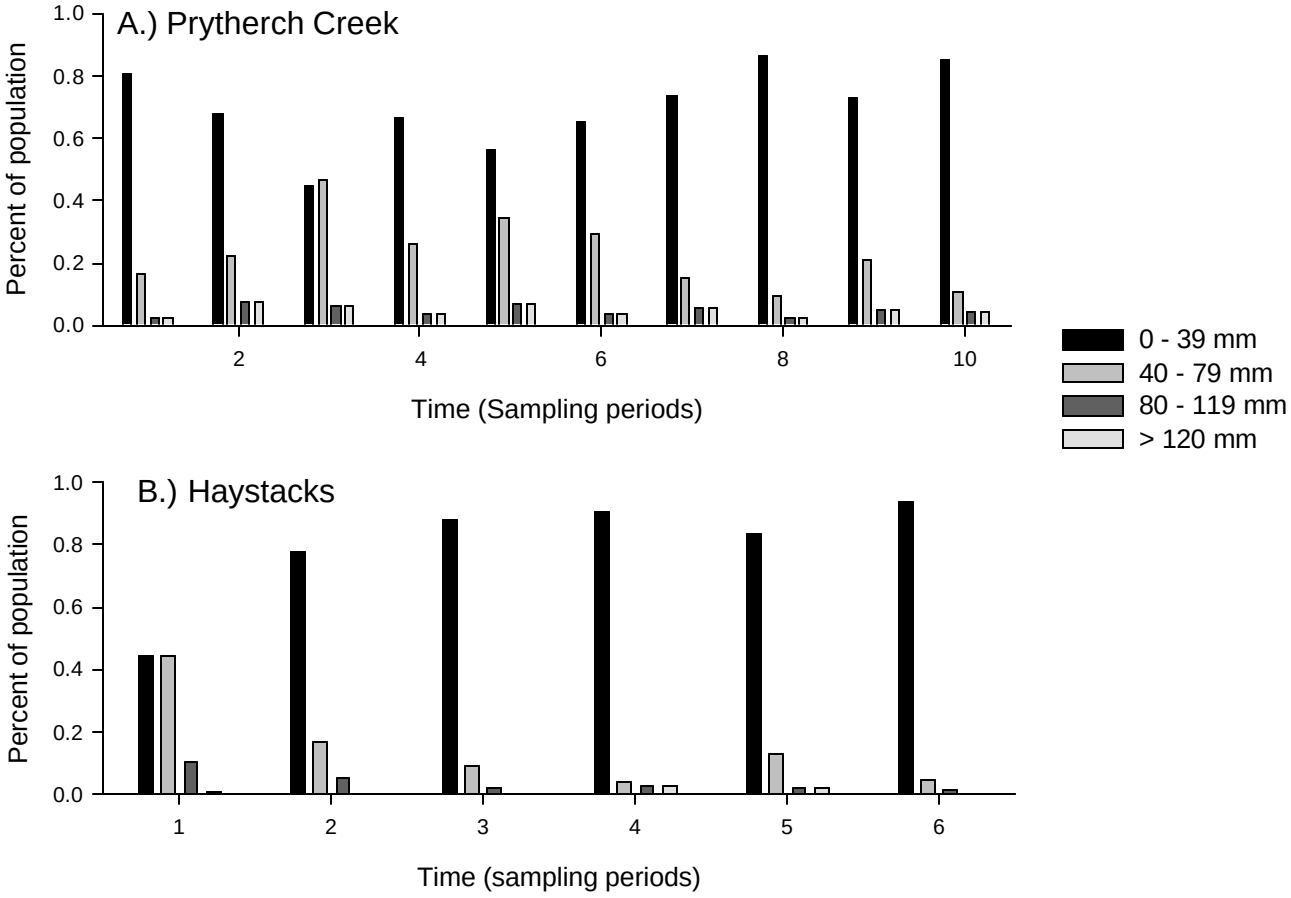


Figure 2. Proportional abundance of four size classes of blue crabs in both Prytherch Creek (A) and Haystacks (B) study sites for each sampling period. The duration between sampling periods averaged 4 d for Prytherch Creek and 7.8 d for Haystacks.

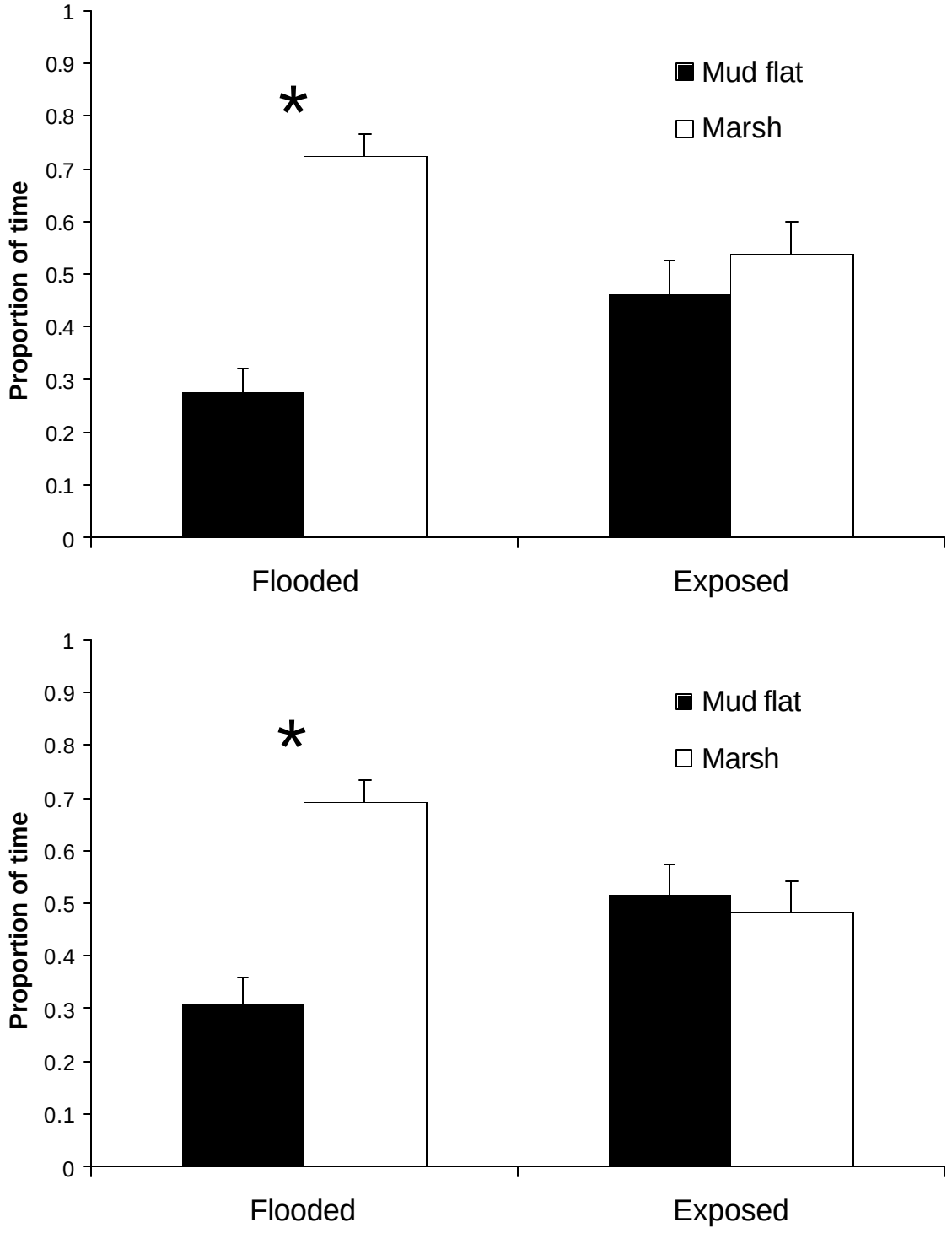


Figure 3. The mean proportion ± SE of time spent in microhabitat types (marsh and mud) during periods in which the marsh was tidally flooded or exposed at Prytherch Creek (A) and Haystacks (B) study sites.

Appendix Table 1. Capture-recapture summary statistics for populations of blue crabs at Prytherch Creek (A) and Haystacks (B) from June to October 2001, following standard Jolly-Seber capture-recapture notation (Jolly 1965): n_i is the number of crabs captured in the ith sample; m_i is the number of tagged blue crabs captured in the ith sample; R_i is the number of crabs captured in i and released; r_i is the number of crabs released at i and subsequently recaptured; z_i is the number of crabs captured before i, but not at i, that are subsequently recaptured.

A.) Prytherch Creek

Date	Period	n_i	m_i	R_I	r_i	z_i
June 11	1	115		115	31	
June 15	2	188	16	172	21	15
June 19	3	100	10	90	17	26
June 23	4	138	21	107	10	22
June 27	5	65	13	52	7	19
July 1	6	83	10	73	4	16
July 5	7	49	8	41	3	12
July 9	8	52	7	45	1	8
July 13	9	104	4	100	3	5
July 17	10	78	8	70		

B.) Haystacks

Date	Period	n_i	m_i	R_I	r_i	z_i
August 22	1	79		79	24	
August 28	2	145	21	124	41	3
August 31	3	82	33	49	7	11
September 7	4	34	8	26	8	10
September 18	5	83	14	69	15	4
October 1	6	74	19	55		

Appendix Table 2. Quasi-adjusted Aikaike's Information Criterion (QAICc), ? $QAIC_c$, Aikaike's weights, and number of parameters (*Np*) from JS capture-recapture models for Prytherch Creek (A) and Haystacks (B) sampling sites. Models are grouped into those that did not incorporate covariates (base models) and those that included covariates. Models were sorted by QAICc with best fitting models having the lowest $QAIC_c$ values. The model used for each site is bolded. While many models including covariates produced lower QAICc values, these models were not selected due to limitations in size range of crabs in the data set.

A.) Prytherch Creek

Model	Survival (ϕ)	Recapture (p)	$QAIC_c$	? $QAIC_c$	$QAIC_c$ weight	Model likelihood	Np	Qdeviance
I. Base models								
1	**Constant**	**Time**	**624.8**	**3.4**	**0.06**	**0.17**	**10**	**604.6**
2	Time	Constant	626.5	5.1	0.03	0.08	8	610.3
3	Constant	Constant	628.1	6.7	0.01	0.03	2	624.1
4	Time	Time	638.2	16.8	0.00	0.00	18	601.3
II. Models including covariates								
5	Constant	Time; quadratic	621.4	0	0.35	1	12	597.0
6	Constant	Time; linear	622.1	0.7	0.24	0.69	11	599.8
7	Constant; linear	Time; quadratic	623.4	2	0.13	0.37	13	596.9
8	Constant; quadratic	Time; quadratic	623.9	2.5	0.1	0.29	14	595.3
9	Constant; linear	Time; linear	624.2	2.8	0.09	0.25	12	599.8

B.) Haystacks

Model	Survival (ϕ)	Recapture (p)	$QAIC_c$	? $QAIC_c$	$QAIC_c$ weight	Model likelihood	Np	Qdeviance
I. Base models								
1	**Constant**	**Time**	**527.3**	**5.2**	**0.03**	**0.07**	**6**	**515.1**
2	Time	Time	531.0	8.8	0.00	0.01	10	510.3
3	Time	Constant	531.8	9.7	0.00	0.00	6	519.6
4	Constant	Constant	544.2	22.1	0.00	0.00	2	544.2
II. Models including covariates								
5	Constant; linear	Time; quadratic	522.2	0	0.4	1	9	503.6
6	Constant	Time; quadratic	522.9	0.7	0.27	0.69	8	506.5
7	Constant; quadratic	Time; quadratic	524.1	1.9	0.15	0.39	10	503.4
8	Constant	Time; linear	524.2	2	0.14	0.36	7	509.9

Appendix Table 3. Apparent survival (ϕ) and capture probabilities (p) from Jolly-Seber (JS) capture-recapture models for Pytherch Creek. Models are grouped into those that did not incorporate covariates (base models) and those that included covariates. The descriptors in parenthesis indicate whether a parameter was held constant (c) or allowed to vary (t) over time, and whether a parameter was a linear or quadratic function of size (carapace width; mm). No values for ϕ and p are presented for the final period (i = 10) since these values are confounded and can not estimated individually (see Lebreton et al. 1992).

Base models (no covariates)

phi (c), p (c)					phi (c), p (t)					phi (t), p (c)					phi (t), p (t)				
Period	phi	SE	p	SE	Period	phi	SE	p	SE	Period	phi	SE	p	SE	Period	phi	SE	p	SE
2	0.70	0.04	0.08	0.01	2	0.80	0.06	0.17	0.05	2	1.00	0.00	0.08	0.01	2	1.00	0.00	0.14	0.04
3					3			0.05	0.02	3	0.56	0.13			3	0.57	0.16	0.07	0.03
4					4			0.10	0.03	4	1.00	0.00			4	1.00	0.00	0.09	0.03
5					5			0.05	0.02	5	0.51	0.15			5	0.57	0.24	0.07	0.04
6					6			0.04	0.02	6	0.81	0.27			6	1.00	0.00	0.05	0.02
7					7			0.03	0.02	7	0.52	0.20			7	0.72	0.49	0.04	0.03
8					8			0.03	0.02	8	0.74	0.31			8	1.00	0.00	0.03	0.02
9					9			0.02	0.01	9	0.49	0.24			9	0.62	0.59	0.02	0.02
10					10			0.03	0.02	10	0.59	0.27			10				

Models including covariates

phi (c), p (t; quadratic)					phi (c), p (t; linear)					phi (c, linear), p (t, quadratic)					phi (c; quadratic), p (t; quadratic)				
Period	phi	SE	p	SE	Period	phi	SE	p	SE	Period	phi	SE	p	SE	Period	phi	SE	p	SE
2	0.82	0.06	0.19	0.05	2	0.81	0.06	0.19	0.05	2	0.82	0.07	0.19	0.05	2	0.81	0.07	0.19	0.05
3			0.05	0.02	3			0.05	0.02	3			0.05	0.02	3			0.05	0.02
4			0.09	0.03	4			0.09	0.03	4			0.09	0.03	4			0.09	0.03
5			0.05	0.02	5			0.05	0.02	5			0.05	0.02	5			0.05	0.02
6			0.04	0.02	6			0.04	0.02	6			0.04	0.02	6			0.04	0.02
7			0.03	0.01	7			0.03	0.02	7			0.03	0.02	7			0.03	0.02
8			0.03	0.02	8			0.03	0.02	8			0.03	0.02	8			0.03	0.02
9			0.02	0.01	9			0.02	0.01	9			0.02	0.01	9			0.02	0.01
10			0.03	0.01	10			0.03	0.02	10			0.03	0.01	10			0.03	0.02

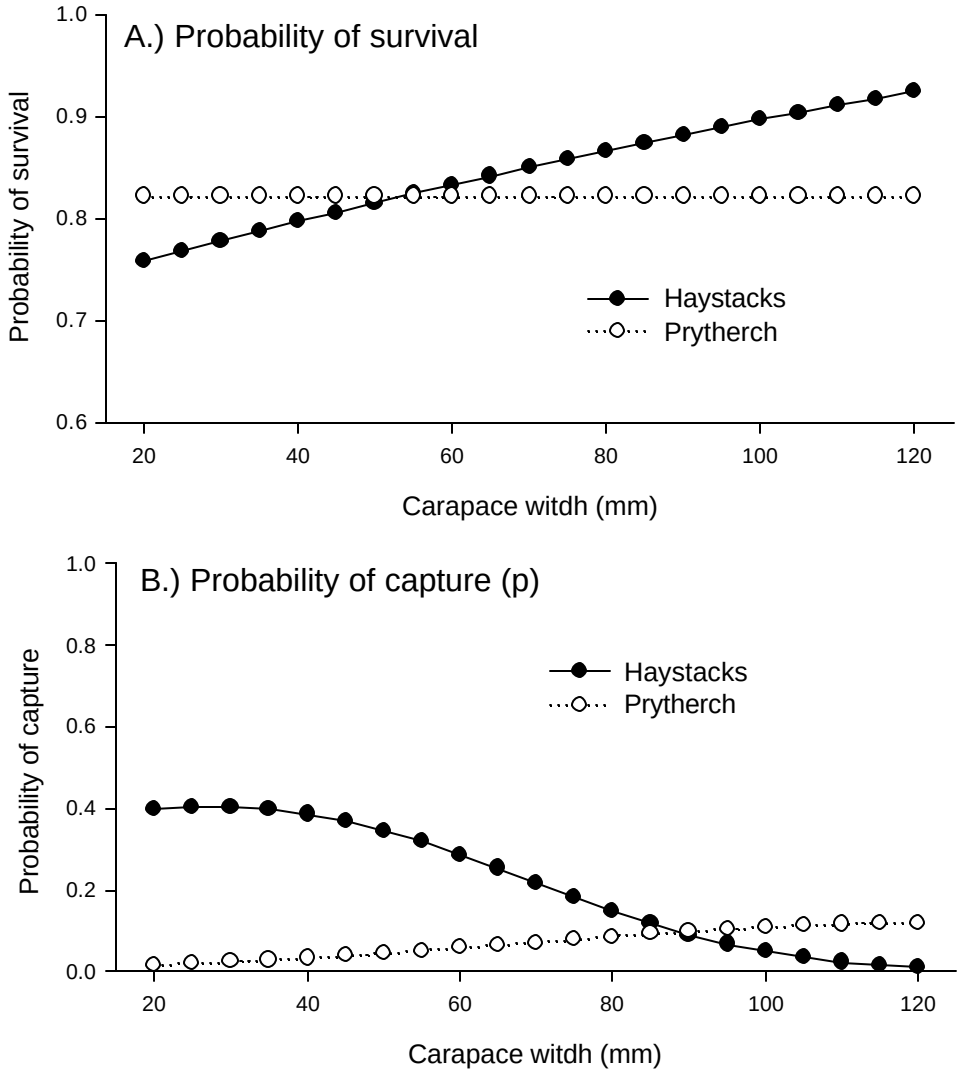
Appendix Table 4. Apparent survival (phi) and capture probabilities (p) from Jolly-Seber (JS) capture-recapture models for Haystacks. Models are grouped into those that did not incorporate covariates (base models) and those that included covariates. The descriptors in parenthesis indicate whether a parameter was held constant (c) or allowed to vary (t) over time, and whether a parameter was a linear or quadratic function of size (carapace width; mm). No values for ϕ and p are presented for the final period (i = 6) since these parameters are confounded and can not be estimated individually (see Lebreton et al. 1992).

Base models (no covariates)

phi (c), p (c)					phi (c), p (t)					phi (t), p (c)					phi (t), p (t)				
Period	phi	SE	p	SE	Period	phi	SE	p	SE	Period	phi	SE	p	SE	Period	phi	SE	p	SE
2	0.77	0.03	0.34	0.05	2	0.74	0.03	0.54	0.10	2	0.72	0.07	0.39	0.06	2	0.62	0.06	0.70	0.13
3					3			0.32	0.05	3	0.61	0.11			3	0.83	0.26	0.30	0.10
4					4			0.15	0.05	4	0.62	0.06			4	0.65	0.11	0.20	0.09
5					5			0.55	0.14	5	0.92	0.06			5	0.85	0.09	0.43	0.15
6					6			0.73	0.20	6	0.84	0.06			6				

Models including covariates

phi (c; linear), p (t; quadratic)					phi (c), p (t; quadratic)					phi (c, quadratic), p (t; quadratic)					phi (c), p (t; linear)				
Period	phi	SE	p	SE	Period	phi	SE	p	SE	Period	phi	SE	p	SE	Period	phi	SE	p	SE
2	0.73	0.025	0.628	0.118	2	0.728	0.032	0.599	0.133	2	0.723	0.027	0.629	0.114	2	0.72	0.028	0.642	0.116
3			0.287	0.051	3			0.295	0.051	3			0.293	0.053	3			0.311	0.052
4			0.138	0.051	4			0.142	0.052	4			0.141	0.052	4			0.147	0.054
5			0.577	0.14	5			0.573	0.152	5			0.592	0.142	5			0.598	0.143
6			0.877	0.151	6			0.825	0.288	6			0.919	0.157	6			0.905	0.226



Appendix Figure 1. Relationships between blue crab carapace width and Cormack-Jolly-Seber estimates of survival (A), and capture probabilities (B) for both Prytherch Creek and Haystacks study sites. Survival probabilities (A) were modeled as a linear functions of CW, and capture probabilities (B) were best described by quadratic functions. See text for justification for fitting linear and quadratic functions.

CHAPTER 2

A STOCHASTIC, DISCONTINUOUS GROWTH MODEL FOR BLUE CRABS

ABSTRACT: Growth models commonly used in fisheries and ecological modeling assume growth is a continuous function of age. While this approach is appropriate for finfish, the validity of these models for crustacean species, which grow discontinuously, has been questioned. There is a critical need to compare the predictions of discontinuous and continuous models for a given species simultaneously to identify if potential biases are introduced by the assumption of continuous growth. A lack of long-term studies, including both field-tagging efforts and controlled laboratory experiments, has been cited as a contributing factor in the poor quantitative understanding of crustacean growth. We used complementary laboratory and field experiments to examine growth of blue crabs (*Callinectes sapidus*). Our laboratory experiment provided observations of (1) molt increment (MI) in mm carapace width (CW), (2) exact intermolt period (IP) in days, and (3) the time to first molt (days), and allowed for a direct comparison with free-ranging individuals from field experiments. Further, the rate of tag loss was explicitly estimated in laboratory experiments. Growth of free-ranging blue crabs varying in initial size from 23.2 – 107.3 mm CW was quantified in two tidal salt marsh creeks in the Newport River estuary, Beaufort, North Carolina, USA during June – October 2001. The discontinuous nature of crustacean growth was modeled as the combination of two functions describing (1) molt increment (MI; i.e. growth-per-molt), and (2) the intermolt period (IP; i.e. time between successive molts). A positive and highly significant ($r^2 = 0.98$, $p = 0.0001$) relationship between premolt-CW and postmolt-CW was identified using linear regression, and a cubic model was used to describe the positive and significant ($r^2 = 0.67$, $p = 0.04$) relationship between premolt-CW and IP. Simulated growth trajectories for 500 individuals were generated from the model and provided estimates of mean growth and variability in individual growth rates. The

results were compared to predictions from a traditional growth model (von Bertalanffy growth function; VBGF) commonly used in fishery stock assessments that assumes growth is a continuous function of age. A VBGF predicted the mean size-at-age from the discontinuous model simulations very well ($r^2 = 0.99$, $p < 0.0001$), suggesting that continuous growth models can adequately predict the growth of blue crabs. The results from our study support the applicability of continuous growth models in fishery stock assessments and ecological modeling of blue crab population dynamics.

INTRODUCTION

Accurate growth data are necessary for modeling the demographics of a fish species, and a required component for a comprehensive stock assessment. Information on growth is also critical for more ecologically based models such as individually based models (IBMs) and matrix models. Broadly defined, growth is the change (increase) in some measure of size (length, weight, carapace width, etc.) over time. Traditionally, length has been used as the measure of body size in most fisheries modeling efforts (von Bertalanffy 1938, Schnute 1981), due in large part to the ease of collecting length measurements. For crustaceans, length measurements are almost always used because of the precise aging techniques are not available (Miller and Smith 2003). The growth process of crustaceans precludes the use of aging techniques that are frequently applied to finfish (i.e., otolith, scales, spines) because all hard parts are shed during the molting process. An approach for aging blue crabs using lipofuscin, a compound which accumulates in nervous tissue with age, has been developed (Ju et al. 2001, 2003), however estimates of age from this technique are imprecise (Miller and Smith 2003). Field tagging studies are a common source of growth information for animals, and are advantageous because they are conducted in natural conditions. The lack of such long-term studies for crustaceans, including both field-tagging efforts and controlled laboratory experiments, has been cited as a contributive factor in the poor quantitative understanding of crustacean growth (Smith 1997, Miller and Smith 2003).

Traditional growth models most commonly used in fishery stock assessments (von Bertalanffy 1938, Schnute 1981) assume growth to be a continuous function of age. While these approaches may be valid for finfish, the application of these models to crustacean species, which grow discontinuously, has been questioned (Miller and Smith 2003). For

example, predicted growth rates for the mud crab, *Scylla olivacea*, modeled using continuous growth functions described observed growth rates poorly (Moser et al. 2002). Thus, there is a critical need to compare the predictions of discontinuous and continuous models fit to observed growth data simultaneously for a given species. Such analyses (Restrepo 1989) can identify potential biases, if any, introduced by the assumption of continuous growth for an animal that grows incrementally via molting.

Despite the ecological importance of the blue crab (*Callinectes sapidus*) as an estuarine predator, as well as its commercial importance along the Atlantic and Gulf coasts of the United States, there are no growth estimates from free-ranging natural populations of individually tagged blue crabs. Since growth is examined under natural conditions, field studies of free-ranging individuals represent the best estimates of growth. Growth has been estimated primarily from studies of crabs held in captivity (Gray and Newcombe 1938, Newcombe et al. 1949). Many of these studies have focused on the effects of environmental factors, such as salinity and temperature on growth (Holland 1971, Leffler 1972, Cadman and Weinstein 1988), and have been mainly qualitative in nature. The quantitative aspect of blue crab growth under laboratory conditions was described by Fitz and Wiegert (1991); however, their study focused primarily on juvenile crabs (29 – 67 mm CW) and used a batch tagging protocol, which did not allow for unique identification of individual crabs. Additionally, Smith (1997) described a discontinuous model of blue crab growth using estimates of growth from laboratory data, but did not compare discontinuous model results with those of continuous models, which are traditionally used in fishery and ecological modeling. Tagatz (1968) examined the growth of blue crabs held in floating cages in the field. The crabs were exposed to natural environmental conditions, but confined to individual compartments and be

fed artificial diets. Application of growth rates estimated from laboratory or field caging studies to natural populations can be problematic. For example, risk of predation (Hines and Ruiz 1989, Ryer et al. 1997) and the unavailability of the marsh surface to blue crabs to forage at low tide (this dissertation, Chapter 1, Ryer 1987) may limit the growth potential of wild crabs relative to laboratory individuals, which are not subject to predation risk and often fed to satiation.

The overall objectives of this study were: (1) to estimate growth rates of free-ranging juvenile and adult blue crabs in tidal salt marsh habitats using capture-recapture techniques, (2) compare growth rates of free-ranging blue crabs to those of individuals held under laboratory conditions, (3) use estimates of growth to construct a stochastic, discontinuous growth model, and (4) compare growth trajectories predicted from our discontinuous growth model with a more commonly used approach (von Bertalanffy 1953) that assumes continuous growth. The results are then used to assess the applicability of continuous growth models in stock assessments of the blue crab and other commercially important crustacean fishery species. The present capture-recapture study is novel in that (1) the growth rates of blue crabs were examined under natural conditions (free-ranging), (2) blue crabs were individually identifiable (uniquely coded microwire tags), and (3) the growth of a broad range of size classes (early juveniles-adults) was investigated.

MATERIALS AND METHODS

Laboratory tagging

A 37 d laboratory experiment (August 8 – September 12, 2002) tested the effects of tagging using CWT's on blue crab growth and mortality, and allowed the rate of tag retention (θ) to be estimated directly (see Chapter 1 for a detailed description of methods). Crabs were

checked daily for mortality and molting. Recently molted crabs were allowed ~ 1 - 2 d to harden prior to being measured and checked for tag retention, and allowed for tag loss to be explicitly estimated. Tag loss around the time of molting would result in a decreased estimate of the proportion of molted animals since they are effectively removed from the population and overestimate the IP in the field. An estimate of the rate of tag loss, and whether the rate of tag loss increases during molting, allows for biases in IP to be corrected (Restrepo and Hoenig 1988).

The discontinuous nature of crustacean growth was modeled as the combination of two functions describing (1) molt increment (MI; i.e. growth-per-molt), and (2) the intermolt period (IP; i.e. time between successive molts). MI can be described using a Hiatt diagram (Hiatt 1948) which examines the relationship between premolt-CW and postmolt-CW, and the IP for a range of size classes can be estimated by examining the relationship between IP and premolt-CW. The two functional relationships described above can be combined to construct a growth trajectory (Hiatt 1948, Caddy 1987, Smith 1997).

Our laboratory experiment provided (1) 46 observations of molt increment (MI; postmolt-CW – premolt-CW), (2) 29 observations of exact intermolt period (IP), and (3) 30 observations of the time-to-first-molt in captivity, and allowed for a direct comparison of MI and IP with free-ranging individuals from field experiments (see below). A two-way, fixed factor analysis of covariance (ANCOVA) model using tag status and sex as factors, and pre-molt CW as a covariate, was used to test whether or not the response variables (MI, IP, and time to first molt) were significantly different between treatments.

Field tagging

Growth of free-ranging juvenile blue crabs was studied in two tidal marsh creeks, Prytherch Creek (PC) and Haystacks (HS), located in the Newport River estuary near Beaufort, North Carolina, USA during June-October 2001 (see Chapter 1 for a detailed description of methods). The field tagging data yielded individual records of sex, carapace widths (CW; mm) at initial release and recapture, and the time (days) at liberty. A total of 155 recaptures obtained from tagging were used to estimate growth of free-ranging individuals, varying in initial size from 23.2 – 107.3 mm CW.

Analysis of laboratory growth data

MI in crustaceans is commonly described using a Hiatt diagram (Hiatt 1948) which plots premolt versus postmolt-CW. The relationship between and premolt and postmolt-CW varies by species (Botsford 1985), and has been described using both linear (Kurata 1962, Somerton 1980) and hyperbolic (Mauchline 1976) models. We compared the fit of a (1) linear regression, and (2) a hyperbolic model (Mauchline 1976) to observed laboratory blue crab growth data using Akaike's Information Criterion (AIC; Akaike 1975; Table 2). AIC is a commonly employed maximum-likelihood approach that incorporates a penalty for over-parameterization and provides an objective method for selecting the most parsimonious model from a candidate set that adequately explains the observed data (Akaike 1975).

We estimated the IP for blue crabs in the laboratory by allowing each animal to molt once, then recording the time until the second molt. This procedure allowed for exact measurements of IP from laboratory crabs. Three models were fitted to the observed relationship between premolt-CW and IP from laboratory experiments: (1) linear, (2) cubic, and (3) exponential (Table 2) since the relationship varies in different species (Hartnoll

1982). Models were selected based on their previous application in crustacean growth studies (Mauchline 1977, Restrepo 1989), and the ability to biologically describe growth dynamics. Growth in crustaceans generally follows the simple allometric relationship ($y = a*x^b$; Hartnoll 1978). For example, as an individual blue crab increases in length (one-dimensional), the concurrent increase in body volume (three-dimensional) is proportionally larger (Olmi and Bishop 1983, Rothchild et al. 1991). A simple, intuitive biological explanation is that successive molts allow for increasing growth capacity (volume) and increase the time necessary to acquire sufficient food resources for the next successive molt if a large increase in foraging efficiency does not occur. Thus, as size increases, IP will become longer. Both the exponential and cubic models can adequately describe this relationship. Model fits were compared using AIC.

Analysis of field growth data

Similar to the analysis of laboratory data, we compared the fit of (1) one-phase (simple) linear and (2) a hyperbolic model (Mauchline 1976) to the observed relationship between premolt-CW and MI from the free-ranging crabs in the field using AIC (Akaike 1975; Table 2). Because the field data for MI was available for a wider range of size classes than in the laboratory experiments, we also fitted a two-phase (segmented) linear regression ("bent-line") model (Gray and Newcombe 1938; Table 2). This model allows for possible changes in the slope of the relationship between pre- and postmolt-CW that may accompany the onset of sexual maturity as somatic growth declines and energy resources are diverted into reproduction. This ontogenetic shift in growth has been reported in many crustacean species (Restrepo 1989, Wainwright and Armstrong 1993), including blue crabs (Gray and Newcombe 1938).

Prior to fitting models to the relationship between premolt-CW and MI, a two-way analysis of covariance (ANCOVA) using site (PC vs. HS) and sex as factors, and premolt-CW as a covariate was applied to field data from recaptured blue crabs, and tested whether or not MI was significantly different between treatments, and varied significantly with premolt-CW.

The relationship between premolt-CW and IP for blue crabs was estimated from field observations of molting from free-ranging blue crabs. Unlike laboratory methods that allow for daily monitoring and exact measurements of IP, IP must be estimated from field tagging experiments since exact times of molting are unknown. To identify the functional relationship between premolt-CW and IP from field tagging data, we first grouped individual recaptured blue crabs into size classes. Crabs were assigned to size bins using 10 mm intervals. For example, all crabs between 20 and 30 mm CW were assigned to the 25 mm size class. For each size class (*i*), the daily probability of molting (Pm) was calculated as:

$$\frac{\text{Observed number of crabs molting in size class } i}{\text{Total number of days at large in size } i} \qquad (1)$$

For each size class, the approximate IP was determined by dividing 1 by the P_m. Similar to previous methods for estimating IP (Munro 1974, 1983), this method assumes that there is no synchronicity in molting (i.e., the probability of molting for individual crabs is independent). A significant bias can be introduced if tag loss primarily at the time of molting. Tag losses were estimated to be12% from laboratory experiments, and was similar to earlier reported estimates (van Montfrans 1987; Fitz and Wiegert 1992) using microwire tags. Two tags were lost, both during the first molt following tagging. To correct for biased estimates of IP

due to tag loss, we applied the following correction as suggested by Restrepo and Hoenig (1988):

$$IP_{correct} = IP_{uncorrected} * (1 + PRT)/2 \qquad (2)$$

where PRT is the proportion of crabs that retain their tags. As with laboratory data, three models were fitted to field observations of IP to describe the relationship between premolt-CW and IP for free-ranging crabs: (1) linear model, (2) cubic model, and (3) exponential model (Table 2), and model fits were compared using AIC.

Construction of growth trajectories from field capture-recapture data

The relationships between MI, IP, and premolt-CW were combined to generate a discontinuous model of blue crab growth. Data from the field CWT tagging study were chosen over laboratory data for this analysis because: (1) growth rates of blue crabs were examined under natural conditions (free-ranging) and represent the best estimates for growth in the wild, (2) this data set contained growth information for a wider range of sizes (23.2 – 107.3 mm CW) than examined in the laboratory, (3) of the longer duration of the study (143 d) as opposed to 37 d in the laboratory experiment, and (4) of the larger sample size (n = 155 for field vs. 46 for laboratory). Despite the large size range of blue crabs for which information on MI and IP was available, the lack of data for MI and IP for both very small individuals (CW < 23 mm) and large individuals (CW > 107.3 mm) required extrapolation of growth predictions to these size ranges. Limitations of the tagging method precluded using CWTs to examine MI and IP for small crabs, and information for the MI and IP of large crabs was difficult to obtain due to the longer IP of these individuals.

We constructed a discontinuous model of blue crab growth to describe size-at-age using a combination of the linear model for MI and the cubic model for IP. The initial size of blue crabs was assumed to be 2.5 mm CW (Newcombe et al. 1949), corresponding to the mean size at the first benthic instar. All subsequent sizes were determined using a linear model to relate premolt-CW to postmolt-CW:

$$CW_{POST} = a*CW_{PRE} - b + \varepsilon \qquad (3)$$

The error term (ε) was assumed to be normally distributed, $e \sim N(0, s^2)$, and the magnitude of the variance (s^2) was based on the fit of equation (3) to the observed field data. Thus, the model was able to incorporate stochasticity explicitly, and provide information on the mean size-at-age, as well as the distribution of sizes at a given age. The relationship between premolt-CW and IP was described using a cubic model:

$$IP = a + b*(CW_{PRE})^3 + \varepsilon \qquad (4)$$

Similar to equation 3, the error term (ε) was assumed to be normally distributed, $e \sim N(0, s^2)$, however, the variance (s^2) was estimated from the fit of equation (4) to the observed field data. When combined, equations (3) and (4) can be used to describe the growth trajectory of an individual blue crab as a discontinuous function resembling a staircase. We simulated growth trajectories for 500 individuals. Individual growth trajectories provided estimates of variability in individual growth rates, and were used to calculate mean and 95% confidence intervals for size-at-age. Although growth of crustaceans is an inherently discontinuous

process, most fishery models used in stock assessments rely on growth described as a continuous function of time (Rugolo et al. 1997, 1998, Miller and Houde 1999, Helser and Kahn 1999, 2001). Therefore, we fitted a von Bertalanffy growth function (VBGF) to predicted mean size-at-age from our discontinuous growth model. The VBGF is the most commonly used model for predicting growth. Further, the VBGF has been used to describe growth in numerous stock assessments for the blue crab (Rugolo et al. 1997, Helser and Kahn 1999, Miller and Houde 1999). The VBGF (von Bertalanffy 1953) is defined by the following equation:

$$L_t = L_{inf}(1 - e^{k(t - t0)}) \qquad (5)$$

where L_t is the length at time t, k is the curvature (Brody growth coefficient) and L_{inf} = asymptotic maximum size, and t_0 is the theoretical age at length 0. Assessing the ability of the continuous functions (VBGF) to predict simulated mean size-at-age from a discontinuous model will address whether or not these models may be appropriate for use in stock assessment modeling of animals which inherently grow discontinuously, such as crustaceans.

RESULTS

Effects of tagging on growth, tag retention and tag-induced mortality

Proportional mortality of juvenile blue crabs in the laboratory was low in both tagged and control treatments, and was not significantly different between treatments ($\chi^2 = 0.28$, *df* = 1, p = 0.60; Table 1). Of the 15 tagged individuals, 13 retained the tag through the entire experiment (37 d) for an overall tag retention of 88%. In both cases in which tags were shed, tag loss occurred during the first molt following tagging. All crabs that retained the tag

through the first molt, retained the tag through all subsequent molts. Mean time to first molt was not significantly different (ANCOVA, F = 0.009, *df* = 1, 28, p = 0.93) between tagged and control treatments or between sexes (ANCOVA, F = 0.004, *df* = 1, 28, p = 0.95; Table 1). Premolt-CW, included in the model as a covariate, had a significant effect on time to first molt (ANCOVA, F = 15.35, *df* = 1, 28, p = 0.03). The relationship between time to first molt and premolt-CW was positive. The IP between first and second molts was also not significantly different (ANCOVA, F = 0.05, *df* = 1, 17, p = 0.83) between tagged and control treatments or between sexes (ANCOVA, F = 1, 17, p = 0.73). Premolt-CW was included in the ANCOVA model as a covariate and had a significant effect on the intermolt period (ANCOVA, F = 4.99, df = 1, 17, p = 0.04). The relationship between time to first molt and premolt-CW was positive, indicating that IP increases with size. Differences in proportional size increases were not significant between tagged and control treatments after the first molt (student's t-test, t = 0.35, *df* = 1, 28, p = 0.56; Table 1), but marginally significant after the second molt (student's t-test, t =3.61, *df* = 1, 17, p = 0.08; Table 1), with size increases in the tagged treatment being higher than in the control. This result is likely spurious since tagging would likely have a negative impact on growth.

Relationship between premolt and postmolt-CW from laboratory data

Linear and hyperbolic regression models (Mauchline 1976) were fitted to the laboratory observations of the relationship between premolt and postmolt-CW. Although both models produced good fits to the data, AIC (Akaike 1973) indicated the linear model provided the best fit to the data (AIC = 66.95, AIC weight = 0.99) as compared to a hyperbolic model (AIC = 79.3, AIC weight = 0.01). A positive and highly significant (r^2 = 0.97, p = 0.0001) relationship was identified using linear regression (Fig. 1).

Relationship between premolt-CW and intermolt period from laboratory data

We estimated the IP for blue crabs in the laboratory by allowing each animal to molt once and recording exact measurements of IP, and subsequently plotting IP as a function of premolt-CW (Fig. 2). Although the linear model produced the lowest AIC, all models produced good fits to the data and no single model was clearly favored as the best fit to the data (Linear: AIC = 8.10, AIC weight = 0.35; Cubic: AIC = 8.24, AIC weight = 0.31; Exponential: AIC = 8.17, AIC weight = 0.33). The AIC weights ($0.35 \approx 0.31 \approx 0.33$) indicated that all models were approximately equally likely to best describe the relationship between premolt CW and IP. The similar fit of both linear and non-linear models to observed IP in the laboratory may be a result of the relatively small size ranges of blue crabs (22.8 – 44.0 mm CW) for which data was available. Since all models produced similar fits, we chose the simplest model (linear) to describe the positive and significant ($r^2 = 0.32$, $p = 0.007$) relationship between premolt-CW and IP (Fig. 2).

Effects of site and sex on molt increment of blue crabs in the field

Mean MI was not significantly different (ANCOVA, $F = 0.022$, $df = 1, 62$ $p = 0.88$) between the PC (10.71 mm $\pm$ 0.85) and HS (10.21 mm $\pm$ 0.99) study sites or between sexes (males = 10.47 mm $\pm$ 0.92 versus females = 10.16 d $\pm$ 1.46; ANCOVA, $F = 0.004$, $df = 1, 62$ $p = 0.95$). The interaction between site and sex was not significant ($p > 0.05$). Premolt-CW, included in the model as a covariate, had a highly significant effect on MI (ANCOVA, $F = 21.82$, $df = 1, 62$ $p < 0.0001$). The relationship between time to first molt and premolt-CW was positive, indicating that MI increases with size

Relationship between premolt and postmolt-CW from field data

Simple and "bent-line" linear models as well as the hyperbolic regression model (Mauchline 1976), were fitted to the field observations of the relationship between premolt and postmolt-CW (Table 2). AIC indicated the one-phase linear model provided the best fit to the observed pre- vs. postmolt CW data (AIC = 62.95, AIC weight = 0.99) as compared to either a two-phase linear (AIC = 76.40, AIC weight ≈ 0), or hyperbolic (AIC = 79.82, AIC weight ≈ 0) model. A positive and highly significant ($r^2 = 0.98$, $p = 0.0001$) relationship was identified using a simple linear regression (Fig. 3) and was defined by the following equation:.

$$CW_{POST} = 1.18*CW_{PRE} + 1.43 + \varepsilon \qquad (6)$$

The error term (ε) was assumed to be normally distributed with mean 0, ($\varepsilon \sim N(0, 6.66)$), and the magnitude of the variance ($s^2 = 6.66$) was based on the fit of equation (6) to the observed field data.

Relationship between premolt-CW and intermolt period from field data

We estimated the IP for blue crabs from field recapture data for both sites (PC and HS) combined. In total, field recaptures yielded information for 155 individual blue crabs. Eighty-three of the 155 recaptured individuals had molted, and in total, recaptured individuals spent 1677 days-at-large. Individual recaptures were pooled by 10 mm CW size classes using observed premolt-CW, and the number of molts and days-at-large for each size class were used to calculate the probability of molting (P_m) and IP. (Table 3). The cubic model produced the lowest AIC, but generated only a marginally better fit than alternative models (linear: AIC = 5.63, AIC weight = 0.29; cubic: AIC = 5.33, AIC weight = 0.38;

exponential: AIC = 5.51, AIC weight = 0.32). The AIC weights (0.39 ≈ 0.32 ≈ 0.29), indicated substantial support for all models. We chose the following cubic model to describe the positive and significant ($r^2 = 0.67$, $p = 0.04$) relationship between premolt-CW and IP (Fig. 4):

$$IP = 17.67 + 0.0001*CW_{PRE}3 + \varepsilon \qquad (7)$$

Similar to equation (6), error was assumed to be normally distributed with mean 0 ($\varepsilon \sim N(0, 29.48)$, and the magnitude of the variance ($s^2 = 29.48$) was based on the fit of the cubic regression model (Fig. 4) to observed field data for IP.

Comparison of laboratory and field data

To investigate potential differences between MI of blue crabs under laboratory and field conditions, we used a two-factor ANCOVA using environmental condition (laboratory vs. field) and sex as fixed factors, and premolt-CW as a covariate. Because there was no significant difference for blue crab MI between sites, we pooled data from PC and HS for this analysis. Mean MI was not significantly different (ANCOVA, F = 0.334, *df* = 1, 108 p = 0.57) between laboratory (10.12 mm $\pm$ 0.92) and field (8.15 mm $\pm$ 0.39) conditions or between sexes (males = 9.81 mm $\pm$ 0.61 versus females = 9.15 mm $\pm$ 0.54; ANCOVA, F = 0.071, *df* = 1, 108 p = 0.79). The interaction between environmental condition and sex was not significant (p > 0.05). Premolt-CW, included in the model as a covariate, had a highly significant effect on MI (ANCOVA, F = 39.61, *df* = 1, 108 p < 0.0001). Formal statistical analysis to test for differences in IP between field and laboratory blue crabs was not feasible since field data were pooled to estimate IP for a given size range. Nevertheless, the IP for

laboratory crabs was generally lower than the IP for free-ranging crabs for a given size (Fig.4), and suggests that blue crabs held in laboratory conditions in our study molted more frequently than free-ranging individuals.

Construction of growth trajectories from field tagging data

The relationships between premolt-CW, MI, and IP (Figs. 3, 4) from field data were used initially to construct a deterministic growth trajectory for the blue crab (Figure 5a). Because the deterministic model provides no information on the variability of individual blue crabs about a given mean size, we used a random number generator and estimates of variability (σ^2) from model regressions to simulate growth trajectories for 500 individual blue crabs. This allowed for the quantification of variability in length for a given size (Figure 5b).

A von Bertalanffy growth function (VBGF) was fitted to the simulated mean size-at-age data and resulted in estimates of L_{inf} = 237.7 mm CW, k = 0.74, and t_0 = 0.02 months, obtained from a non-linear regression model (Fig. 6). The VBGF provided a good first order approximation to the simulated mean length-at-age data (Fig. 6), but examination of the residuals suggested that predicted values were underestimated at intermediate ages, and overestimated at older ages. The magnitude of the errors, however, were small. Regardless, the fit of the VBGF predicted the mean size-at-age from the model simulation extremely well (r^2 = 0.99, $p < 0.0001$), suggesting that continuous growth models can adequately predict the growth of blue crabs, and potentially other crustaceans.

DISCUSSION

Capture-recapture studies using microwire tags are extremely valuable to estimating growth of animals under natural environmental conditions. The important findings of this

study were: (1) Growth was similar across two independent salt marsh creek systems during summer-fall (Prytherch Creek and Haystacks), (2) MI was similar between animals held under laboratory and field conditions, (3) blue crabs held in the laboratory molted more frequently than free-ranging individuals of similar size, (4) tag retention was high (88%), and tag loss was associated with the first molt following tagging, and (5) continuous and discontinuous growth models yielded similar predictions for size-at-age. This capture-recapture study illustrates the utility of CWTs to investigate the growth of crustacean species for which many conventional tagging methods can not be applied.

Assumptions of the tagging method

Capture-recapture experiments provide a powerful tool for estimating growth, however, these methods require several assumptions: (1) the tagging process does not adversely effect growth, (2) mortality and tag loss are not associated with the molting process, and (3) a lack of synchrony in molting in the population (i.e., the probability of molting for each individual is independent). Estimated growth rates from free-ranging, tagged blue crabs can be applied to wild populations only if the tagging process does not alter natural growth patterns. Laboratory studies (van Montfrans et al. 1986, Fitz and Wiegert 1991, this study) demonstrated that microwire tagging has negligible effects on growth in blue crabs. In this study, MI, time to first molt, and IP were similar for tagged and untagged individuals.

Tag loss and mortality result in a positive bias for estimates of IP if these processes are associated with the time of molting. This occurs because the observed proportion of animals molting will be lower than the actual proportion since molting individuals are effectively removed from the population when they lose their tags (Restrepo and Hoenig

1988). Both cases of tag loss in the present study occurred during the first molt following tagging. The estimate of IP can be corrected, however, if tag loss and mortality can be quantified. We estimated tag loss to be 12%, and corrected estimates of IP following the method of Restrepo and Hoenig (1988). Mortality at the time of molting is also likely to be increased; blue crabs are particularly vulnerable to predation immediately following molting while soft (Ryer et al. 1997). Since the magnitude of mortality associated with molting was unknown, we were unable to correct IP for this bias, however, estimates of IP have been demonstrated to be robust to the failure of this assumption (Restrepo and Hoenig 1988).

Molting of blue crabs is assumed to be asynchronous. Blue crabs held under laboratory conditions in this study did not appear to molt synchronously. While molting is likely asynchronous for our study population of crabs in the Newport River estuary during summer and fall, estimation of IP from mature females during the spring may be problematic. In the mid-Atlantic, prepubertal female blue crabs exhibit an annual period of synchronous molting to sexual maturity in the spring. For example, the "peeler" fishery in North Carolina that targets these molting females captures 51% of the annual catch during the month of May (NC DMF 1998). Thus, whether or not the assumption of asynchrony is violated must be considered critically in future studies when calculating IP from capture-recapture data.

Comparison of laboratory and free-ranging blue crabs

Growth rates of animals estimated from laboratory studies are frequently used to make inferences about growth rates in natural populations (Restrepo 1989, Wainwright and Armstrong 1993, Smith 1997). The extension of laboratory results to describe growth of wild individuals is often required for crustaceans because of the difficulty of estimating MI and IP in the field relative to the laboratory (Miller and Smith 2003). The application of

growth rate estimates obtained from laboratory experiments assumes growth to be similar to individuals in natural populations. While potential differences in growth rates between laboratory and wild individuals is generally acknowledged in studies which extrapolate laboratory growth estimates to natural populations (Hoenig and Restrepo 1989, Restrepo 1989, Wainwright and Armstrong 1993), data are frequently not available to test for violations of this assumption. The simultaneous field and laboratory components in this study allowed for this assumption to be examined.

The relationship between premolt-CW and MI in blue crabs in this study was similar for laboratory and field individuals, as has been found in other crustaceans (Restrepo 1989), suggesting that estimates of MI for blue crabs from laboratory studies are applicable to wild populations. Our study suggests, however, that blue crabs in the laboratory molted more frequently than similar sized individuals in the field. These differences may be explained by environmental variables or differences in diet since IP in crustaceans is often influenced by temperature, salinity and diet (Hartnoll 1982). For example, IP is negatively correlated with temperature in blue crabs (Tagatz 1969, Holland et al. 1971, Leffler 1972, Cadman and Weinstein 1984) and growth throughout the mid-Atlantic ceases during winter months at low temperatures (Smith 1997, Miller and Smith 2003). Our laboratory experiment was conducted in close proximity to field sites and utilized a continuous flow-through design that supplied water from nearby Core Sound. As a result, temperatures were similar between field and laboratory blue crabs, and were probably not responsible for observed differences in IP. Longer IPs for blue crabs in the field may be the result of decreased feeding rates relative to laboratory crabs that were fed to satiation daily. As the marsh became exposed at low tide, crabs buried within the marsh and unvegetated creek bottom (see Chapter 1). Since crabs

were unable to actively forage while buried, food intake of blue crabs in the field was probably reduced relative to laboratory individuals. Gut fullness of blue crabs in a Chesapeake Bay marsh creek was greatest when captured during high tide and lowest just prior to the beginning of ebb tide, indicating blue crabs were utilizing the vegetated marsh surface to forage (Ryer et al. 1987). Further, the amount of energy expended for blue crabs in the field may have been increased relative to individuals in the laboratory that did not actively forage and had reduced movement rates. The exact mechanism underlying the shorter IP in blue crabs in the laboratory study, relative to those in the field is not clear. Nevertheless, the results of our concurrent laboratory and field studies suggest that estimates of IP for blue crabs derived from laboratory experiments may differ from those of individuals in the wild. Estimated growth rates of blue crabs held in the laboratory may impart significant bias when these estimates are extrapolated to natural populations. Advances in tagging technology (i.e., uniquely identifiable CWTs) have eliminated many of the difficulties associated with estimating growth rates from free-ranging animals. Whenever possible we recommend estimating growth rates in the field, and when necessary, extrapolation of laboratory results should be considered carefully.

Application of capture-recapture estimates to natural populations

The observed IPs in this study probably represent maximum molt frequencies attainable during summer and fall, and likely overestimate growth rates during colder winter months when IP is longer (Tagatz 1968, Leffler 1972, Smith 1997). The present study was conducted during June-October, a period when water temperatures are at or near the annual maximum in North Carolina. Estimated von Bertalanffy parameters ($L_{\text{inf}} = 237.7, k = 0.74$) were similar to values reported for blue crabs in Delaware Bay ($L_{\text{inf}} = 234.7, k = 0.75$;

Helser and Kahn 1999) and Chesapeake Bay (L_{inf} = 262.5, k = 0.59, Rugolo et al. 1997), but were considerably higher than values for North Carolina derived from length-based modeling of length-frequency data (L_{inf} = 216.9, k = 0.47; see this dissertation, Chapter 3). The higher observed growth rates may be a result of the timing of this study (June-October) relative to length-frequency analysis of fishery-independent data sets which reflect annual changes in growth rates throughout the year. Blue crabs grow faster at increased temperatures as a result of shorter IPs (Tagatz 1968, Winget et al. 1976).

Lowered growth rates as a result of decreased MI often accompany the onset of sexual maturity, as somatic growth declines and energy resources are diverted into reproduction. This drop in growth rate has been reported in many crustacean species (Restrepo 1989, Wainwright and Armstrong 1993), including blue crabs (Gray and Newcombe 1938). While this change in growth rate can be adequately modeled using a two-phase regression model, we lacked sufficient information on large crabs to justify fitting one. If our model is less appropriate, it may overestimate the MI of large crabs, and could partially account for the greater predicted size-at-age relative to estimates from length-based modeling of length-frequency data (see this study, Chapter 3). For the reasons above, growth rates are probably overestimated relative to wild populations that experience large annual fluctuations in growth rates with seasonal changes in water temperature. Nevertheless, this study provides important information on the growth of free-ranging blue crabs during summer-fall, and allows the predictions of size-at-age from discontinuous and continuous models to be compared.

Comparison of predicted size-at-age from discontinuous and continuous models

The mean sizes-at-age predicted from the VBGF were very similar to simulated

growth trajectories from the discontinuous model (Fig. 6a). Similar to Restrepo (1988), a plot of residuals (Fig. 6b) suggested that the VBGF underestimated the size of intermediate age crabs (0.3 – 1.2 years) and overestimated the size of older crabs (1.2 – 3 years) relative to simulated data. The differences between the predictions from the VBGF and the discontinuous model were relatively small, and likely would not introduce a significant bias into stock assessment models. Unfortunately, our growth model required extrapolation of growth rates to large crabs (CW > 107.3 mm) for which no recapture data were available. The magnitude of the potential bias introduced by our lack of data for large individuals is unknown. While discontinuous models provide a more realistic representation of crustacean growth by implicitly considering the molting process, the VBGF has several advantages: (1) it is considerably simpler, (2) is less data intensive, and (3) is integrated into current stock assessment analysis software. Thus, the results from our study support the current practice of using continuous growth models in fishery stock assessments, as well as more ecologically based modeling (i.e., IBMs and matrix models) of the blue crab and other commercially important crustacean fishery species.

ACKNOWLEDGEMENTS

We thank the following graduate and undergraduate students, technicians and fishermen for assistance in field and laboratory experiments: G. Bell, D, Blackmon, D. Doxey, R. Doxey, W. Elis, H. Johnson, G.T. Kellison, N. Reyns, S. Searcy, C. Taylor, and D. Taylor. Special thanks are required to my committee members: Dave Eggleston, Joe Hightower, Ken Pollock, and Tom Wolcott for constructive critique. I thank Jacques van Montfrans and the Virginia Institute of Marine Science for access to the microwire tagging equipment, and for

providing technical training. Funding for this research was provided by the North Carolina Sea Grant Fishery Resource Grant Program (99-FEG-10 and 00-FEG-11), NSF grant (OCE-97-34472) to D. Eggleston, and the PADI foundation to E. Johnson.

LITERATURE CITED

Akaike H. (1973) 2nd International Symposium on Information Theory, Chapter Information theory and an extension of maximum likelihood principle, pp. 267-281. Budapest: Akademia Kiado.

Cadman, L. R. and M.P. Weinstein. 1988. Effects of temperature and salinity on the growth of laboratory-reared juvenile blue crabs *Callinectes sapidu*s Rathbun. J Exp Mar Biol Ecol 121:193-207.

Caddy, J. (1987). Size-frequency analysis for Crustacea: moult increment and frequency models for stock assessment. Kuwait Bulletin of Marine Science 9:43-61.

Fitz H.C., Wiegert R.G. (1991) Tagging juvenile blue crabs, *Callinectes sapidus*, with microwire tags: retention, survival, and growth through multiple molts. Bull Mar Sci 11:229-235

Fitz H.C., Wiegert R.G. (1992a) Utilization of the intertidal zone of a salt marsh by the blue crab Callinectes sapidus: density, return frequency, and feeding habits. Mar Ecol Prog Ser 86:249-260

Fitz H.C., Wiegert RG. (1992b) Local population dynamics of estuarine crabs: abundance, recruitment and loss. Mar Ecol Prog Ser 87:23-40

Gilliam J.F., Fraser D.F. (1987) Habitat selection under predation hazard: Test of a model with foraging minnows. Ecology 68(6)1856-1862

Gray, E. H., C. L. Newcombe. (1938). Studies of moulting in *Callinectes sapidus* Rathbun. Growth 2:285-296.

Hartnoll, R. G. (1978). The determination of relative growth in Crutacea. Crustaceana 34(3): 281-293.

Hartnoll, R. G. (1982). Growth. In: L. G. Abele (*ed*) The Biology of Crustacea, Vol. 2, Embryology, morphology and genetics. pp. 111-196. Academic Press, Inc. Ney York.

Helser T.E., Kahn.D.M. (1999) Stock assessment of Delaware Bay blue crab (*Callinectes sapidus*) for 1999. Dept. of Natural Resources, Delaware Division of Fish and Wildlife, 89 Kings Highway, Dover DE 19901

Hines A.H., and Ruiz G.M. (1995). Temporal variation in juvenile blue crab mortality: nearshore shallows and cannibalism is Chesapeake Bay. Bull Mar Sci 57:884-901

Hiatt, R. W. (1948). The biology of the lined shore crab *Pachygrapsus crassipes* Randall. Pacif Sci 2:135-213.

Hoenig, J. M. and R. G. Restrepo (1989). Estimating the Intermolt periods in asynchronously molting crustacean populations. Biometrics 45:71-82.

Holland J.S., D.V. Aldrich, and K. Strawn. 1971. Effects of temperature and salinity on growth, food conversion, survival, and temperature resistance of juvenile blue crabs *Callinectes sapidus* Rathbun. Sea Grant Program Publication SG-71-222.

Ju, S-J, D. H. Secor, and H. R. Harvey. (2003) Demographic assessment of the blue crab (*Callinectes sapidus*) in Chespaeake Bay using extractable lipofuscins as age markers. Fish Bull 101:312-320.

Ju, S. J., D. H. Secor, and H. R. Harvey. (2001). Growth rate variability and lipofuscin accumulation rates in the blue crab *Callinectes sapidus.* Mar Ecol Prog Ser 224:197-205.

Ju, S-J, D. Secor, and H. R. Harvey. (1999). The use of extractable lipofuscin for age determination of the blue crab, *Callinectes sapidus*. Mar Ecol Prog Ser 185:171-179.

Kurata, H. (1962). Studies of the age and growth of Crustacea. Bull Hokkaido reg Fish Res Lab 24:1-115.

Leffler, C.W. 1972. Some effects of temperature on growth and metabolic rate of juvenile blue crabs, *Callinectes sapidus*, in the laboratory. Mar Biol 14:104-110.

Mauchline J. (1977). Growth of shrimps, crabs and lobsters – an assessment. J Cons Int Explor Mer 37:162-169.

Moser, S. M., D. J. Macintosh, S. Pripanapong, and N. Tongdee. (2002). Estimated growth of the mud crab *Scylla olivacea* in the Ranong mangrove ecosystem, Tahiland, based on a tagging and recapture study. Mar Fresh Res 53:1083-1089.

Munro, J. L. (1974). The biology, ecology and bionomics of Caribbean reef fishes: crustaceans: (spiny lobsters and crabs). *In* JL Munro (*ed*). Caribbean coral reef fishery resources. ICLARM studies and reviews 7, Manila, Phillipines.

Munro, J. L. (1983). The biology, ecology and bionomics of spiny lobsters (Palinuridae), spider crabs (Majiidae) and other crustaceans. *In* JL Munro (*ed*). The biology, ecology, exploitation and management of Caribbean reef fishes: Sci. Rep. 3, part V.1. of the the ODA/UWI fisheries ecology project 1962-1973. University of the West Indies, Dept. of Zoology, Kingston, Jamaica.

Miller, T. J. and E. D. Houde. 1998. Blue crab target setting. Final Report for Living Resources Subcommittee, Chesapeake Bay Program, U.S. EPA, 410 Severn Ave., Annapolis, MD 21403.

Miller T., S. G. Smith. (2003). Modeling crab growth and population dynamics: Insights from the Blue Crab Conference. Bull Mar Sci 72(2):537-541.

Newcombe, C.L., F. Campbell, and A. M. Eckstine. (1949). A study of the form and growth of the blue crab *Callinectes sapidus* Rathbun. Growth 13:71-96.

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. J Crust Biol 3(4):575-581

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. Mar Ecol Prog Ser 41:283-294

Restrepo, V.R. (1989). Growth estimates for male stone crabs along the southwest coast of Florida: A synthesis of available data and methods. Trans. Amer. Fish. Soc. 118:20-29.

Restrepo, V.R., J.M. Hoenig. (1988). Munro's method for estimating intermolt period of tropical decapods is robust. Bull. Mar. Sci. 42(3) 488-492.

Rugolo, L., K. Knotts, A. Lange, V. Crecco, M. Terceiro, C. Bonzek, C. Stagg, R. O'reilly and D. Vaughn. (1997). Stock Assessment of the Chesapeake Bay Blue Crab (*Callinectes sapidus*). Maryland Department of Natural Resources, 267 p.

Ryer C.H. (1987). Temporal patterns of feeding by blue crabs (*Callinectes sapidus*) in a tidal marsh creek and adjacent seagrass meadow in the lower Chesapeake Bay. Estuaries 10:136-140

Ryer C.H., van Montfrans J., Moody K.E. (1997). Cannibalism, refugia and the molting blue crab. Mar Ecol Prog Ser 147:77-85

Schnute, J.T. (1981). A versatile growth model with statistically stable parameters. Can J Fish Aquat Sci 38:1128-1140.

Smith, G. (1997). Models of crustacean growth dynamics. Ph.D. thesis, University of Maryland, College Park. 337 p.

Somerton, D.A. (1980). Fitting straight lines to Hiatt growth diagrams: a re-evaluation. J Cons Int Explor Mer 39:15-19.

Tagatz, M.E. 1968. Growth in juvenile blue crabs, *Callinectes sapidus* Rathbun, in the St. John's River, Florida. Fish. Bull. 67:281-282.

van Montfrans J., Capelli J., Orth R.J., Ryer C.H. (1986) Use of microwire tags for tagging juvenile blue crabs (*Callinectes sapidus* Rathbun). J Crust Biol 6(3):370-376

van Montfrans J., Ryer C.H., Orth R.J. (1991). Population dynamics of the blue crab *Callinectes sapidus* Rathbun in a lower Chesapeake Bay tidal marsh creek. J Exp Mar Bio Ecol 153:1-14.

Von Bertalanffy, L. (1938). A quantitative theory of organic growth. Human Biol. 10:181-213.

Wainwright, T.C., Armstrong D.A. (1993). Growth patterns in the dungeness crab (*Cancer magister* Dana): synthesis of data and comparison of models. J Crust Bio 13(1):36-50.

Winget, R.R., Epifanio, C.E., Runnels, T., Austin P. (1976). Effects of diet and temperature on growth and mortality of blue crab, callinectes sapidus, maintained in a recirculating culture system. Proceedings National Shellfisheries Association 66:29-33

Table 1. Mean (± SE) initial and final juvenile blue crab carapace width, mortality, tag retention estimates, and first and second molt increments for tagged and untagged (control) crabs using coded microwire tags in a laboratory experiment. N = 15 crabs tagged and 15 crabs untagged (control). Overall tag retention was not applicable (N/A) to control groups since they did not receive a microwire tag.

	Tagged	Control
Initial CW (mm)	27.58 ± 1.16	27.99 ± 0.88
Final CW (mm)	41.28 ± 1.64	39.86 ± 1.95
Mortality (%)	6.70	13.33
Time to first molt (d)	5.93 ± 0.53	6.13 ± 0.46
(Overall tag retention (%))	87.67	N/A
Time between first and second molts (d)	12.70 ± 0.84	14.33 ± 1.11
(Tag retention between first and second molts (%))	100.00	N/A
Molt increment (mm)	8.17 ± 0.39	8.14 ± 0.41
Size increase at first molt (%)	26.7 ± 0.9	25.8 ± 1.2
Size increase at second molt (%)	28.9 ± 0.9	26.4 ± 1.0

Table 2. Functional relationships between molt increment (MI), intermolt period (IP) and premolt carapace width (X).

Model	Equation		Source
	Molt increment		
Linear	$Y = a + b*X + \varepsilon$		Hiatt (1948)
Bent-line model	$Y = a + b*X + \varepsilon$	$x \leq X_0$	Somerton (1980)
	$Y = a + b*X + c(X - X_0) + \varepsilon$	$x \geq X_0$	
Hyperbolic	$Y = K/(X - X_0) + Y_0 + \varepsilon$		Mauchline (1976)
	Intermolt period		
Linear	$Y = a + b*x + \varepsilon$		Mauchline (1977)
Cubic	$Y = a + b*X^3$		Kurata (1962)
Exponential	$Y = a*e^{b*X}$		Mauchline (1977)

Table 3. Size class (mm), days-at-large, number of crabs molting, Pm (daily probability of molting), and uncorrected and corrected IP for recaptured free-ranging blue crabs in North Carolina. Corrected IP was calculated using the procedure of Restrepo and Hoenig (1988).

Size class (mm)	Days-at-large	No. of crabs molting	P_m	$IP_{uncorrected}$	$IP_{corrected}$
25	591	39	0.07	15.15	14.17
35	362	18	0.05	20.11	18.80
45	263	9	0.03	29.22	27.32
55	187	9	0.05	20.78	19.43
65	80	3	0.04	26.67	24.93
75	194	5	0.03	38.80	36.28

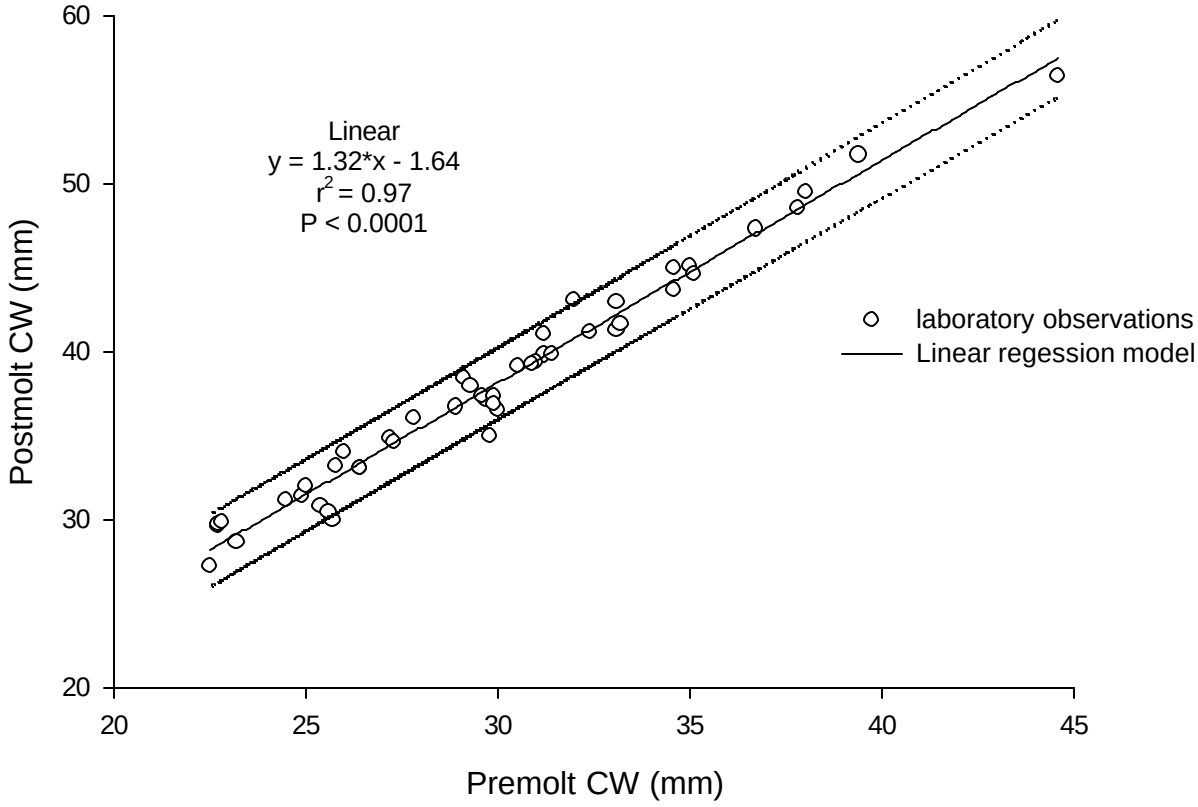


Figure 1. The relationship between premolt and postmolt carapace width (CW) for tagged and untagged juvenile blue crabs in a laboratory experiment. Molt increment for tagged and untagged crabs did not differ statistically (see text for results of statistical tests), and results were pooled for both treatments. The solid black line corresponds to a linear regression and dotted lines represent 95% confidence intervals (n = 46).

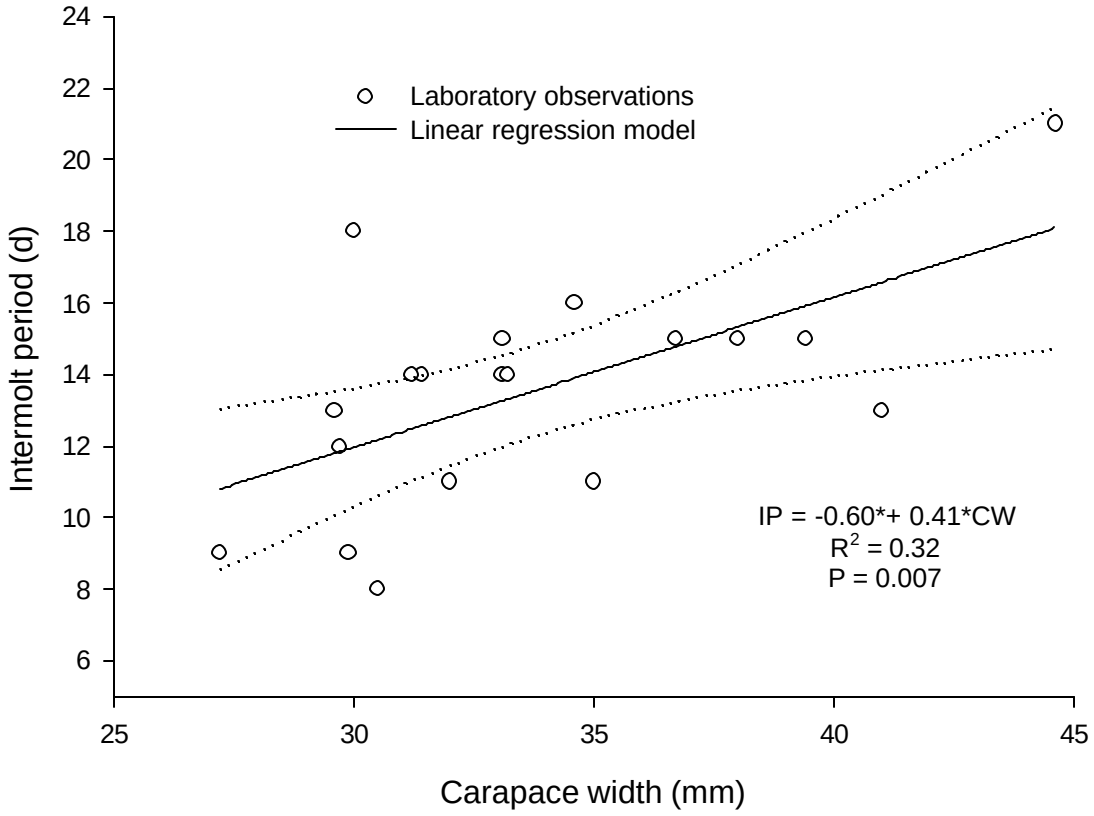


Figure 2. Relationship between premolt carapace width (CW) and exact intermolt period (IP) in days for juvenile blue crabs in a laboratory experiment. IP for tagged and untagged crabs did not differ statistically (see text for results of statistical tests), and results were pooled for both treatments. The solid black line corresponds to a linear regression and dotted lines represent 95% confidence intervals (n = 30).

.

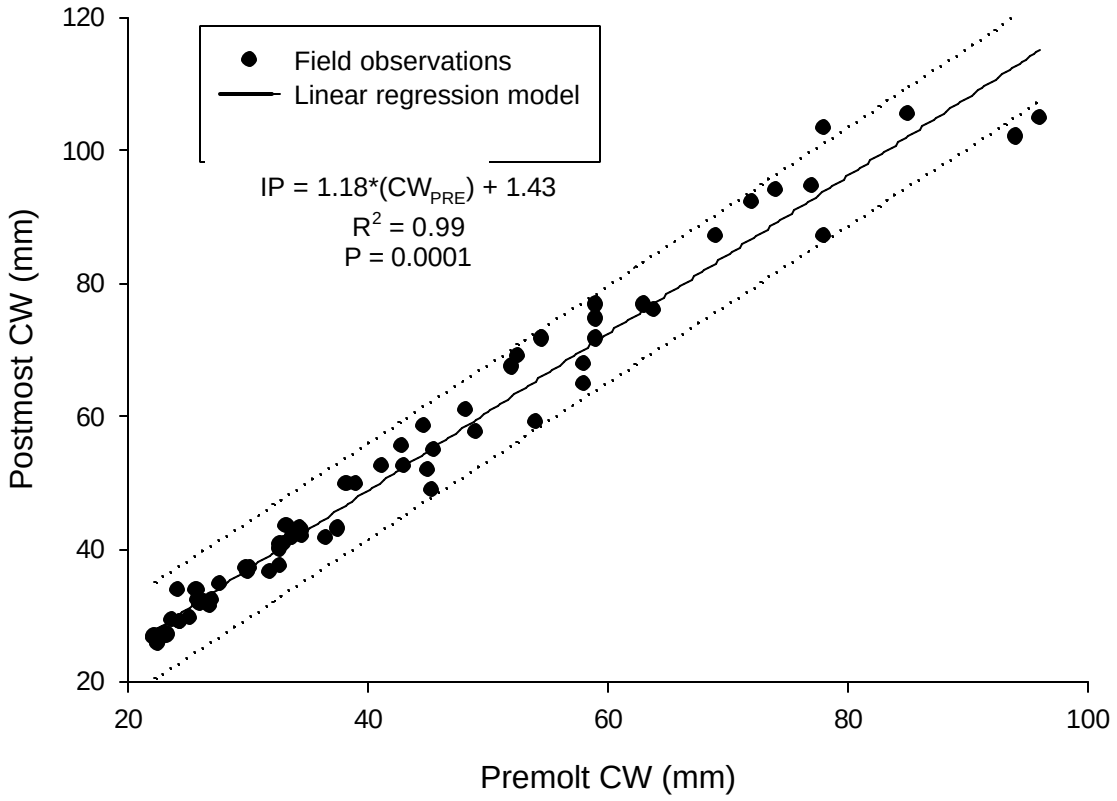


Figure 3. The relationship between premolt and postmolt carapace width (CW) for free-ranging blue crabs in the field. Molt increment for two field sites did not differ and results were pooled for both locations (PC and HS). The solid black line corresponds to a linear regression and dotted lines represent 95% confidence intervals (n = 66).

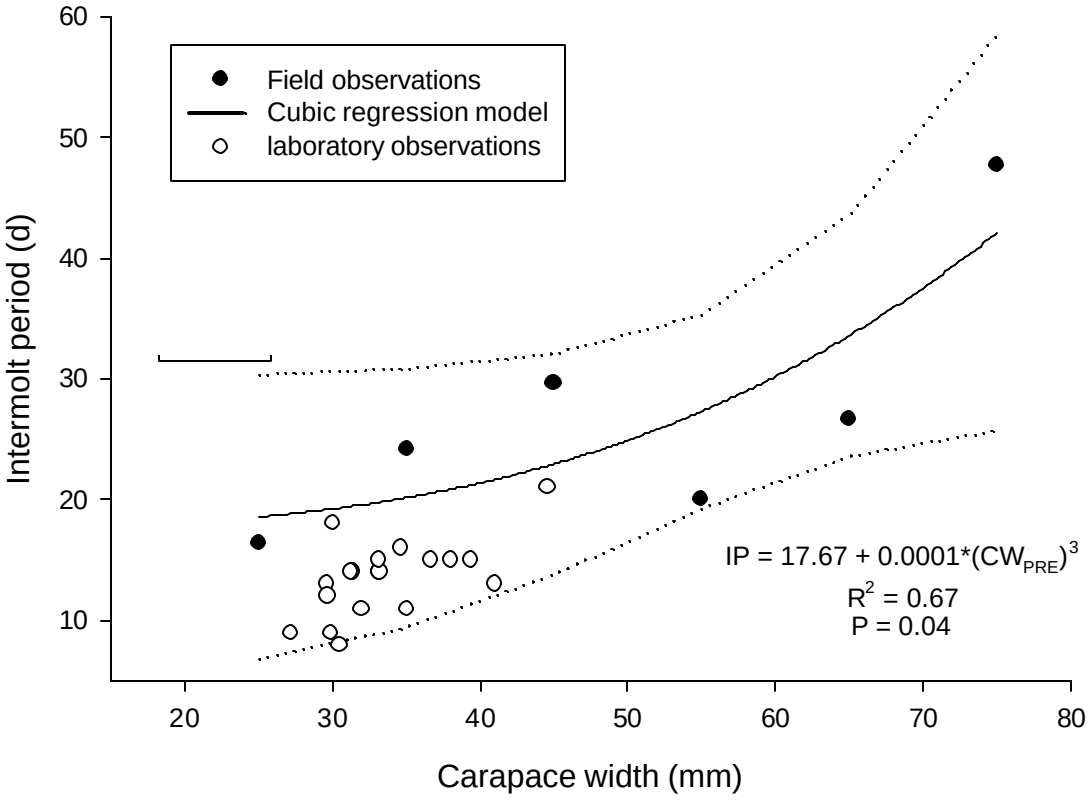


Figure 4. Relationship between premolt carapace width (CW) and estimated intermolt period (IP) for blue crabs under laboratory and free-ranging conditions. Individual data points represent the pooling of data for each size class (n = 155; see text for details.). The solid black line corresponds to a cubic regression and dotted lines represent 95% confidence intervals (n = 6).

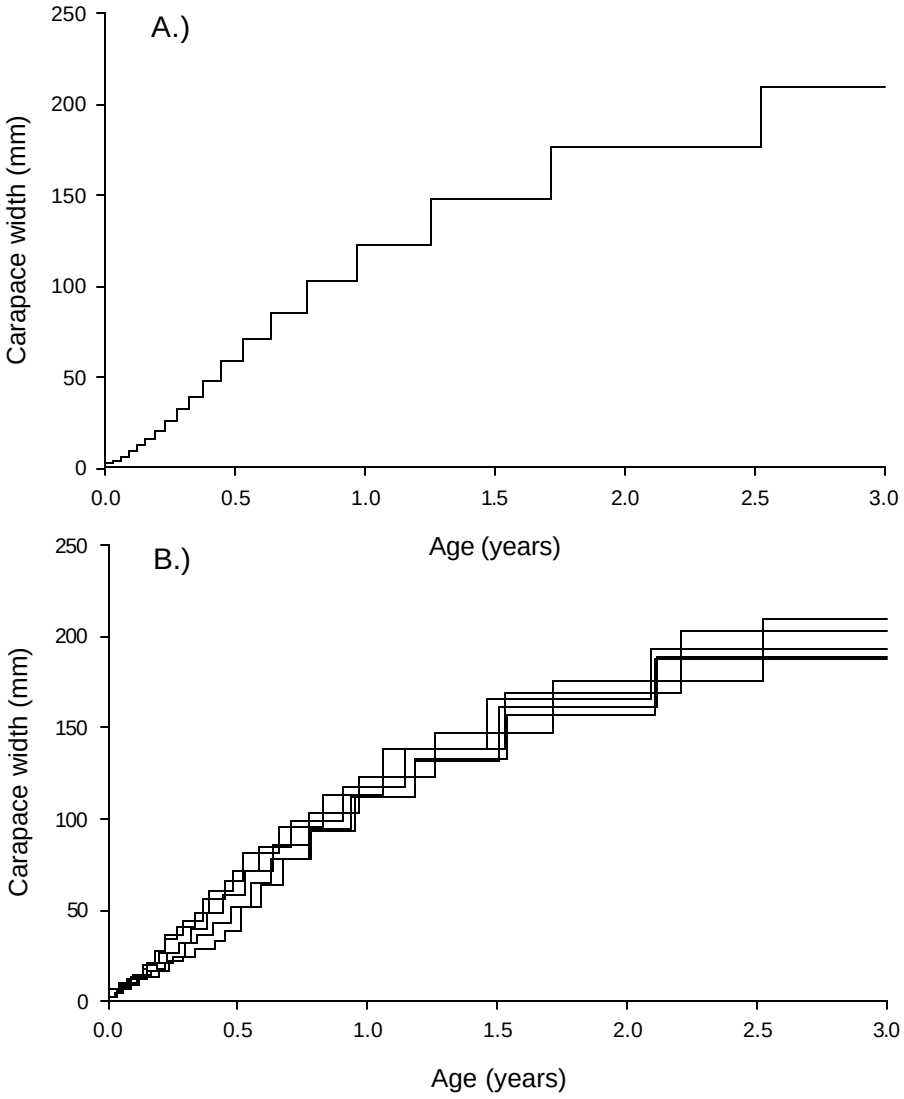


Figure 5. Simulated growth trajectories for A.) a single individual blue crab using a deterministic discontinuous growth model, and B.) five individual blue crabs using a stochastic discontinuous growth model. The magnitude of variability was estimated from relationships of premolt-CW to MI and IP from field data. See text for model details.

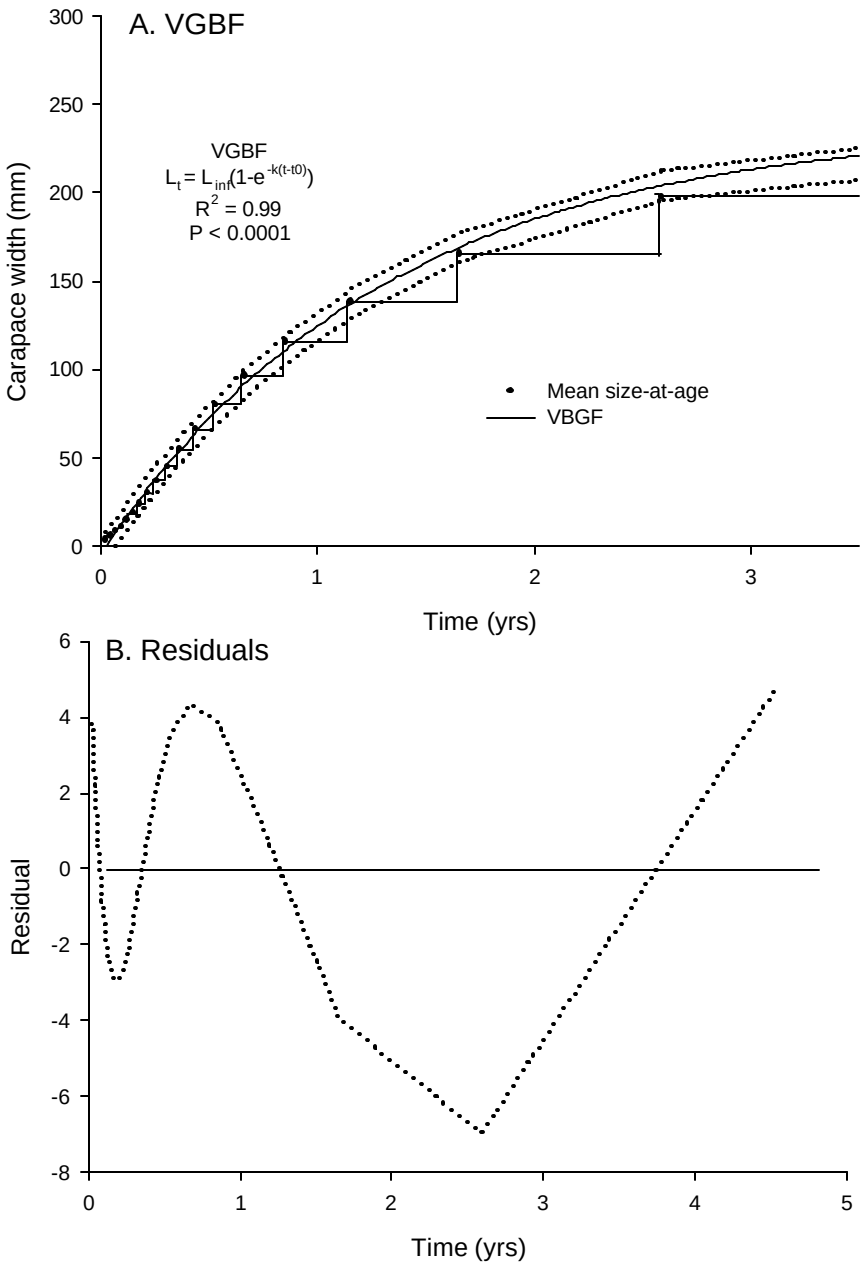


Figure 6. A.) A von Bertalanffy growth function fit to simulated mean size-at-age values from 500 simulations using the discontinuous growth model (this study). The solid black stairstep represents growth of an individual crab from the deterministic growth model (this study). The solid black curve represents the fit of the VBGF to the mean size-at-age. Dotted lines are 95% confidence for the VBGF predictions. B.) Plot of residuals (simulated mean size – VBGF prediction) for all ages.

CHAPTER 3

STOCK ASSESSMENT OF THE BLUE CRAB IN NORTH CAROLINA

EXECUTIVE SUMMARY

The blue crab (*Callinectes sapidus*) is an ecologically important estuarine predator and represents North Carolina's most important commercial fishery. Recent fishery-dependent and -independent data suggest the population is declining. An initial description of the population dynamics of the blue crab in North Carolina was provided in 1998 (Eggleston 1998). The present report builds on the previous assessment by incorporating six additional years of data (1998-2003), generating objective indices of annual blue crab abundance using length-based models, using additional modeling techniques (e.g., Collie-Sissenwine), incorporating the uncertainty involved with fisheries data and model outputs, addressing the effects of environmental variability (e.g., salinity) on spawning stock biomass and mean size of mature females, and incorporating additional information on postlarval abundance. The goal of this study was to increase our understanding of the status and population dynamics of the blue crab in North Carolina by addressing the following objectives: (1) identify long-term trends in blue crab abundance as measured with fishery-independent research surveys; (2) describe the relationship between fisheries-independent catch-per-unit-effort (CPUE) and commercial harvest; (3) identify potential relationships between stock and recruitment, as well as between different cohorts (Age 0, Age 1, Age 2); (4) estimate historical biomass and fishing mortality rates; (5) estimate fisheries management targets such as Maximum Sustainable Yield (MSY); and (6) generate biological reference points using yield-per-recruit (YPR) and spawning stock biomass-per-recruit (SSBR) analyses.

The blue crab stock in North Carolina currently sustains heavy exploitation by the commercial fishery, and information on the recreational fishery is generally lacking. There has been a systematic increase in commercial landings from 1987-1999, followed

by a period of reduced landings from 2000-2002. During this period fishery-independent indices of abundance have remained stable, or have shown a significant decline. In no case have any indices of abundance shown an increasing trend. Moreover, adult and relative spawning stock abundance (SSB) during 2000-2001 were at the lowest levels recorded since 1987. Increases in the index of relative SSB during 2002-2003, however, may indicate a recovery. We detected a significant stock-recruit relationship for the blue crab in North Carolina using certain estimates of recruit abundance. Non-parametric stock-recruit modeling (Myers and Barrowman 1996) found that recruitment was higher when relative SSB was above median values for four of six potential measures of juvenile recruitment. Estimates of annual maximum sustainable yield (MSY) from surplus production models ranged from 26.3-51.7 million pounds, similar to previous estimates of MSY for this fishery (Eggleston 1998). Average landings were near or above the maximum estimated MSY (51.7 million pounds) from 1996-1999 (e.g., 65 million pounds in 1996). Collie-Sissenwine models estimated higher abundance of legal-sized crabs in the early 1990's due to estimated strong year classes and lower fishing mortality rates, then abundance declined from 1992-2002. Estimated Fs during 1995-2001 ranged from 1.0-1.5 for the most likely estimates of M (0.55 and 0.87). Biological reference points from YPR and SSBR suggest a reduction in fishing mortality for lower rates of assumed natural mortality (M = 0.55 and 0.87) may be warranted due to both growth and recruitment overfishing concerns. We encourage decision makers to use the information and recommendations in this report as soon as possible to manage the blue crab fishery in NC in a sustainable manner.

The following sections provide a brief summary of each of the specific goals of the

study.

1. **Temporal variation in commercial effort and landings**

   Total annual hard crab landings in North Carolina steadily increased from 1953-1997, with peak landings of approximately 65 million pounds in 1996. This general increase in landings was most likely due to increased effort, landings, and reporting in Albemarle and Croatan Sounds, rather than an increase in stock size. Recent increases in landings in Pamlico Sound were likely due to new, more rigorous commercial landings reporting requirements initiated in 1994 by the NC DMF. Although there is no statistical evidence of a decreasing trend in landings, commercial landings for the blue crab for 2000-2002 were the lowest in the last 10 years (Fig. 1). A concomitant reduction in commercial effort also occurred over this same period (2000-2002). Commercial effort, which was relatively stable and low from 1953-1975, showed a sharp increase from 1976-2000 (Fig. 1). During 1976-2002, effort has been increasing at an average annual rate of 17%. Commercial effort has leveled off during 2001-2002, potentially in response to lowered catch rates in the fishery during this period (Fig 1).

2. **Criteria for selecting fishery-independent indices of blue crab abundance**

   We examined two fishery-independent trawl survey time series of blue crab catch-per-unit-effort (CPUE) collected by the NC DMF: juvenile trawl survey Program 120 (P120): 1987-2002; and adult trawl survey Program 195 (P195): 1987-2003 to provide a first order approximation of the status of juvenile and adult blue crab stocks in North Carolina. Overall, there was a general lack of coherence in trends among survey indices of blue crab abundance creating considerable uncertainty regarding current stock status. Due to this uncertainty, we considered all indices of abundance in our analyses.

Because of the up-estuary nature of sampling, P120 was biased against sampling mature females since females tend to mate in the mesohaline zone of estuaries, and then migrate seaward to inlets and spawning areas. The CPUE of mature female crabs captured in P195 in September provided a useful index of spawning stock abundance (see section: V. INDEX OF SPAWNING STOCK BIOMASS). Evidence from this index of relative SSB indicates that spawner abundance has declined in recent years (although not significantly according to statistical models) and has reached historically low levels. SSB between 2000 and 2002 was the lowest on record, 72% below the previous 10-year average. Estimates of relative SSB in 2003 suggest both an increase in SSB to average levels, and an increase in availability of mature females to P195 trawl surveys because of low salinities. Any decline in SSB is especially troubling considering the concurrent decrease in average size of mature females, the positive relationship between spawning stock and recruitment for the blue crab in North Carolina, and the possibility of recruitment overfishing.

3. **Relationship between survey indices of abundance and commercial landings**

There was no relationship between research survey indices of abundance for Age 0 crabs and commercial landings one year later. There was, however, a significant relationship between the CPUE of Age 2 crabs from P195 in September and commercial landings in the same year. Both linear and hyperbolic statistical regression models adequately described the relationship between the abundance of Age 2 crabs and commercial landings. There was also a significant relationship between the CPUE of Age 0 and 1 crabs from P120 in June and commercial landings in the same year. Although several indices were significantly correlated with landings in the same year, none of the indices

were able to predict future landings. The inability to forecast landings in advance using fishery survey data was likely due to the uncertainty of estimated indices of abundance. This uncertainty in estimated indices of abundance may be due to annual changes in availability of crabs to NC DMF trawl surveys and to changes in the magnitude of commercial landings data due to fishing effort rather than abundance.

4. Identify potential stock-recruit and relationships between cohorts

There was a relatively strong and highly significant spawning stock-recruit relationship using an index of relative SSB from P195 in September, and an index of recruits based on the CPUE of small crabs (< 60mm CW) from P195 in September of the same year. Additionally, a significant stock-recruit relationship was identified using our index of relative SSB from P195 in September and an index of recruits based on the CPUE of Age 0 crabs from P120 surveys in May and June in the following year. Statistically significant stock-recruit relationships were identified using both parametric (Ricker, Beverton-Holt, and linear models) and non-parametric methods. The Ricker function provided the best fit to observed stock-recruit data in both cases. Other potential measures of recruitment failed to produce significant fits. Correlation analyses on survey indices at appropriate lags (e.g. Age 0 in year t vs. Age 1 in year t + 1), were used to determine the extent to which surveys were able to track cohorts through successive years. Cohorts could only be tracked in the P195 survey in June. In this survey, Age 0 crabs in June were positively correlated with Age 1 crabs in the following year. No other survey programs were able to follow cohorts at appropriate lags.

5. Crab mortality rates.

Based on a maximum age (t_{max}) of 5 years from tagging studies in North Carolina (Fischler 1965), M was estimated to be 0.87 using a regression equation developed by Hoenig (1983). While we believe $t_{max} = 5$ to be the best estimate for blue crabs in North Carolina, a wide range of reported values for t_{max} have been used in previous assessments (ranging from 3 to 8; Rugolo et al. 1997, 1998, Helser and Kahn 1999). To address this uncertainty, we also calculated estimates of M using Hoenig's equation (1983) based on t_{max} values of 3 and 8. Thus, three estimates of M (0.55, 0.87, and 1.44) based on t_{max} values of 8, 5, and 3, respectively, were used in subsequent analyses.

Annual total instantaneous mortality rates (Z) were estimated with length-based methods (Hoenig 1987). Length-based estimates of mean total instantaneous annual (Z) crab mortality from 1987-2003 were 1.03 (range: 0.91 – 1.22) from P195. These estimates are similar to Zs reported for the blue crab in Chesapeake Bay (~1.0-1.5; Rugolo et al. 1998), but lower than estimates from Delaware Bay (1.19-2.90; Helser and Kahn 1999). Length-based estimates of Z were generally considerably lower than annual Zs estimated from Collie-Sissenwine modeling from over the same period (1987-2001; 1.04-2.90). There was no significant increase in mortality observed over time. Length-based estimates of Z were not generated using P120 data because the shallow water emphasis of this survey resulted in very few large crabs being captured. Although the sampling gear used in P120 can effectively sample larger crabs if they are present, this survey selects against large crabs by sampling in habitats (depth strata) in which relatively few large crabs are present.

6. Estimation of population and stock assessment parameters

We used a non-equilibrium, biomass-based stock assessment model to estimate historical biomass (B) and fishing mortality rates (F), as well as Maximum Sustainable Yield (MSY). To address the uncertainty in MSY generated from inherent variability in CPUE data, we fitted one fishery-dependent and two fishery-independent time series separately and in combination. The CPUE of legal-sized blue crabs (crabs > 127 mm CW) from P195 in June and September, and NC DMF commercial pot CPUE (Landings/# NC DMF pots) were selected as the most reliable measures of crab abundance and were fitted to the biomass-based models. Estimates of MSY ranged from a minimum of 27.9 million pounds to a maximum of 51.7 million pounds. Average landings were near or above estimated MSY from 1994-1999 (e.g., 65 million pounds in 1996). During 1996-2002, relative blue crab biomass declined steadily while fishing mortality increased sharply. Relative fishing mortality rates above 1 are inefficient and may lead to a decline in the resource; current fishing mortality rates are likely above this threshold (e.g., estimated F in 2002 was between 0.87 and 3.01). Our estimates of relative F_{MSY} and B_{MSY} indicate that the stock is currently overfished and at a low stock size (B_{2002}/B_{MSY} range: 0.43 – 0.81), and that the fishery has operated above F_{MSY} during 1996-2002. Given: (1) the known limitations of surplus production models; (2) uncertainty associated with landings prior to 1994; (3) inherent variability in CPUE data; and (4) the difficulty obtaining biologically reasonable model fits with many time series, a cautionary approach should be taken to the interpretation of biomass-based modeling results. These difficulties are not surprising, as biomass-based models have historically been applied to long-lived species, and can be unreliable for

species which exhibit high rates of intrinsic population growth (Punt and Hilborn 1996). The results, however, do suggest that the blue crab stock is currently at low biomass, and current fishing pressure likely exceeds that required to produce MSY, leading to reduced yields.

Additionally, we employed a two-stage population model (C-S; Collie and Sissenwine 1983) that has proven very useful for crustacean assessments (see Smith and Addison (2003) and references therein). The model has been used to describe blue crab population dynamics in Delaware Bay (Helser and Kahn 1999; Helser and Kahn 2001) and in Chesapeake Bay (L. Fegley, MD Department of Natural Resources, personal communication). The C-S model estimates recruit and fishable population size, as well as annual harvest and fishing mortality (F) rates. Predicted numbers of legal-sized crabs were higher in the early 1990s due to estimated strong year classes and lower Fs, then generally declined from 1992 through 2002. The estimated harvest or exploitation rate generally increased over time, although values were substantially lower and showed less of a trend for the highest M. The 10-20% exploitation rates for an assumed M of 1.44 seem unlikely, and we suspect that the M=0.55 and 0.87 cases are more realistic. For those two Ms, exploitation rates ranged from about 0.2 in 1989 to 1995-2001 levels of about 0.50-0.75. Estimated Fs in 1995-2001 for Ms of 0.55 and 0.87 ranged from about 1.0 to 1.5.

7. Biological Reference Points

Yield-per-recruit modeling suggests that current fishing mortality rates in North Carolina exceed the conservative biological reference point, $F_{0.1}$, and exceed F_{MAX}, under likely values of assumed M (0.55 and 0.87). A fishing target between $F_{0.1}$ and

F_{MAX} has been recommended for blue crabs in Delaware Bay (Helser and Kahn 1999). When the most conservative approach of M = 0.55 is used, the analyses yield a target F between 0.36 ($F_{0.1}$) and 0.51 (F_{MAX}) which suggests a reduction in fishing effort should be implemented, since current estimated Fs ($F_{1995\text{-}2001}$ = 1.28) from C-S models exceed this value. Under the assumption of M = 0.87, which we believe to be the best estimate of M, a target F would be somewhere between 0.45 ($F_{0.1}$) and 0.64 (F_{MAX}). Estimates of F from C-S models exceed F_{MAX} from 1994-2001 and range from 0.68 to 2.03. At levels of F that exceed F_{MAX}, the fishery is considered to be growth overfished. Mace and Sissenwine (1993) have advocated the use of $F_{20\%}$ (fishing mortality rate at which the SSBR is 20% of the unexploited SSBR) as a recruitment overfishing threshold. Current estimated Fs ($F_{1995\text{-}2001}$ = 0.90) from C-S models exceed $F_{20\%}$ (0.81) in North Carolina for M = 0.55, but not M = 0.87 ($F_{20\%}$ = 1.12). Particular concern regarding the status of the spawning stock is warranted, since female blue crabs are harvested at the beginning of their sexual maturity (peeler fishery) and mature females have no size protection in the hard crab fishery. Given the uncertain status of the blue crab spawning stock in North Carolina, a reduction in fishing pressure on mature females may be warranted. Further, non-parametric stock-recruit models estimate that levels of recruitment are generally greater (up to ~ 4 times greater) when relative SSB is above the median value. With the exception of 2003, relative SSB has been below the median since 1999, suggesting levels of recruitment may be inadequate replenish the SSB.

8. Conclusions

There was a systematic increase in commercial landings from 1987-1998, followed by a period of decreased landings from 2000-2002. Overall, fishery-independent indices of abundance are conflicting regarding whether or not a decline in the blue crab stock has occurred. Some indices suggest that the stock has not declined, while others suggest a decline has occurred. In no cases, however, did we find a significant increasing trend in survey indices, suggesting conservative, risk-averse management as a preferred option.

Key findings that should be considered in terms of effort management for the blue crab fishery in North Carolina include: (1) a general lack of coherence among survey indices of abundance resulting in considerable uncertainty regarding current stock status; (2) extremely low estimates of relative SSB during 2000-2002, although an increase in relative SSB in 2003 suggests a recovery of SSB to average levels; (3) the major role that environmental variation due to rainfall, hurricanes, wind-stress and temperature appear to play in annual postlarval recruitment of the blue crab, as well as crab availability to fishery-independent trawl surveys, and vulnerability to fishing; (4) a significant spawning stock-recruitment relationship with certain indices of recruitment; (5) generally increased recruitment when at levels of relative SSB above the median value; (6) females are harvested at the beginning of their sexual maturity (peeler fishery) and mature females have no size protection in the hard crab fishery; (7) a decreasing size of mature females and increasing proportion of small (< 100 mm CW) females; (8) the range of best estimates of MSY for the blue crab in North Carolina was 27.9 to 51.7 million lbs, and landings were at or above this level from 1994-1999; (9) steadily decreasing biomass and sharply increasing fishing mortality rates (0.87-3.01 times levels at MSY); (10)

decreasing numbers of legal-sized crabs from 1992-2002, concurrent with a generally increasing exploitation rate over the same period; and (11) biological reference points from YPR and SSBR that suggest a reduction in fishing mortality may be warranted due to growth and recruitment overfishing concerns.

I. INTRODUCTION

Due to the decline in fisheries resources and concomitant increase in fishing effort in North Carolina over the past decade, a moratorium was placed on the issuance of additional commercial fishing licenses in 1994. The North Carolina General Assembly then charged the NC Sea Grant College Program to conduct comprehensive studies of the fishing industry to supplement information needed by a Moratorium Steering Committee, which was responsible for making changes in fisheries management and legislation. As a part of this effort, Eggleston and McKenna (1996) evaluated fisheries resource data collection, analysis and availability for the blue crab (*Callinectes sapidus*) in North Carolina. Key information gaps identified through their study, which are relevant to this report, included a lack of information on: (1) long-term trends in blue crab abundance as measured with fishery-independent research surveys; (2) the relationship between fisheries-independent catch-per-unit-effort (CPUE) and commercial harvest; (3) spawning stock biomass; (4) stock-recruit and recruit-juvenile-adult relationships; (5) historical biomass and fishing mortality rates; and (6) fisheries management targets such as Maximum Sustainable Yield (MSY; Eggleston and McKenna 1996). In 1998, an initial assessment of the blue crab stock and population dynamics was undertaken (Eggleston 1998), the principal goals of which were to address the information gaps identified in Eggleston and McKenna (1996) by analyzing long-term fisheries data

generated by the North Carolina Department of Marine Fisheries (NC DMF). One of the key findings from the initial study by Eggleston (1998) was that annual harvest of the blue crab during 1994-1997 was above levels deemed sustainable; however, there was considerable uncertainty in estimates of MSY that necessitated a more rigorous and comprehensive stock assessment (Eggleston 1998). Such information should help produce an efficient and cost-effective stock-assessment program, facilitate forecasting of year-class strength and setting biologically-based management targets, and increase our understanding of blue crab population dynamics in North Carolina. Better information on the stock status of the blue crab in NC is urgently needed given that the moratorium on the issuance of new crab licenses was lifted in 2000, and commercial landings declined 35% from 1998-2002. This report builds on the previous assessment (Eggleston 1998) by generating age-specific indices of relative stock abundance for the blue crab using statistical length-based models, incorporating six additional years of data (Program 195: 1998-2003; Program 120: 1998-2002), including information on postlarval abundance, invetgitating the effects of environmental variability (e.g., salinity) on estimates of relative SSB and mean size of mature females, using additional modeling techniques (e.g., Collie-Sissenwine model), and incorporating the uncertainty involved with the fisheries data.

II. DESCRIPTION OF THE FISHERY

The blue crab supports North Carolina's most valuable commercial fishery in terms of total landings, the amount of gear used, employment, and value (both dockside and post-processing). For example, landings in 1996 were 65 million pounds (Table 1,

Fig. 1) with a value exceeding $40 million. Processed crab products annually range in value from $25-$50 million; this value is in addition to the harvest dockside value. Historically, many types of harvest gear have been used in North Carolina's commercial blue crab fishery, including trotlines, dredges, crab pots, and trawls. The use of crab pots has steadily increased since the 1950s (Fig. 1). Since 1994, the crab pot has accounted for, on average, 95% of the total hard blue crab harvest (Table 1; McKenna et al. 1998). The peak months of pot landings in North Carolina are May through October, which contain, on average, 89% of the total landings (Fig. 2; NC DMF Trip Ticket Data 1994-2002), with a relatively small percentage of annual landings taken from November through April (Fig. 2). Male and female blue crabs greater than 127 mm (5 in.) carapace width (CW), as well as all mature females are harvested in the crab pot fishery.

Peeler crabs are harvested through peeler pots, directed peeler trawling, or as bycatch associated with trawling for hard blue crabs and shrimp. Peelers are held in onshore-shedding systems until the crabs complete the molting cycle. Soft crabs are shipped alive or cleaned and frozen. The recent development of onshore-shedding systems and peeler pots has contributed to the steady growth in this segment of the fishery during the 1980s-2000 (McKenna et al. 1998, Chaves and Eggleston 2003). Nevertheless, the peeler and soft crab fishery accounts for, on average, only 3-4% of the total blue crab harvest in North Carolina (McKenna et al. 1998, and see this section, A. Fishery-dependent data). For example, annual peeler and soft crab landings have averaged 0.93 million and 0.68 million pounds, respectively since 1994 (Table 1, Fig. 3; NC DMF Trip Ticket data, 1994-2002). Prior to 1994, annual peeler and soft crab landings were not separated, and landings data for these segments of the fishery are

available only as the sum of peeler and soft crab landings (Table 1). The impact of the peeler fishery may be underestimated, however, as many crabs that die in shedding operations are not sold to dealers and therefore are not reported. Nevertheless, the fishery-dependent data used in this study focused on hard blue crabs landed by crab pots, since pots have accounted for 95% of the total NC landings since 1994 and have the longest time series (see this section, A. Fishery-dependent data).

Blue crabs are harvested recreationally in North Carolina with crab pots (rigid and collapsible), trawls (crab and shrimp), hand lines, and dip nets (McKenna et al. 1998). Prior to 1999, no license required to harvest blue crabs recreationally, unless a vessel is used. The bag limit on recreationally caught crabs is 50 crabs per person per day, not to exceed 100 per vessel. Beginning in 1999, all recreational fishermen harvesting blue crabs with commercial gear were required to obtain a recreational commercial gear license (RCGL; NC BC FMP: Draft 2 2004). A survey of RCGL license holders estimated that 108,050 lbs of blue crabs were harvested by RCGL license holders in 2001, and 133,421 lbs of blue crabs were harvested in 2002 (NC BC FMP: Draft 2 2004). The harvest from RCGL holders was less than 0.5% of the total blue crab harvest for 2001-2002 (NC BC FMP: Draft 2 2004). Recreational fishermen employing collapsible crab pots, cast nets, dip nets, and seines, as well as a single hard crab pot fished from privately owned land or piers are exempt from this license (NC BC FMP: Draft 2 2004). Thus, estimates of total recreational harvest for North Carolina are unavailable; however, this unaccounted segment of the fishery could be significant. For example, estimates of the Maryland recreational harvest of blue crabs in 1990 were 11.5 million pounds, whereas the commercial harvest was approximately 30 million pounds (Rugolo et al.

1997). The absence of landings data for the recreational fishery in North Carolina could be a substantial bias in population estimates that are based solely on commercial landings data.

A. Fishery-Dependent Data.

North Carolina commercial hard crab landings have averaged 21.5 million pounds during 1953-2002 (Table 1, Fig. 1). The U.S. National Marine Fisheries Service collected commercial effort statistics for the blue crab until 1984 (Fig. 1). The NC DMF initiated and augmented the collection of hard blue crab landings data in 1982 as a part of the NMFS/North Carolina Cooperative Statistics Program (Fig. 1). Both programs were based entirely upon voluntary reporting. In 1994, the NC DMF implemented a mandatory Trip Ticket program, which records landings for each commercial harvest trip. During 1994, 131 seafood dealers who had not previously reported hard blue crab landings under the voluntary collection program reported approximately 14 million pounds (26% of the total landings; McKenna et al. 1998). Thus, reliable fishery-dependent data for landings are only available since 1994. One potential solution to correct for underreporting in commercial landings was to adjust commercial landings upwards by 26% prior to 1994. While this option was considered, it was concluded that although 26% of landings in 1994 came from dealers that did not report in 1993, this value would likely result in the over-inflation of catches prior to 1993 (S. McKenna, NC DMF, pers. comm.). Thus, unadjusted landings were used throughout this report, as they were considered to be a more accurate estimate of catch over the entire time series than were adjusted landings. The use of historical landings data in this report should be

viewed cautiously and only as a general indicator of fishing trends, since they are influenced by different data collection methods, market demand, price, fishing effort, weather, availability of alternate species, regulations, and stock abundance.

Commercial crab pot landings have been reported from all coastal waters of North Carolina. The major water bodies of pot-caught hard crabs from 1994 through 2001 were Pamlico Sound (28%), Albemarle Sound (25%), Pamlico River (11%), Neuse River (7%), and Croatan Sound (5%). Although total catch for 2002 was known at the time of this report, regional landings were not. Since 1978, when a standardized fishery-independent survey of juvenile blue crabs was initiated (see section: III. FISHERY-INDEPENDENT RESEARCH SURVEY INDICES, A. Juvenile Survey (NC DMF Program 120)), hard blue crab landings have steadily increased in Albemarle and Croatan sounds (Fig. 3), most likely due to rapidly increasing fishing effort in this region (S. McKenna, NC DMF, pers. comm.). Although mean landings for the period 1978-2002 was approximately 4 million pounds in both the Neuse and Pamlico rivers, the patterns of annual landings differed between rivers. Annual landings for the Neuse and Pamlico rivers were among the most variable of all the major water bodies in North Carolina (Fig. 3). For example, with the exception of 1984, annual landings for the Pamlico River were at or below average from 1978 to 1993, above average from 1994-99, but decreased sharply in 2000-2002 (Fig. 3). Sharp increases in landings in the Pamlico River beginning in 1994 most likely reflect the NC DMF mandatory trip-ticket reporting procedures initiated in 1994. The below average landings from 1986 to 1993 (Fig. 3) in the Pamlico River may reflect increasing water quality problems rather than increased crab trawling-induced mortality rates (McKenna and Camp 1992). With the exception of

the period 1980-85, when annual landings in the Neuse River were slightly above average, landings have fluctuated above and below average on a nearly annual or biannual basis (Fig. 3). Neuse River landings for 2000 and 2001 are the lowest catches since 1978, and likely represent a large-scale decrease in abundance rather than a trend specific to the Neuse River. Annual landings in Pamlico Sound were also somewhat variable, with a steady decline from 1980 to 1986, a period of relatively constant and high landings from 1987 to 1994, followed by extremely low landings in 1995 (Fig. 3). Total annual hard crab landings from the five major water bodies combined show steadily increasing landings from 1986 to 1999, with highest landings of 65 million pounds recorded in 1996, followed by a sharp decline from 2000 to 2002 (Table 1, Fig. 1). The general increase in total annual landings was most likely due to increased effort and landings in Albemarle and Croatan sounds, as described above, rather than an increase in stock size, while the relatively low landings since 1999 reflect a lowered population size. Although soft crabs generally contributed only 3-4% to the total annual landings, they accounted for approximately 20% of the total annual landings in Croatan Sound in 1997 (Fig. 3). We re-emphasize the need for better reporting statistics on commercial effort for hard blue crabs, as well as more reliable data on landings, effort, and mortality during shedding for the peeler fishery, soft crabs, and the recreational fishery.

III. FISHERY-INDEPENDENT RESEARCH SURVEY INDICES

A. Juvenile Survey (NC DMF Program 120)

NC DMF Program 120 (P120) was initiated in 1970 as a shallow water (< 2 m) juvenile survey in primary nursery habitats, which are defined by the North Carolina

Marine Fisheries Commission (NC MFC) as those areas in the estuarine system where initial post-larval development occurs. The principal goal of P120 is to develop indices of abundance for a number of recreationally, commercially, and ecologically important species, including the blue crab. Although data generated through P120 was standardized in 1978, we present data beginning in 1987 to remain consistent with the available data from P195 data which was initiated in 1987 (see this section, B. Adult survey (NC DMF Program 195)). The gear in P120 is standardized to a 4-m otter-trawl with 0.64 cm mesh, and a towing distance of ~ 75 m. Blue crabs are separated by sex and maturity, and stations subject to commercial trawling are identified. Initially, selection of station locations was haphazard, however, since 1978 sampling stations were stratified according to eight water bodies: (1) Croatan Sound; (2) Northwest Pamlico Sound (Stumpy Pt. Bay to Abel's Bay); (3) Pamlico and Pungo rivers; (4) Southwest Pamlico Sound (Pamlico Pt. to Cedar Pt.); (5) Neuse River; (6) Outer Banks (Oregon Inlet to Ocracoke Inlet); (7) Core and Bogue sounds (Cedar Island to Bouge Inlet); and (8) Southern area (Bogue Inlet to S. Carolina line) (Table 2, Fig. 4). The number of stations has ranged from 48-109 since 1978. Presently, there are 109 core stations for this sampling program (Table 2, Fig. 4). P120 represents a relatively reliable 16-year data set (1987-2002); although the survey occurs predominantly in May-June, prior to the major recruitment period for blue crab in NC. Thus, indices of Age 0 generated from NC DMF P120 generally reflect both spring recruitment, as well as recruitment from the previous fall. Data for NC DMF P120 were not available for 2003 for inclusion in this report.

B. Adult Survey (NC DMF Program 195)

NC DMF Program 195 (P195) was initiated in 1987 as a deep water (> 2m),

survey of adult blue crabs in North Carolina. The gear used is a 9.1 m "Mongoose" trawl with a 1.9 cm cod-end. This is a stratified random sampling scheme based on area, with a total of 54 stations that were initially sampled in March, June, September and December of each year. In 1990, the sampling frequency was reduced to twice per year (June and September). Presently, there are 54 core stations (Table 3, Fig. 5); the number of sampling sites within a station has ranged from 1-341 (Fig. 6). The spatial coverage of sampling is very comprehensive for Pamlico Sound, and ranges geographically from the mouth of Albemarle Sound to the Southwest portion of Pamlico Sound, as well as the Neuse and Pamlico rivers (Fig. 6). Most of the sampling effort for P195 has been concentrated in Pamlico Sound (Table 3, Fig. 6). Similar to P120, the data for P195 were divided into eight major water bodies: (1) Albemarle Sound (Camden Point to Ned Bees Point); (2) Croatan Sound (Caroon Point to Croatan Sound); (3) Northwest Pamlico Sound (off Stumpy Point to Rose Bay); (4) Outer Banks (Gull Island to Howard Reef); (5) Pamlico River (Sandy Point to upstream of Maules Point); (6) Pamlico Sound (Long Shoal to west of Bluff Shoal); (7) Southwest Pamlico Sound (Bay River to West Bay); and the (8) Neuse River (Gum Thicket Shoal to South River) water bodies (Table 3).

C. Calculation of annual indices of abundance

Blue crab catch-per-unit-effort (CPUE) from P120 and P195 were used as relative indices of stock abundance and in various population models. Although techniques for aging blue crabs are being developed (Ju et al. 2002, 2003), direct aging of blue crabs with precision is not possible at this time. Past assessments have assigned crabs to age classes using size class proxies based on carapace-width (CW mm) increments (Rugolo et al. 1997, Helser and Kahn 1999). The size-specific indices of blue

crab abundance used by Rugolo et al. (1997) and Helser and Kahn (1999) were: 0-60 mm CW; 60-120 mm CW; and > 120 mm CW. These individual size classes are defined as Age 0, Age 1, and Age 2 crabs in the Chesapeake Bay stock assessment (Rugolo et al. 1997), and as Young-of-the-year (YOY), medium crabs, and large crabs in the Delaware Bay stock assessment (Helser and Kahn 1999). While these conventions may be appropriate for the Chesapeake and Delaware bay stocks of blue crab, application of these size/age classes to the North Carolina blue crab stock is problematic given potential differences in the timing of spawning, individual growth rates, and extended growing season. To address this concern, the catch data from the NC DMF survey programs were used to calculate age-specific indices of relative stock abundance for the blue crab using a statistical length-based model.

The length-based model estimates the proportion of crabs in each age class for each year using a maximum likelihood approach to fit a predicted length-frequency distribution to the observed fishery-independent data (P120 and P195). The predicted length-frequency distribution is generated from the three von Bertalanffy growth function (VBGF) parameters, L_∞, k, t_0, as well the standard deviation of crab CW (s). We assumed a single VBGF described the pattern of blue crab growth for all years; however, the model allowed for year-specific estimation of proportions in each age class for each survey Program (P120 and P195) and month (May, June, September). All model parameters were allowed to vary without constraint, with the exception of L_{inf}. We fixed L_{inf} at 216.9 mm CW based on an average of previous estimates for L_{inf} (187.0, 200.3, 200.6, 235.7, and 262.5; mean = 216.9 mm CW) from earlier stock assessments (Rothschild et al. 1991, Rugolo et al. 1997, Helser and Kahn 1999). This was required

since in this heavily exploited fishery, the fishery-independent surveys captured very few large, older individuals. Consequently, P120 and P195 surveys lacked sufficient information about maximum size, and did not produce biologically reasonable estimates of L_{inf} when this parameter was allowed to vary. This resulted in similar model fits over a wide range of values, since k and L_{inf} were inversely related. Similar difficulties estimating L_{inf} (values as high as several thousand mm CW) for the blue crab were encountered in Delaware Bay (Helser and Kahn 1999) using MULTIFAN (Fournier et al. 1990).

We used the Akaike Information Criterion (AIC; Akaike 1973) to determine the best fitting model from our candidate set of models. The AIC is a commonly used approach, which provides an objective method for selecting the most parsimonious model that still provides an adequate fit to the observed data. The model makes several assumptions regarding the length distribution of crabs: (1) the CWs of the crabs in each age class are distributed normally; (2) the mean CW of each age class can be described using the VBGF; and (3) the dispersion of the carapace widths of each age class about the mean length is described by the standard deviation (σ). All crabs were assumed to be born on September 15th of a given year based on life history information (see section: V. INDEX OF SPAWNING STOCK BIOMASS), and fishery-independent survey trawls were assumed to occur at the mid-point of each month (i.e. for May all trawls were assumed to occur on May 15th). Additionally, the number of age classes in the population must be assumed *a priori*; in all cases we assumed two age classes were present. The assumption of two age classes was based on the visual examination of the observed length-frequency distributions from fishery-independent trawl survey data (P120 and

P195) in which two distinct modes were generally present. While it is likely that older age classes are present in the population, given the heavy exploitation in this fishery these ages represent a small fraction of the population and do not produce a distinct mode in the data. Similar fits over a wide range of assumed ages are common when these older age classes do not represent a large portion of the population and do not exhibit distinct modes in the observed length-frequency distribution (Fournier et al. 1990).

Four sets of indices of annual abundance were generated based on data collected by P120 and 195 between 1987-2003: (1) P120 data collected from tows conducted in May; (2) P120 data collected in June; (3) P195 data collected in June; and (4) P195 data collected in September. Thus, indices of Age 0, Age 1 were generated for each trawl survey program (P120 and 195) and for each month (P120: May and June; P195 June). For example, since a September 15th birthdate is assumed for all crabs, Age 0 crabs in May are 0.66 years old (241d / 365d = 0.66), and Age 1 crabs were 1.66 years old. The only exception was P195 in September in which only indices of Age 1 and Age 2 crabs were generated. No index of abundance for Age 0 crabs was available for this time series because the timing of the survey (September 15th) relative to the assumed birthdate of September 15th (August-September; see section V. INDEX OF SPAWNING STOCK BIOMASS) and the deep water focus of this trawl program failed to capture large numbers of Age 0 crabs. Thus, the first mode in the observed length-frequency for P195 in September is crabs that are effectively one year old (see this section: B. Adult survey (NC DMF Program 195)). Since a September 15th birthdate is assumed for all crabs, and surveys are assumed to occur at the mid-point of month (i.e. September 15th) Age 1 crabs in the P195 September survey are 1.0 year old (365d / 365d = 1.0), and Age 2 crabs were

2.0 years old. A single growth curve was fitted to the P120 data from both months (May and June) simultaneously. The joint analysis of two points in time (May and June) should capture additional information on growth based on the shift in size modes from May to June within a given year. Similarly, a single growth curve was fitted to P195 in June and September simultaneously.

In general the length-based model provided a resonable fit to the observed length-frequency data from the trawl surveys in most years (Figs. 7-10). AIC values were used to select the best fitting model for each trawl survey program and month. Model parameters from best fitting model runs (Tables 4, 5) were used to estimate size/age classes for a given year, and to estimate growth rates of blue crab in North Carolina (Tables 4, 5; see section VII. LIFE HISTORY CHARACTERISTICS, A. Estimation of growth rates for details).

D. Correlation analyses of length-based indices of abundance

We conducted correlation analyses on our annual length-based estimates of abundance for three purposes: (1) to determine whether the multiple indices of abundance for a given year class covaried (i.e., Do the indices of Age 0 abundance from P120 trawls in May, P120 trawls in June, and P195 trawls June, and Age 1 abundance from P195 show similar patterns within a given year?); (2) to determine whether individual cohorts could be tracked over successive years (i.e., Does Age 0 abundance in a given survey in year t predict Age 1 abundance in year t + 1?); and (3) to determine whether indices of abundance for all age classes were correlated within a single year (i.e., Do the indices provide an accurate estimation of abundance, or do they reflect changes in the annual availability of blue crabs to the survey gear?).

To determine the extent to which different indices of abundance (Table 6) covaried, we conducted correlation analyses for all survey indices within the same year. If the indices of abundance for Age 0, Age 1 and Age 2 crabs from the different survey programs and months were significantly correlated within years, it would provide a greater level of confidence in survey data. Given the timing of the survey programs, the estimates of P120 Age 0 crabs in May (0.66 years), P120 and P195 Age 0 crabs in June (0.75 years) and P195 Age 1 crabs in September (1.0 years) were considered to represent a single age class over time and used for within year calculations. Similarly, P120 Age 1 in May and June, P195 Age 1 in June and P195 Age 2 crabs in September were also considered for within year analyses. The results indicated that only indices of Age 0 crabs for P120 May and P120 June were positively correlated ($r = 0.485$, $P = 0.028$; Table 7). Indices of Age 1 crabs for P120 May and P120 June were positively correlated, but the correlation was only marginally significant ($r = 0.403$, $P = 0.061$; Table 7). No other indices of Age 0, Age 1 or Age 2 abundance were significantly correlated, indicating considerable variation within annual estimates of abundance. Due to this uncertainty, we considered all indices of abundance in our analysis.

Correlation analyses on survey indices at appropriate lags (e.g. Age 0 in year t vs. Age 1 in year t + 1), were used to determine the extent to which surveys were able to track cohorts through successive years. Cohorts could only be tracked in the P195 survey in June. In this survey, Age 0 crabs in June were positively correlated ($r = 0.537$, $P = 0.016$) with Age 1 crabs in the following year (Table 7). The relationship between P195 June Age 0 and Age 1 blue crabs was described by a statistically significant linear regression model (Fig. 11). No other survey programs were able to follow cohorts at

appropriate lags (Table 7). The inability of P120 in both May and June to track cohorts may be a result of the timing and spatial coverage of this survey. The length-frequency data from P120 suggests that this survey collects a large abundance of small crabs (CW < 20 mm, Figs. 7, 8) in the spring. These crabs are too small to have recruited to the estuary in the fall, and these indices are partially tracking recruitment of juvenile crabs from spring spawning females. Data also suggests that the offshore concentration of megalopae in the late summer and fall is much greater than in the spring (see section: V. INDEX OF SPAWNING STOCK BIOMASS; Relative abundance of blue crab larvae and megalopae), suggesting that the primary recruitment of crabs into the estuary occurs in the fall. Thus, the index of Age 0 crabs from P120 surveys seems to partially reflect the abundance of spring spawned crabs, but also effectively captures larger Age 0 crabs (40 – 80 mm CW) that presumably resulted from the fall spawn of the previous year.

We also tested for correlations between indices of abundance for all age classes within the same year. If indices are an accurate measure of abundance, one would expect to see high correlation between age classes in successive years, but not in the same year. High correlation between different age classes within a single year may be a result of changing availability to the survey gear due to environmental factors that result in large or small numbers of all age classes of crabs being available to the survey gear. Similar to analyses from Chesapeake Bay (Rugolo et al. 1997), we found a high level of correlation between age classes within years (Table 8) suggesting that certain survey indices may better reflect availability of crabs to the survey gear than relative abundance. The correlation between indices of Age 0 and Age 1 crabs in the same year for P120 in May was not significant. P120 indices of abundance in June for Age 0 and Age 1 crabs,

however, were significantly and positively correlated ($r = 0.74$, $P < 0.001$, Table 8). P195 indices of abundance in June were also significantly correlated between Age 0 and Age 1 ($r = 0.581$, $P = 0.01$). P195 September indices of Age 1 and Age 2 crabs were not significantly correlated (Table 8). These results suggest that certain P120 and P195 blue crab trawl survey indices reflect availability to the survey gear to an extent, and annual availability may mask any cohort signal over time. This finding underscores the need to examine the effect of environmental factors on the distribution and abundance of blue crabs in North Carolina relative to the current spatial coverage of current NC DMF survey programs, and how this environmental variation drives crab availability to the surveys.

E.) TRENDS IN INDICES OF ABUNDANCE

1. Size-frequency analysis of Program 120 data

Carapace width-frequency distributions were prepared for each survey program (sexes combined). Crabs were pooled by CW into 5-mm length groups. From 1987-2002, P120 in May (Fig. 7) and June (Fig. 8) collected early juvenile through adult stages of blue crabs ranging in size from 5 to 200 mm CW. As intended, however, P120 captured primarily small juvenile crabs less than 40 mm CW (Figs. 7, 8). The general increase in size frequency of juvenile crabs to a peak of approximately 20-40 mm CW (Figs. 7, 8) may suggest that crabs were not fully recruited to the sampling gear used in P120 until this size, and suggests that these surveys are primarily tracking the abundance of a spring cohort. This survey, however, may also effectively track the abundance of fall spawned Age 0 crabs, as it collects larger Age 0 crabs as well (40 – 80 mm CW). Crabs

of this size (40-80 mm CW) presumably resulted from the fall spawn of the previous year. The P120 survey is not as effective at capturing larger individuals, probably because larger crabs occupy deeper waters (> 2m) and are not available to the survey.

2. Trends in the Program 120 indices of abundance

Overall, mean juvenile CPUE in May was higher for Age 0 blue crabs (mean = 6.34 crabs per tow) than for Age 1 (mean = 1.17 crabs per tow) crabs (Table 6, Figs. 12, 13). No long-term pattern in the time series of Age 0 crabs from P120 May between 1987-2002 was evident (Fig. 12), and linear regression revealed no significant trends. The abundance of Age 0 crabs in May for the most recent year for which data was available (2002) was similar to the long-term (16 year) average (Table 6, Figs. 12, 13). Similar to the May time series, the mean CPUE for P120 in June was higher for Age 0 crabs (mean = 5.46 crabs per tow) than for Age 1 (mean = 3.22 crabs per tow; Table 6, Fig. 12); however, the June time series is slightly more variable (coefficient of variation (CV) = 0.44) than the May series (CV = 0.36; Table 6). This increased variation in crab abundance from May to June is largely a result of the large CPUE value in 1998 (Fig. 12). No long-term pattern in the time series of Age 0 crabs from P120 June (Fig. 12) was identified using linear regression models, and the abundance of Age 0 crabs in June 2002 was just below the long-term (16 year) average (Fig. 12). Similarly, the index of Age 1 crabs from P120 May did not show any statistical trends in abundance over time (Fig. 12), and abundance of Age 1 crabs in 2002 is just above the long-term average (Fig. 12). The index of Age 1 crabs from P120 June was also trendless, but exhibited a large spike in 1998 (Table 6, Fig. 12). Overall, no trends in abundance were evident over time for Age 0 or 1 blue crabs from the P120 May or June surveys (Fig. 12) and abundance in

2002 appears to be at or near the long-term average.

3. Size-frequency analysis of Program 195 data

The size frequency of blue crabs captured in P195 ranged from 20-200 mm CW, and was skewed towards larger sized crabs (> 60 mm CW, Figs. 9, 10). In most years, length-frequency distributions exhibit clear modes suggesting the existence of individual cohorts (e.g. Fig. 9, 1987, Fig. 10, 1996). Although crabs > 127 mm CW are harvested by the fishery, relatively large numbers of crabs above this size class were captured in most years (Figs. 9, 10).

4. Trends in Program 195 indices of abundance

Overall, mean CPUE from P195 June was higher for Age 0 crabs (mean = 34.56 crabs per tow) than for Age 1 (mean = 14.04 crabs per tow) crabs. (Table 6, Figs. 14, 15). No long-term pattern in the time series of Age 0 crabs from P195 June (Fig. 14) was evident, and a linear regression model revealed no significant trends. The abundances of Age 0 crabs in June of 2002 and 2003 were well above the long-term (17 year) average and the second and third highest on record, respectively (Table 6, Fig. 14). A statistically significant ($r^2 = 0.28$, $P = 0.03$) decline in the abundance of P195 June Age 1 crabs, however, was identified using linear regression (Fig. 14), and current abundance was estimated to be well below the long-term average (2003 = 4.47 vs. mean = 12.12; Fig. 14). Mean CPUE from P195 September was lower for Age 1 blue crabs (mean = 5.27 crabs per tow) than for Age 2 (mean = 6.31 crabs per tow) crabs (Table 6, Fig. 14). Linear regression identified a significant ($r^2 = 0.37$, $P = 0.01$) decline in CPUE of Age 1 blue crabs from P195 September (Fig. 14). The mean CPUE of P195 September Age 2 crabs did not exhibit a trend over time, and abundance in 2003 was the highest observed

between 1987-2003 (Fig. 14).

Overall, there was a general lack of coherence in trends among survey indices of blue crab abundance suggesting considerable uncertainty regarding current stock status. P120 surveys for Age 0 and Age 1 crabs indicate that population size has remained at or near a long-term average. It should be recognized, however, that these surveys were not designed to target Age 1 and Age 2 blue crabs and may not provide the best estimates of larger individuals. In some cases, P195 data exhibited a statistically significant trend toward declining population abundance over time (P195 June Age 1, September Age 1; Fig. 14). The 2003 values for P195 June Age 0 and September Age 2 (Fig. 14) were well above the long-term average, but were not consistent with a single strong year class (the record CPUE value for Age 2 crabs in September 2003 should be evident in Age 1 CPUE in June). The values for P195 June Age 0 and September Age 2 were well above the long-term average (Age 2 crabs in P195 September was the highest on record; Fig. 14). Overall, indices of relative abundance are conflicting between P120 and P195 regarding whether or not a decline in stock abundance has occurred. Nevertheless, in no case did we find a significant increasing trend in survey indices, suggesting that a conservative, risk-averse management strategy would be advisable.

IV. RELATIONSHIP BETWEEN SURVEY INDICES AND LANDINGS

Identifying the relationship between research survey indices of blue crab abundance and commercial landings is essential for forecasting fishery year class strength. The abundance of blue crab recruits from fishery-independent surveys has been used to predict harvest for both the Chesapeake and Delaware bays (Speir et al. 1995).

The CPUE of mature crabs (> 4.7 inches or 120 mm CW) is positively correlated with commercial landings and effort in Chesapeake Bay (Lipcius and Van Engel 1990, Speir et al. 1995). Conversely, in NC McKenna and Camp (1992) did not find a correlation between the CPUE of juvenile crabs in the Pamlico River and subsequent commercial landings.

We used correlation analyses, as well as linear and non-linear regression procedures to identify possible relationships between blue crab fishery-independent CPUE estimates generated from length-based models for NC DMF P120 and 195, and commercial landings. For P120 in May, there was no relationship between the CPUE of Age 0 or Age 1 blue crabs and commercial landings with or without annual lags (Table 9). Conversely, there was a positive and statistically significant relationship between both P120 June indices of crab abundance (Age 0 and 1) and landings the same year (Table 9). The relationship between P120 Age 1 blue crabs in June and commercial landings the same year was described by a non-linear (hyperbolic) regression model (Fig. 16) when all years were considered. The relationship between P120 Age 1 crabs in June and commercial landings was described by linear model when data from 1998 is removed (Fig 16). The relationship between P120 Age 0 blue crabs in June and commercial landings in the same year is likely spurious; a result of autocorrelation of the Age 0 and Age 1 indices due to availability to the survey gear (see section: III. FISHERY-INDEPENDENT RESEARCH SURVEY INDICES, D. Correlation analyses of length-based indices of abundance). There was no relationship between P120 indices of blue crab abundance in June and landings lagged by one or two years (Table 9). For P195 June, there was no relationship between the relative abundance of Age 0 and 1 blue crabs,

and landings with or without annual lag (Table 10). Conversely, there was a positive and statistically significant relationship between P195 September Age 2 crabs and commercial landings the same year; none of the other P195 September indices were correlated with landings (Table 10). The relationship between P195 Age 2 blue crabs in September and commercial landings the same year was described equally well by linear and non-linear regression models (Fig. 17). Thus, although several fishery-independent indices of blue crab abundance are correlated with landings the same year, none of the indices are capable of predicting landings 1 to 2 years in advance.

V. INDEX OF SPAWNING STOCK BIOMASS

There are two primary fishery-independent surveys in NC (P120 and P195), each of which includes several monthly sampling events, and 2-size/age classifications, providing a number of potential indices of spawning stock at various points in time. Both crab sex and maturation stage are recorded in the NC blue crab surveys. Thus, rather than use a size-based proxy to estimate abundance of mature females, we used a direct measure, which avoided underestimating the spawning stock size given an apparent decline in mean size at maturity (see this section: Trends in spawning stock biomass). The relative abundance of mature females was converted to relative spawning stock biomass (SSB) to better capture the decline in mean size-at-maturity. Conversions from crab size (mm CW) to biomass are described in the yield-per-recruit section below (see section: VIII. BIOLOGICAL REFERENCE POINTS, A. Yield- and Spawning Stock Biomass-per-Recruit Analyses).

We used CPUE data from P195 in September for our index of spawning stock based on biological evidence that the offshore larval concentrations and subsequent poastlaval recruitment to Pamlico Sound are highest in August and September, respectively, and that relative abundance of mature females on the major inlet spawning sanctuaries in NC is relatively high in August. Moreover, P195 uses sampling gear that targets adult crabs in Pamlico Sound, as opposed to P120, which uses gear and samples in shallow areas to target juveniles. In addition, indices of mature females in September from P195 should better reflect the abundance of mature females available to spawn than the abundance of mature females measured in June, the only other month P195 samples, given the intense fishing pressure during July and August. Lastly, there is a significant spawning stock-recruit relationship using P195 September spawners, but not using June spawners (see section: VI. SPAWNING STOCK-RECRUIT RELATIONSHIP, A. Parametric stock-recruit relationships). In the paragraphs below, we provide information in support of our decision to use September P195 data for an index of blue crab spawning stock in NC.

Relative abundance of mature females on spawning sanctuaries.

Newly inseminated female blue crabs either migrate to seaward inlets in NC or the lower Chesapeake Bay during summer, or migrate in fall, overwinter, and then spawn the following year (Van Engel 1958; Tagatz 1968; S. McKenna, NC DMF, unpubl. data). The collective evidence from published and unpublished data indicates that egg-bearing female blue crabs are present and spawn on the inlet sanctuaries from spring through fall in NC and Chesapeake Bay (Dudley and Judy 1971; Prager et al. 1990; Ballance and Ballance 2002; Eggleston 2003; Lipcius et al. 2003; Medici 2004). Peak abundance of

mature female crabs in the major NC inlets occurs in May and August (Dudley and Judy 1971, Ballance and Ballance 2002, Eggleston 2003). For example, Eggleston's (2003) trawl surveys at all of the inlet spawning sanctuaries in NC in 2002 indicated similar relative abundance of mature females within the sanctuary versus a ~ 5 km distance away from the sanctuary (inshore & offshore) during June-September, with peak abundance in August (Fig. 18). Fishery-independent crab pot surveys from Ocracoke Inlet indicate peak abundance of mature female blue crabs in May and August, with peak abundance of egg-bearing females in May (Ballance and Ballance 2002).

Relative abundance of blue crab larvae and megalopae.

Nichols and Keney (1963) found peak concentrations of blue crab larvae and megalopae off North Carolina in August compared to other months (Fig. 19). Dudley and Judy (1971) found highest larval concentrations in June-August, with highest megalopal concentrations in September-November. Similarly, Eggleston (unpubl. data) identified a relatively weak pulse of blue crab megalopae that settled to artificial settlement substrates near Oregon Inlet in spring, followed by a major pulse in fall (Fig. 20). The fall recruitment pulse of megalopae to Pamlico Sound has been observed annually since 1996 (Etherington and Eggleston 2003, Eggleston unpubl. data). Thus, irrespective of the origin of blue crab larvae to Pamlico Sound, or the fact that mature, egg-bearing female crabs are present on the spawning grounds throughout the summer, the main recruitment period of blue crabs to Pamlico Sound appears to be late summer-early fall. Given that the larval duration of the blue crab is documented at ~ 30 d (Van Engel 1958; McConaugha et al. 1983), the blue crab spawning stock sampled by P195 in September appears to better reflect the relative abundance of those crabs available to

spawn in August compared to the relative abundance of mature females surveyed by P195 in June, since the abundance of crabs sampled in June declines greatly during the summer (Fig. 21). It remains to be determined if the relatively high blue crab larval concentrations offshore of NC and SC in August and subsequently high megalopal settlement in Pamlico Sound in September is due to (1) peak spawning of blue crabs in Pamlico Sound in August, or (2) continual spawning of blue crabs during spring-fall with oceanographic conditions most favorable for inshore transport only during early fall. Mechanisms underlying #2 could involve both active (delayed metamorphosis) or passive (storm-driven transport) recruitment processes.

Trends in relative spawning stock biomass (SSB) and size of mature females

Spawning stock biomass. No statistically significant decline in SSB was observed from 1987-2003 (Fig. 22). The mean index of SSB from 2000-2002, however, declined 72% from the previous 10-year average, and produced the three lowest recorded values for SSB since P195 was initiated in 1987 (Fig. 22). Following this period of low abundance, SSB has appeared to rebound in 2003, and was the second highest value recorded since 1987 (Fig. 22). While the 2003 index of spawning stock may indeed reflect an increase in SSB from low levels, a precautionary approach is warranted when interpreting the 2003 value because blue crabs shift their distribution within Pamlico Sound depending on salinity, which determines their availability to P195 surveys. For example, we suggest that blue crabs shift their distribution downstream during wet years as was the case following hurricane floodwaters in 1999 (Fig. 23), which makes them more available to P195. Conversely, blue crabs likely shift their distribution upstream during dry years (S. McKenna, NC DMF pers. comm.), which would make blue crabs less available to P195

surveys. To determine the extent to which availability of mature females to the P195 trawl survey was driven by annual fluctuations in salinity, we examined the relationship between our index of SSB and mean annual salinity. We fit both linear and hyperbolic regression models to the relationship between the index of SSB and mean salinity from P195. A statistically significant ($r^2 = 0.49$, $P = 0.008$) relationship was identified using non-linear hyperbolic regression (Fig. 24a) and provided the best fit to the observed data. We then examined the residuals (i.e., observed SSB - predicted SSB) from the regression of salinity on relative SSB to examine the trend over time while controlling for effect of salinity (Fig 24b). The residuals from regression models are used frequently in statistical analyses to remove the confounding effects of variables (Garcia-Berthou 2001, Freckleton 2002). Although multiple regression and ANCOVA are recommended as more powerful techniques that control for autocorrelation (Garcia-Berthou 2001, Freckleton 2002), these approaches were precluded due to the summary of data into annual means. Nevertheless, our approach is valid since no autocorrelation existed between salinity and year. Two major differences are apparent in the patterns of the residuals when the effects of salinity are removed, (1) SSB was underestimated by P195 in 2002, and (2) SSB was overestimated by P195 in 2003 (compare Figs. 22 and 24b). Thus, it appears the large increase in relative SSB in the P195 September survey in 2003 (Fig. 22) reflects both an actual increase in spawning stock from historic lows observed during 2000-2001 to average levels, and an increase in availability of mature females to survey gear due to low salinity. P195 surveys were conducted in October rather than September 2003 due to delays from the passage of hurricane Isabel in mid-September.

Size of mature females. Concurrent with the decline in SSB between 1996-2002 are two

related trends: (1) a declining trend in the average size of mature females from 1987-2002, and (2) an increasing proportion of extremely small mature females (CW < 100 mm CW) in the spawning stock (Fig. 25). Mature females were identified using the semi-circular morphology of the female abdominal apron that is characteristic of maturity. The average carapace width of mature females over time was variable, potentially due to annual fluctuations in salinity; blue crabs mature at a smaller size as temperature and salinity increase (Fisher 1999). Although untested, a negative correlation between size and salinity was suggested for blue crabs in Chesapeake Bay (Tagatz 1968), and results of laboratory experiments have suggest blue crabs will achieve maximum size in low salinity waters at high temperatures (Cadman and Weinstein 1988). The physiological mechanism for crabs achieving a relatively large size at low salinities is unknown.

To determine if annual fluctuations in salinity affected the mean size of mature females in NC, we examined the relationship between mean CW of mature females and salinity from the P195 trawl survey. A marginally significant ($r^2 = 0.18$, $P = 0.10$) relationship was identified using linear regression (Fig. 26a). We then examined the residuals (i.e., observed CW– predicted CW) from the regression of salinity on mean CW of mature to determine if there was still a decline in mean size of mature females (Fig. 26b) over time. A linear regression on the residuals identified a statistically significant ($r^2 = 0.37$, $p = 0.01$) decline in mean size of mature female blue crabs over time after removing the effects of salinity (Fig 26b). There also appears to be an increasing and marginally significant ($r^2 = 0.23$, $P = 0.06$) trend in the proportion of small (CW < 100 mm) mature females in the population (Fig. 25b).

This decline in mean size of mature females may be the result of the implementation of cull rings, mandated by NC DMF in 1989, leading to increasing proportion of escapement from crab pots by small females (< 127 mm CW), although cull rings have been exempted by proclamation in the Outer Banks area since 1994. A decline in average size-at-maturity may also reflect a compensatory response by the population to reproduce as soon as possible under intense exploitation rates (Bertelsen and Cox 2001). A similar pattern of concurrent decline in spawning stock abundance and average size has been documented for Chesapeake Bay (Lipcius and Stockhausen 2002). Similar to the North Carolina fishery, crab pots in both the Maryland and Virginia waters of Chesapeake bay must have at least 2 cull rings (one at least 2 3/16" and a second at least 2 5/16"); however, cull rings may be closed on the seaside of the eastern shore within areas open to crab dredging. Because blue crab fecundity increases with size (Prager et al. 1990), a simultaneous decline in both spawning stock abundance and size-at-maturity will produce a synergistic reduction in spawning potential.

Overall, the evidence from trends in the index of SSB and size-at-maturity for female blue crabs indicates that spawner abundance and biomass declined to historic low levels during 2000-2001, but increased during 2002-2003 to near the long-term (17 year) average (Fig. 24b). We believe the low SBB values from 2000-2001 accurately reflect a low abundance in spawning stock during this period because: (1) intense, localized fishing of crabs migrating to high salinity waters following multiple hurricanes in 1999 (Dennis, Floyd, and Irene; Fig. 23) resulted in an increase in catchability within Pamlico Sound that was 369% above the average from 1987 – 1998 (Fig 27), and (2) there were concurrent declines in varying life history stages of the blue crab in 2000-2001. Thus, it

appears that the blue crab spawning stock is susceptible to overfishing during extreme flooding events (1999), and the large increase in relative SSB in 2003 reflects both an actual increase in spawning stock from historic lows observed during 2000-2001 to near average levels, and an increase in availability of mature females to survey gear due to annual changes in salinity.

VI. SPAWNING STOCK RECRUIT RELATIONSHIP

A. Parametric stock-recruitment relationships

The relationship between spawner abundance and subsequent recruitment is one of the most fundamental issues in fisheries management because in the absence of a stock-recruit relationship, managers would only be concerned with maximizing yield-per-recruit (YPR; Hilborn and Walters 1992). The goal of stock-recruit analyses was to determine if a fishery-independent index of spawning stock abundance (Relative spawning stock biomass of mature females collected in Program 195 September trawls; SSB) and several potential indices of recruitment could be described with standard stock-recruit functions (Ricker, Beverton-Holt), as well as non-parametric methods (Myers and Barrowman 1996). Specifically, we examined the relationship between relative SSB in year t and six potential indices of recruitment: (1) postlarval index of abundance in year t; (2) P195 CPUE of crabs 0 – 60 mm CW collected in September of year t; (3) P195 CPUE of Age 0 crabs collected in June of year t + 1; (4) P120 CPUE of Age 0 crabs collected in May of year t + 1; (5) P120 CPUE of Age 0 crabs collected in June of year t + 1; and (6) P120 CPUE of Age 0 crabs collected in May and June in year t + 1 combined. The Ricker stock-recruitment model (Ricker 1954) is one of the two most commonly used

models. According to this model, maximum recruitment is at an intermediate stock size and declines in a density-dependent manner towards zero as spawning stock size increases. The equation relating recruitment (R) to spawning stock size (S) is:

$$R = aS*e^{(-bS)}$$

where a and b are model parameters. Some possible biological mechanisms for the density-dependence assumed in Ricker's model include (1) cannibalism of early juvenile crabs by older juveniles and adults (Lipcius and Van Engle 1990, Hines and Ruiz 1995), and (2) density-dependent mortality of early juvenile crabs (Pile et al. 1996, Etherington and Eggleston 2000).

The Beverton-Holt (B-H) model (Beverton and Holt 1957) has also been widely used to fit stock-recruitment data. According to this model, recruitment is essentially constant over a wide range of spawning stock levels. The equation relating recruitment (R) to spawning stock size (S) is:

$$R = \frac{1}{(a + b/S)}$$

where a and b are model parameters.

Ricker, B-H, and linear stock-recruit models were fitted to the various indices of blue crab recruitment and the index of relative SSB (Figs. 28, 29). There was a relatively strong and highly significant spawning stock-recruit relationship using an index of relative SSB from P195 in September, and an index of recruits based on the CPUE of small crabs (<

60mm CW) from P195 in September of the same year. Although Ricker, B-H, and linear relationships all produced significant fits, we used the Akaike Information Criterion (AIC; Akaike 1973) to determine the best fitting model from our candidate set (Ricker, B-H and linear). Using this selection criterion the Ricker model generated the best fit to the data (AIC weight = 0.51). A good model fit was also generated using the B-H stock-recruit function (AIC weight = 0.44) indicating that the Ricker and B-H models were both able to adequately describe the observed stock-recruit relationship. The linear model generated a much poorer fit to the entire data series (AIC weight = 0.05). A significant stock-recruit relationship was also identified using our index of relative SSB from P195 in September and an index of recruits based on the CPUE of Age 0 crabs from P120 surveys in May and June in the following year. We chose to model the stock-recruit relationship of the blue crab in NC using a Ricker model because it produced the lowest AIC value for both indices of recruitment (P195 September crab < 60 mm CW and P120 Age 0 crabs in May and June), and because of known density-dependent mortality in this species (Pile at al. 1996, Etherington and Eggleston 2000).

Since the index of SSB varied with annual changes in salinity, we examined the relationship between relative SSB adjusted for salinity (compare Figs 22 and 24b) in year t and two potential indices of recruitment: (1) P195 CPUE of crabs 0 – 60 mm CW collected in September of year t, and 2) P120 CPUE of Age 0 crabs collected in May and June in year t + 1 combined (Fig 30). The significant stock-recruit relationships identified earlier (Figs 28, 29) were also identified using our salinity-adjusted index of relative SSB from P195 in September (Fig. 30).

A significant relationship between spawning stock abundance of blue crabs and

recruit abundance (i.e., Ricker S-R function) has been identified for the blue crab in Chesapeake and Delaware bays (Tang 1985, Lipcius and van Engel 1990, Helser and Kahn 1999). We detected a significant stock-recruit relationship in two of six potential indices of recruitment.

B. Non-parametric stock-recruitment modeling

Several authors have suggested the utility of non-parametric stock-recruit models (Getz and Swartzman 1981; Hilborn and Walters 1992). These approaches can be advantageous because they allow for a greater variety of functional forms (Getz and Swartzman 1981, Rothschild and Mullen 1986, Hilborn and Walters 1992), and can be useful in management because they lack assumptions about the underlying relationship between spawning stock and recruitment (Miller and Houde 1999). We employed a simple, non-parametric method (Myers and Barrowman 1996) to further investigate the stock-recruit relationship for the blue crab in North Carolina. This method provides answers to three simple questions: (1) Does the highest recruitment occur at high levels of spawner abundance?; (2) Does the lowest recruitment occur at low levels of spawner abundance?; and (3) Is recruitment higher if spawner abundance is above historic median levels rather than below the median? (Myers and Barrowman 1996).

To determine whether the largest recruitment was associated with the highest levels of spawning stock abundance (see above: Question 1), we followed the procedure of Myers and Barrowman (1996) and computed a relative rank, $r_{\max} = (\text{rank}(SR_{\max}) - 1)/(n - 1)$, where $SR_{\max}$ is the spawning stock abundance that produced the maximum subsequent recruitment, and n is the number of observations in the stock-recruit series. The value of r_{max} can take values between 0 and 1, with $r_{\max} = 0$ implying that the highest

level of recruitment is produced from the lowest level of spawning stock abundance, and conversely $r_{max} = 1$ implies that the highest level of recruitment is associated with the highest level of spawner abundance. The average value of r_{max} for our six stock-recruitment time series was 0.74, and ranged from 0.36 to 1.0 (Figs. 31, 32). To determine whether the smallest recruitment was associated with the lowest levels of spawning stock abundance (see above: Question 2), we computed a relative rank, $r_{min} = (\text{rank}(SR_{min}) - 1)/(n - 1)$, where SR_{min} is the spawning stock abundance that produced the minimum subsequent recruitment, and n is the number of observations in the stock-recruit series. The value of r_{min} can take values between 0 and 1, with $r_{min} = 0$ implying that the lowest level of recruitment is produced from the lowest level of spawning stock abundance, and conversely $r_{min} = 1$ implies that the highest level of recruitment is associated with the lowest level of spawner abundance. The average value of r_{min} for our six stock-recruitment time series was 0.24, and ranged from 0.07 to 0.67 (Figs. 31, 32). Thus, overall the largest observed recruitment in each time series tends to be associated with larger values of SSB, and the lowest observed recruitment tends to be associated with lower values of SSB. The results suggest a qualitative positive relationship between SSB and recruitment, and that at low levels of SSB, we may expect to see low subsequent recruitment.

To determine whether mean recruitment was higher at larger spawning stocks (see above: Question 3), we split each stock-recruitment data series into two subsets divided by the median spawning stock (Figs. 31, 32). One group comprised all the values of the spawning stock larger than the median, and the other group contained all values below the median. The mean recruitment for each group was then calculated. We followed the

notation of Myers and Barrowman (1996) and denote the mean recruitment below the median spawning stock as R_{below} and the mean recruitment above the median spawning stock as R_{above}, and then calculated the ratio of the two values (R_{above}/R_{below}). When mean recruitment does not differ between the groups this ratio is near 1. This ratio for our postlarval index of abundance in year t was 3.87, indicating that mean recruitment resulting from spawning stock sizes above the median is on average 3.87 times greater than mean recruitment resulting from lower stock sizes (Fig. 31). Similar values calculated for P195 CPUE of crabs 0 – 60 mm CW in year t and P195 CPUE of Age 0 crabs in June of t + 1, were 1.68 and 0.96, respectively (Fig. 31). For P120, values of R_{above}/R_{below} for P120 CPUE of Age 0 in May, June, and May and June combined of year t + 1, were 0.92, 1.21, 1.39, respectively (Fig 32). In four of the six recruitment series, recruitment is higher when SSB is above the median value. This result suggests that maintaining spawning stock above median levels will result in greater overall recruitment of blue crabs in North Carolina.

VII. LIFE HISTORY CHARACTERISTICS

A. Estimation of Natural Mortality

The natural mortality rate (M) is a critical parameter for fishery stock assessments, yet this parameter is among the most difficult to estimate. A lack of direct estimates of M for the blue crab has hampered stock assessment efforts for the blue crab, and necessitated the use of rules of thumb to estimate M. Given the lack of a direct estimate for M, previous assessments for the blue crab (Rugolo et al. 1997, 1998; Helser and Kahn 1999) have estimated M using the convention of M = 3/maximum age (t_{max}).

Following this convention, M is estimated as the value that results in 5% of the individuals in a cohort surviving to the maximum age. Based of tagging data (McConaugha 1991), the maximum age for blue crabs in Chesapeake Bay was assumed to be 8 (Rugolo et al. 1997), resulting in an estimate of M = 0.375 ($3/t_{max} = 8$). Helser and Kahn (1999) noted that blue crabs in Delaware Bay are near the northern most extent of the species distribution, and suggest a lower maximum age of 3-4 years is appropriate for blue crabs in Delaware Bay. Thus, M for blue crabs in Delaware Bay was estimated to be between 0.75 and 1.0 ($3/t_{max} = 4$ and 3, respectively). Tagging studies suggest the maximum age of blue crabs in North Carolina is 5 years (Fischler 1965), and would result in M = 0.60 ($3/t_{max} = 5$).

Unlike previous assessments, however, we have chosen not to adopt the $3/t_{max}$ convention based on recent criticisms of the method (Hewitt and Hoenig *in review*), and alternatively estimate M using Hoenig's (1983) regression estimator. This method (Hoenig 1983) uses the following regression:

$$\ln(Z) = 1.44 - 0.982*\ln(t_{max})$$

to predict Z from the maximum age (t_{max}) and is based on empirical data from 134 fishery stocks. This method has been recommended (Hewitt and Hoenig *in review*) to replace the $3/t_{max}$ convention when direct estimates of M are not available. The regression is based on lightly exploited fish stocks so that $Z \approx M$. Based on a t_{max} of 5 years estimated from tagging studies in North Carolina (Fischler 1965), M was estimated as 0.87 using Hoenig's equation (Hoenig 1983). We believe $t_{max} = 5$ to be the best estimate for blue crabs in North Carolina, and represent a good estimate of maximum age under light exploitation. A wide range of reported values of t_{max} have been used in previous

assessments ranging from 3 to 8 (Rugolo et al. 1997, 1998, Helser and Kahn 1999). To address the uncertainty regarding estimates of M, we also calculated estimates of M using Hoenig's equation (1983) based on t_{max} values of 3 and 8. Thus, three estimates of M (0.55, 0.87, and 1.44) based on t_{max} values of 8, 5, and 3, respectively, were used in subsequent analyses.

B. Length-based estimation of total mortality rates

The goal of this analysis was to derive estimates of total instantaneous mortality (Z) for the North Carolina blue crab population using length-based methods. Both Beverton and Holt (1957) and Hoenig (1987) have developed approaches for estimating Z from the mean size in the catch (mean length) and the VBG parameters for growth rate and asymptotic size. Hoenig (1987), however, argues that the Beverton and Holt (1957) formulation induces bias in the estimate of Z when mean size approaches the length of full recruitment to the fishing gear (CW_{FR}). For this reason, and as a means for comparison with similar estimates from Chesapeake Bay (Rugolo et al. 1997, Miller and Houde 1998) and Delaware Bay (Helser and Kahn 1999), we used the Hoenig (1987) length-based approach for estimating Z of blue crabs in North Carolina:

$$Z = \log_e \left[\frac{(e^{-k} * (\overline{CW} - CW_{\inf})) + CW_{\inf} - CW_{FR}}{(\overline{CW} - CW_{FR})} \right]$$

where, k = the curvature (Brody growth coefficient) and $CW_{\inf} = L_{\inf}$ = maximum carapace width parameters from the VBG model; $\overline{CW}$ = mean CW (mm) of crabs from the P195 survey that are larger than the size at full recruitment to the fishery (CW_{FR}). CW_{FR} was 127 mm, the legal minimum size for hard crabs in North Carolina. The total

mortality rate (Z) for crabs > 127 mm would include both fishing and natural mortality. Natural mortality is assumed to be constant over time. Estimates of k and L_{inf}, 0.47 and 216.9, respectively, were derived from length-based modeling of P195 length frequency data in June and September (see section VI. LIFE HISTORY CHARACTERISTICS, C. Estimation of growth). Because estimates of Z are highly dependent on assumptions of growth, estimates of Z were also obtained using growth parameters from previously published stock assessments in Chesapeake Bay (Rugolo et al. 1997) and Delaware Bay (Helser and Kahn 1999). Length-based estimates of Z were not generated using P120 data because the shallow water emphasis of this survey resulted in very few large crabs being captured.

Caution has been advised when interpreting the results of this length-based model, because large variations in recruitment can impact the estimates of Z (Helser and Kahn 1999). For example, a large recruitment year class will have the effect of reducing average size in the population resulting in a larger estimated value for Z. We investigated the relationship of the annual index of P195 Age 0 blue crabs in North Carolina and Z using linear regression analysis, but did not detect any significant relationships.

Based of growth parameters from this study, estimates of Z from P195 June length-frequency data ranged from 0.91 to 1.22 (Table 11, Fig. 33), and averaged 1.03 with no apparent trend in mortality over time (Table 11, Fig. 33). These estimates are similar to Zs reported for the blue crab in Chesapeake Bay (~1.0-1.5; Rugolo et al. 1998), but lower than estimates from Delaware Bay (1.19-2.90; Helser and Kahn 1999). Length-based estimates of Z were generally considerably lower than annual Zs (1.04-2.90) estimated from Collie-Sissenwine modeling from over the same period (1987-2001; see

section: IX. COLLIE-SSISENWINE MODELING).

C. Estimation of Growth Rates.

Accurate growth data are a necessary component of many fishery modeling techniques. Broadly defined, growth is the change (increase) in some measure of size (length, weight, carapace width, etc.) over time. Traditionally, length has been used as the measure of body size in most fisheries modeling efforts (von Bertalanffy 1938; Schnute 1981), due in large part to the ease of collecting length measurements. For crustaceans, length measurements are necessitated due to the current lack of precise aging techniques (Ju et al. 2001, 2003). Growth measured as CW in blue crabs is discontinuous, as crabs must periodically molt to grow. Most attempts to model blue crab growth have assumed continuous growth and fitted various forms of the von Bertalanffy growth function (VGBF; Rothschild et al. 1991, Rugolo et al 1997, Helser and Kahn 1999). Attempts have been made to model growth as a discontinuous process (Grey and Newcombe 1938, Newcombe et al. 1949, Smith 1997), but that approach has not been incorporated into stock assessments. Previous estimates of growth rates have been variable. Rothschild et al. (1991) used a modified version of the VBGF adjusted for molting to produce a growth trajectory defined by $k = 0.51$ and L_{inf} of 186 mm CW. In a recent stock assessment for the blue crab in Chesapeake Bay, Rugolo et al. (1997) predicted growth using $k = 0.59$ and $L_{inf} = 262.5$ mm CW. Helser and Kahn (1999) used MULTIFAN (Fournier et al. 1990) to estimate blue crab growth in Delaware Bay, resulting in estimates of $k = 0.75$ and $L_{inf} = 234.7$ mm CW.

We employed the length-based model described above (see section: III. FISHERY-INDEPENDENT RESEARCH SURVEYS, C. Calculation of age-specific

annual indices of abundance) to generate VBG parameters from P195 trawl survey data from 1987-2002 from P195 June and P195 September. The estimate of L_{inf} was fixed to 216.9 mm CW. A single VBGF was assumed to describe growth in all years, and estimates of k and t_0 from P195 June (Fig. 9) and September (Fig. 10) length-frequency data were 0.47 and 0.02, respectively (Fig 34). The estimate of k (k = 0.51)from analysis P120 length-frequency data was similar to that of P195 (k = 0.47), however the estimate t_0 (t_0 = 0.41) was very different than P195 estimates (t_0 = 0.02). Differences in estimates of t_0 between P120 and P195 were probably due to a violation of the assumed September 15th birthdate in the P120 survey data. The initial mode in the length-frequency data from P120 generally occurs between 10-20 mm CW, and captures crabs recruiting in the spring, not the fall. Thus, growth estimates derived from P195 survey data are a more accurate reflection of growth in NC and were used in length-based estimates of total instantaneous annual mortality rates (Hoenig 1987), as well as yield-per-recruit (YPR) and spawning stock biomass-per-recruit (SSBR) analyses.

VIII. SURPLUS PRODUCTION MODELING

A. Relative Biomass, Fishing Mortality, and MSY

Biomass-based models are one of several approaches for analyzing fishery data to estimate historical abundance and mortality. Unlike age-structured models that track population numbers by age and describe population change in terms of growth, recruitment, and mortality, biomass-based models describe stock dynamics strictly in terms of biomass. Biomass-based models are among the simplest and most commonly used stock assessment method, and have proven valuable in cases where fisheries species

are difficult or impossible to age (e.g., crustaceans), or where sufficient age data are not yet available. Biomass-based and age-structured models may perform equally well and often result in similar management recommendations (Hilborn and Walters 1992). Thus, the additional effort required to obtain age data and fit more complex models may not be justifiable in certain fisheries.

We used a non-equilibrium biomass-based model to estimate relative fishing mortality and biomass over time for the blue crab in North Carolina, as well as estimate Maximum Sustainable Yield (MSY). This model, which is given in Hilborn and Walters (1992), consisted of two equations:

$$B_{y+1} = B_y + rB_y\,(1-B_y/K) - C_y,$$

$$U_y = qB_y,$$

For the first equation, B = biomass, r = the intrinsic rate of population growth, K = carrying capacity (the unfished stock size), and C = catch. This difference equation describes how the change in biomass from year to year depends on the magnitude of surplus production versus catch. The second equation relates the model for biomass to the observed CPUE from fishery-independent and -dependent indices of abundance (Table 6, Fig. 1). CPUE (U) is assumed to be directly proportional to population biomass. We used a maximum likelihood approach to estimate r, K, B_1, and q, so that the sum of squared differences ($S(U_y - \hat{U}_y)^2$) between observed and predicted CPUE was minimized. The parameters r and K were used to estimate MSY ($rK/4$, Hilborn and

Walters 1992). Since MSY is the product of *r* and *K*, this value tends to be more reliably estimated than the individual model parameters themselves (Prager 1993).

We fitted the non-equilibrium, biomass-based model described above to three different time series (1) CPUE of legal-sized crabs (crabs > 127 mm CW) from P195 in June for the period 1987-2002; (2) CPUE legal-sized crabs (crabs > 127 mm CW) from P195 in September for the period 1987-2002; and (3) NC DMF commercial pot CPUE (Commercial landings / NC DMF pot numbers) for the period 1953-2002 (Fig. 1). CPUE was generated from fishery-independent trawl survey data from P195 in all cases except the use of NC DMF commercial crab pot CPUE series, which is a fishery-dependent measure of abundance. In 1994, the NC DMF instigated a mandatory reporting program for the blue crab fishery resulting in a 26% increase in landings from dealers that had not previously reported. As discussed earlier (see section: II. DESCRIPTION OF THE FISHERY, A. Fishery-dependent data), it was concluded that although 26% of landings in 1994 came from dealers that did not report in 1993, this value would likely result in the over-inflation of catches prior to 1993 (S. McKenna, NC DMF, pers. comm.). Thus, unadjusted landings were used, as they were considered to be a more accurate estimate of catch over the entire time series than were adjusted landings (S. McKenna, NC DMF, pers. comm.). Model fits were produced using only the NC DMF commercial pot time series (Table 12), and also by fitting the three time series simultaneously (Table 13). We chose to fit the NC DMF commercial pot CPUE, mean CPUE of crabs > 127 mm CW from P195 in June and September, as these time series provided: (1) a long-term data set 1953 – 2002 (commercial crab pot CPUE); and (2) the most reliable estimates of adult abundance available based on targeted sampling of large crabs in deep water habitats.

The NC DMF commercial pot CPUE was also fitted separately without the fishery-independent data because this data series represents a much longer time series (50 years vs. 16 years).

Our first model run included only the NC DMF commercial pot effort series for the period 1953-2002. Model fitting began by allowing all model parameters (r, K, and B_1) to vary simultaneously. These model fits were difficult to obtain, were extremely sensitive to initial values of B_1 and K, and often resulted in a failure to generate reasonable model parameter values. To avoid these problems, we assumed that the starting model biomass (B_1) was equal to K. This assumption is likely valid for this model given that it estimates starting biomass in 1953, when extremely low fishing pressure was placed on the stock (1953 pot landings = 185,700 lbs vs. 1996 pot landings 61,800,000 lbs.). Despite this simplifying assumption, model fits were still difficult to obtain. To generate an estimate of model parameters over a wide range of possible r and K values, we fixed r at values between 0.2 and 2.0, and allowed the model to obtain a best fit by varying K (Table 12). This fitting also generated a likelihood profile, which can provide information for selecting the best fitting model (Punt and Hilborn 1996; Figure 30). Estimates of MSY varied widely and ranged from 26.3 to 51.1 million pounds (Table 12). The model fit was essentially the same for a large range of biologically reasonable values of r and K (Table 12). Additional management benchmarks from this biomass-based model were estimates of relative fishing mortality (F) and biomass (B) (Table 12). The ratio estimates such as Biomass_{year}/MSY Biomass (B_y/B_{MSY}) and Fishing Mortality_{year}/MSY Fishing Mortality (F_y/F_{MSY}) are more precise estimates than absolute biomass and fishing mortality (Prager et al. 1996). For an

assumed r of 1.0, annual biomass of crabs was high and relatively stable through 1978, then began a decline that continues until present (Figs. 35, 36). Since 1995, concurrent with increased commercial landings from 1995 – 1999, relative biomass has steadily declined to values below B_{MSY} while relative fishing mortality has sharply increased (Fig. 37). For any plausible values of r, relative fishing mortality (F_y/F_{MSY}) values were greater than or equal to 1 (e.g., F_{2002}/F_{MSY} = 2.08 – 6.45 in 2002; Table 12). Values greater than 1 are inefficient and produce a level of harvest less than the MSY. Relative stock biomass values for 2002 (B2002/BMSY) were substantially less than 1 for all assumed values of r (Table 12).

Given the important management implications of the previous findings regarding estimates of relative B and F, as well as MSY, it is critical to assess the reliability of the model results. We used the log-likelihood profile described above (Table 12, Fig. 35), and two additional indicators of the reliability of model results, including indices of (1) nearness and (2) coverage (Prager et al. 1996). "Nearness" (N) ranges from 0 (least reliable) to 1 (most reliable) and indicates how closely a modeled stock has approached the biomass level producing B_{MSY}:

$$\hat{N} = 1 - \frac{|\hat{B}_{MSY} - \hat{B}^*|}{\hat{B}_{MSY}}$$

where B_{MSY} is the biomass at MSY and B* is the smaller value of K or the estimated biomass closest to MSY. "Coverage" ranges from 0 (least reliable) to 2 (most reliable), and indicates how widely stock biomass has varied between 0 and K:

$$C = \frac{\hat{B}^+ - \hat{B}^-}{\hat{B}_{MSY}}$$

where B^+ is the lesser value of K or the largest estimated biomass, and B^- is the smallest estimated stock size. The rationale for these indices is that B_{MSY} will be estimated more reliably if estimated biomass has gone from above B_{MSY} to below (or vice versa). In our case, "nearness" and "coverage" were 1.0 and 1.73, respectively. MSY values from likelihood profiling varied from 26.3 to 51.1 million pounds as F_{MSY} ranged from 0.10 to 1.0 (Table 14). While there was considerable uncertainty regarding model fits, in all cases the model suggests that the stock is currently at low levels of biomass (B_{2002}/B_{MSY} = 0.21 to 0.34) and that the stock is heavily exploited (F_{2002}/F_{MSY} = 2.08 – 6.45).

Our second model run was fit to the NC DMF commercial pot effort series (1953-2002), P195 crabs > 127 mm CW in June, and P195 crabs > 127 mm CW in September. Similar to our first run, model fits were difficult to obtain, and were extremely sensitive to initial values of B_1 and K; often resulting in a failure to generate reasonable model parameter values even after assuming $B_1 = K$. As above, we estimated model parameters over a wide range of possible r and K values by constraining r to values between 0.2 and 2.0 and allowing the model to vary K (Table 13). This fitting procedure also generated a likelihood profile, which can provide information in selecting the best fitting model (Punt and Hilborn 1996; Fig. 38). Estimates of MSY varied widely and ranged from 27.9 to 51.7 million pounds (Table 13). Annual biomass of crabs was high and relatively stable through 1978, then began a decline that continues until present (Figs. 39, 40). From 1979 through 2000, relative biomass steadily declined to values below B_{MSY} while relative fishing mortality has sharply increased (Fig. 40), however, the population stopped declining and showed possible increases in 2001-2002 concurrent with reduced harvest

(average landings 2000-2002 ~ 35 million lbs.; Table 1). Relative fishing mortality (F_y/F_{MSY}) values were greater than or equal to 1 in 2002 for most values of *r* and *K* (e.g., F_{2002}/F_{MSY} = 0.87 - 3.01; Table 13). For all model runs, however, the relative biomass in 2002 was below 1.0 (0.43-0.81; Table 13), suggesting the stock is currently below the MSY level.

Estimates of annual MSY from all surplus production models ranged widely from 26.3-51.7 million pounds (Tables 12, 13). Average landings were near or above the largest estimated value for MSY of 51.7 million pounds from 1994-1999 (e.g., 65 million pounds in 1996). Since 1996, relative crab biomass has declined steadily while fishing mortality has increased sharply (Figs. 37, 40). Relative fishing mortality rates above 1 result in annual yields less than MSY; most current fishing mortality rates are estimated to be above this threshold (e.g., F in 2002 = 0.87 – 6.45 times F_{MSY}, Tables 12, 13). Our estimates of relative F_{MSY} and B_{MSY} indicate that the stock is currently overfished and at low stock size (e.g. $B_{2002} < B_{MSY}$), and that the fishery has operated near or above F_{MSY} since 1996 (Figs. 37, 40). Given: (1) the known limitations of surplus production models; (2) uncertainty associated with landings prior to 1994; (3) inherent variability in CPUE data; (4) uncertainty in fishery-independent surveys (see section: III. FISHERY-INDEPENDENT RESEARCH SURVEY INDICES, D.) Correlation analyses of length-based indices of abundance), and (5) the difficulty of obtaining biologically reasonable model fits with many time series (likely caused by lack of contrast in data sets), a cautionary approach should be taken to the interpretation of these results. The results, however, do suggest that the blue crab stock is currently at low biomass, and current fishing pressure is resulting in reduced yields.

IX. COLLIE-SISSENWINE MODELING

Collie and Sissenwine (1983) developed a two-stage population model that has proven very useful for crustacean assessments (see Smith and Addison (2003) and references therein). The C-S model has been used to describe blue crab population dynamics in Delaware Bay (model referred to as modified DeLury: Helser and Kahn 1999; Helser and Kahn 2001) and in Chesapeake Bay (L. Fegley, MD Department of Natural Resources, personal communication). Another regional application of the model is for white perch in the Choptank River, MD (P. Piavis, MD Department of Natural Resources). The model requires catch data, survey indices for legal-sized and undersized animals, and an external estimate or assumed value for natural mortality (M).

For the simplest case where harvest is assumed to occur in mid-year (Smith and Addison 2003), the population of legal-sized animals in year y+1 (N_{y+1}) is defined as

$$N_{y+1} = \left[\left(N_y + R_y\right)e^{-0.5M} - C_y\right]e^{-0.5M}$$

The population at the start of year y is made up of legal-sized individuals (N_y) plus incoming recruits that will reach legal size within the next year (R_y). This total population at the start of year y ($N_y + R_y$) decreases due to natural mortality for one-half year (i.e., a rate of 0.5M), at which time the catch is removed. After the catch is subtracted, the remaining population decreases due to natural mortality for the other half-year (at rate 0.5M). For the more general case where the fishery occurs at time T (ranging between 0 and 1), the total population declines due to natural mortality for time

T, then the catch is removed, then the remaining population declines due to natural mortality for the remainder of the year (1 - T).

Because population size is not known, the above equation is rewritten in terms of abundance indices representing the legal-sized animals and recruits:

$$n_y = q_n N_y$$

and

$$r_y = q_r R_y$$

where n_y is the abundance index for legal-sized individuals, r_y is the index for recruits, q_n is the catchability coefficient for adults, and q_r is the catchability coefficient for recruits.

An important advantage of this model compared to a biomass-based (surplus production) model is that recruitment can vary annually; for example, due to environmental factors. Thus the model can account for an unusually large (or small) year class as long as it is evident in the recruitment index. In contrast, the biomass-based model assumes that all population changes can be accounted for by the annual harvest and logistic population growth. The biomass-based model works best for longer-lived stocks where fishable biomass changes gradually in response to fishing (Punt and Hilborn 1996). It would be expected to work less well for short-lived species for which incoming recruits have a substantial effect on population size.

Following the approach used by Helser and Kahn (1999), we assumed that September surveys provide a useful index of legal-sized and recruit categories for the following year. The primary spawning period for NC blue crabs is during fall, and

recruits detected in the September P195 survey would be expected to attain legal size over the next year. Also, most of the harvest in NC occurs during May-October (Figure 2) so September indices should be related to abundance the following January. For example, the September 1987 P195 CPUE for recruits and legal-sized blue crabs are used as indices of relative abundance for January 1988. Survey data for 1987-2001 were used to estimate population size between 1988 and 2002.

Helser and Kahn (1999) defined recruit and fully recruited blue crabs to be less than and greater than 120 mm, based on a legal minimum size of 120 mm for New Jersey and 127 mm for Delaware. For NC, the legal minimum size is 127 mm so that was used as the dividing line between recruits and legal-sized blue crabs. Following Helser and Kahn (1999), we assumed that legal-sized and recruiting blue crabs were equally vulnerable to the trawl survey gear ($q_n/q_r = 1$).

The model requires an assumed value for M and we considered three values: 0.55, 0.87, and 1.44. These values are obtained using the regression equation relating maximum age and Z, the total instantaneous mortality rate (Hoenig 1983). We fitted an observation error model, which assumes that differences between predicted and observed CPUE are due to variability in survey catches rather than to a mis-specified population model. Parameter estimates are obtained by minimizing ln-scale differences between observed and predicted CPUE.

The C-S model fitted the survey relative abundance data for legal-sized crabs reasonably well (see results for M=0.87, Figure 36). The model was less successful in fitting CPUE of recruits, because of the lack of an apparent connection between incoming recruits and subsequent numbers of legal-sized blue crabs. For example, the high recruit

CPUE value for 1997 did not result in a large increase in legal-sized blue crabs, nor did the low recruit CPUE value for 2001 result in a large decrease in legal-sized blue crabs in 2002. Because there was no obvious trend in recruitment over time, the model attributed the decrease in relative abundance of legal-sized blue crabs mostly to an increasing rate of fishing.

When results from all three assumed natural mortality rates were compared, specific values depended on M but the trends were similar (Table 14, Figs. 42, 43). Predicted numbers of recruits varied without obvious trend between 1988 and 2002, except for higher estimated recruitment in 1989 and 1991. Predicted numbers of legal-sized crabs were higher in the early 1990s due to those estimated strong year classes and lower Fs, then generally declined from 1992 through 2002 (Table 14, Fig. 42). The estimated harvest or exploitation rate generally increased over time, although values were substantially lower and showed less of a trend for the highest M (Table 14, Fig. 43). The 10-20% exploitation rates for an assumed M of 1.44 seem unlikely, and we suspect that the M=0.55 and 0.87 cases are more realistic. For those two Ms, exploitation rates ranged from about 0.2 in 1989 to 1995-2001 levels of about 0.50-0.75 (Fig. 43). Estimated Fs in 1995-2001 for Ms of 0.55 and 0.87 ranged from about 1.0 to 1.5 (Table 14, Fig. 43).

The specific values obtained depended on the assumed value for M. For the lowest assumed value for M (0.55), abundance was lower and more of the total mortality was attributed to fishing (higher Fs). At higher assumed Ms, abundance was higher but Fs were lower because more of the total mortality was assumed to be due to natural causes.

X. BIOLOGICAL REFERENCE POINTS

A. Yield- and Spawning Stock Biomass-per-Recruit Analyses

Yield-per-recruit analyses (YPR) have been conducted to estimate the appropriate level of fishing mortality for the blue crab in Chesapeake Bay (Rugolo et al. 1997, Miller and Houde 1999) and Delaware Bay (Helser and Kahn 1999). YPR analysis is an optimization in time between two opposing effects, (1) increasing weight of crabs due to growth and (2) decreasing population size due to mortality. Ideally, the fishery should wait until the maximum YPR value, and catch every individual instantaneously at that time. Although theoretically possible, this strategy poses obvious practical impossibilities for the fishery, and disregards the potential problems from a flood of the fishery product into a market driven economic system (decreased product value following increased market supply; Sissenwine 1981).

A recognized weakness of the YPR model is that it is ignorant of recruitment overfishing, in which overfishing a stock leads in future recruitment being lowered (Hilborn and Walters 1992). Therefore, spawning stock biomass-per-recruit (SSBR) is also considered. SSBR is a related approach to YPR, which examines the effects of fishing on the spawning stock. The two analyses (YPR and SSBR) are used to generate several important biological reference points (BRPs) such as F_{MAX} (fishing mortality rate at which yield-per-recruit is maximized), $F_{0.1}$ (Fishing mortality rate at which the slope of the YPR curve is 10% of the slope at the origin; Gulland and Boerema 1973, Deriso 1987), and $F_{30\%}$ and $F_{20\%}$ (fishing mortality rate at which the SSBR is 30% and 20% of the virgin or unexploited SSBR, respectively).

We conducted both YPR and SSBR analyses for the North Carolina blue crab

stock. These models require numerous inputs: (1) information on size-at-age, (2) relationship between size (CW) and weight, (3) a schedule of partial recruitment to the fishery, (4) relationship between size and maturity, and (5) an estimate of natural mortality. Model inputs were estimated using data from North Carolina whenever possible. In cases where estimates were not available, we relied upon previously published information from earlier stock assessments for Chesapeake and Delaware bays (Rothschild et al. 1991, Miller and Houde 1999).

The relationship between size and age was described using a VBGF generated from length-based modeling of length-frequency data from P195 trawl surveys (see section: VI. LIFE HISTORY CHARACTERISTICS, A. Estimation of growth rates). The growth equation was generated from the length-frequency data from P195 June and September (Figs. 9, 10) and was used to conduct YPR and SSBR analyses. The following equations described the change in mean length with age for our YPR analysis:

$$L_t = 216.9(1 - e^{(-0.47(t - 0.02)}$$

The relationship between blue crab length and weight was described using the equation Rothschild et al. (1991) generated for blue crabs in Chesapeake Bay, as this information is not available for North Carolina. Since the commercial catch is comprised of both males and females, we used parameters that relate weight (g) to CW (mm) for both sexes combined for YPR analyses (Rothschild et al. 1991):

$$W_g = 0.001089 * CW^{(2.363)}$$

For SSBR analyses, we used a different weight to CW relationship that was specific to females (Miller and Houde 1998), since spawning stock is composed of only female crabs:

$$W_g = 0.003486 * CW^{(2.1165)}$$

We calculated the partial recruitment (PR) of crabs of various age classes to the fishery using the predicted length-frequency of crabs at age from NC DMF P195 trawl surveys, the size-specific fishery regulations for North Carolina, and the relative contribution of various fishery sectors to the overall landings. Specifically, we considered three distinct sectors of the blue crab fishery in North Carolina when calculating age-specific PR: (1) soft/peeler crab fishery; (2) hard crab fishery for mature females; and (3) hard crab fishery for males and immature females > 127 mm CW. Currently, there is no minimum size regulation for soft/peeler crabs allowing for all ages of crabs (including Age 0 crabs) to be taken in this fishery. Since 1978, the soft/peeler crab fishery has averaged approximately 3-4% of total landings, and the fishery has comprised nearly 5% of total landings since 1994 (Table 1, McKenna et al. 1998). For these analyses, we assumed that 4% of crabs in each age class had recruited to the soft/peeler fishery and were susceptible to harvest. Hard crabs in North Carolina must measure at least 127 mm CW (5 in.) to be legally harvested, however, this regulation does not apply to mature females which can currently be legally harvested at any size. To account for the PR of mature females to the hard crab fishery, we first estimated the percentage of females that are mature at a given age, as these individuals can be legally harvested and are recruited to the fishery. We

used the VBGF parameters and maturity ogive (Fig. 44, see below) to estimate the percentage of crabs that are mature in each age class. We estimated that 4.4% of female crabs are mature by the end of their first year, 67% of crabs are mature by the end of their second year, and the remainder will mature before age 3. Assuming a sex ratio of 1:1 (M:F), and adjusting for the percentage of females captured in the soft/peeler fishery, approximately 4.2% (4.4% * 0.96) of female crabs are mature and have recruited to the hard crab fishery by the end of age 0, and 64% (67% * 0.96) have recruited by the end of Age 1. All female crabs are assumed recruited to the fishery by the end of Age 2. In addition to mature females, hard crabs greater than 127 mm CW can be legally harvested. To estimate age-specific PR for this fishery, we estimated the proportion of male and immature females at each age that have attained 127 mm CW. The proportion of crabs > 127 mm CW in each age class was calculated by assuming that CW followed a normal distribution defined by a mean size-at-age from the VBGF and a standard deviation from the length-based modeling of observed length-frequency data (see section: III. FISHERY-INDEPENDENT RESEARCH SURVEY INDICES, C. Calculation of annual indices of abundance). We estimate that 0.82% of crabs have attained a size of 127 mm CW or greater by the end of their first year, and 77% are greater than 127 mm CW by their second year, and all crabs are greater than 127 mm CW by the end of Age 3. By summing the contribution of each fishery to the PR, we estimate that 7% (4% soft/peeler + 2.2% (4.4%/2) mature females + 0.82% of male and immature female crabs greater than 127 mm CW) crabs are susceptible to the fishery by the end of their first year (Age 0). We estimate 77% of crabs are recruited to the fishery by the end of their second year (Age 1). All crabs are recruited to the fishery by the third year (Age 2).

The previously described relationship between size and maturity was used in SSBR analyses. We estimated that 4.4% of females in North Carolina are mature by the end of their first year, and that 67% of females are mature by the second year. Females Age 3 and above were assumed to all be mature for the SSBR analysis. We assumed a flat-topped maturity ogive such that there was no reduction in fecundity occurred with age, similar to assumption made by Helser and Kahn (1999) for blue crabs in Delaware Bay .

Given the sensitivity of YPR models to assumptions regarding M, we conducted the analysis using three different values of M. Estimates of M (0.55, 0.87, and 1.44) were chosen using based on Hoenig's method (1983; see section: VII. LIFE HISTORY CHARACTERISTICS, Estimation of natural mortality), and correspond to maximum ages of 8, 5, and 3 years, respectively.

YPR estimates were generated for length-based estimates of growth parameters and estimates varied predictably with M values (Table 15, Fig. 45). F_{MAX} ranged from 0.51 to 0.93 as M increased, and resulted in lower absolute values of YPR (Table 15 Fig. 45). For the fishery, this translates to increasing fishing mortality rates (i.e., increasing F_{MAX} and $F_{0.1}$) to catch individuals before they are removed from the system by natural mortality. $F_{0.1}$ ranged from 0.36 to 0.62 with increasing M (Table 15, Fig. 45). Our values of $F_{0.1}$ are similar to those reported by Miller and Houde (1999) for the blue crab in Chesapeake Bay (range $F_{0.1}$ = 0.35 to 0.47), and for Delaware Bay (range $F_{0.1}$ = 0.60 – 0.70; Helser and Kahn 1999). While F_{MAX} produces the highest value of YPR, $F_{0.1}$ is a more conservative reference point, and consistent with risk-averse management. A fishing target between $F_{0.1}$ and F_{MAX} has been recommended for blue crabs in Delaware

Bay (Helser and Kahn 1999). The use of $F_{0.1}$ also increases economic efficiency, and is less likely to lead to declines in spawning stock abundance (Miller and Houde 1999).

Historical fishing mortality rates from length-based modeling were compared to BRPs from YPR analysis to evaluate the status of the blue crab fishery in NC and the concern of growth overfishing under three different assumptions regarding the value of M (M = 0.55, 0.87, 1.44). Although results are presented for all values of M, estimated exploitation rates from C-S modeling for an assumed M of 1.44 seem unlikely, and we suspect that the M = 0.55 and 0.87 cases are more realistic (see section IX. COLLIE-SISSENWINE MODELING). For M = 0.55 and 0.87 the stock would be considered growth overfished and the fishery operating inefficiently when current Fs (1995-2001) are considered ($F_{1995\text{-}2001} > F_{MAX}$; Table 15). We believe the most reasonable estimate of M to be 0.87. Using this natural mortality rate, recent estimated Fs exceed $F_{0.1}$, and F_{MAX}.

Because YPR analysis does not account for declines in spawning stock due to fishing that may result in potential reductions in recruitment, SSBR was also considered. Fishery benchmarks from SSBR are generally reported as percentages of the maximum spawning potential that would result, theoretically, in the absence of all fishing pressure. We calculated the following reference values: $F_{30\%}$ and $F_{20\%}$, which represent the fishing mortality rates which result in a reduction of the spawning stock to 30% and 20% of the unfished value of SSB. When M is assumed to be 0.87, the values of $F_{30\%}$ and $F_{20\%}$ are 0.72 and 1.10, respectively (Table 15). The average estimated F from 1995-2001 from C-S modeling was 0.91 (Table 15), which exceeded $F_{30\%}$, but not $F_{20\%}$.

The results of YPR models suggest that current fishing mortality rates in North

Carolina exceed the conservative fishery benchmark, $F_{0.1}$, and exceed F_{MAX}, under reasonable assumptions for M (M = 0.55 and 0.87). When considering the results of similar analyses for Delaware Bay, Helser and Kahn (1999) suggested a target value for F somewhere between $F_{0.1}$ and F_{MAX}. Under the assumption of M = 0.87, a target F would be somewhere between 0.45 and 0.64 with the estimated current F for 1995-2001 higher than either target level. Current estimated Fs (1995-2001) from C-S modeling exceeded $F_{30\%}$, but not $F_{20\%}$, indicating the potential for recruitment overfishing, however, Mace and Sissenwine (1993) have advocated the use of $F_{20\%}$ as a recruitment overfishing threshold.

XI. CONCLUSIONS

The blue crab stock in North Carolina currently sustains heavy exploitation by the commercial fishery, with additional (generally undocumented) pressure from the recreational fishery. There has been a systematic increase in commercial landings from 1987-1999, followed by a period of reduced landings from 2000-2002. Although recent landings are reduced from the peak landings from 1994-1999 (mean = 52.8 million lbs.), landings from 2000-2002 (mean = 34.6 million lbs.) were similar to catches prior to 1994 (mean landings 1987-1993 = 36.0 million lbs.). Effort, however, during 2000-2002, (NC DMF number of pots) was 1.8 times greater than from 1987-1993. During 1987-2003 fishery-independent indices of blue crab abundance have either remained stable, or have shown significant declines. In no case do any fishery-independent indices of blue crab abundance show an increasing trend. The relative abundance of Age 1 blue crabs and relative SSB in the P195 trawl survey during 1999-2001 were at the lowest levels

recorded since 1987 (Figs. 14, 22), however the index of SSB appeared to rebound in 2003 . While the 2003 index of spawning stock may indeed reflect an increase in SSB from low levels, a precautionary approach is warranted when interpreting the 2003 value because crabs blue crabs shift their distribution within Pamlico Sound depending on salinity, which determines their availability to P195 surveys. For example, we suggest that blue crabs shift their distribution downstream during wet years as was the case following hurricane floodwaters in 1999 (Fig. 23), which makes them more available to P195. Conversely, blue crabs likely shift their distribution upstream during dry years (S. McKenna, NC DMF pers. comm.), which would make blue crabs less available to P195 surveys. To determine the extent to which availability of mature females to the P195 trawl survey was driven by annual fluctuations in salinity, we examined the relationship between our index of SSB and mean annual salinity. Two major differences are apparent in the patterns of the residuals when the effects of salinity are removed, (1) SSB was underestimated by P195 in 2002, and (2) SSB was overestimated by P195 in 2003 (compare Figs. 22 and 24b). Thus, it appears the large increase in relative SSB in the P195 September survey in 2003 (Fig. 22) reflects both an actual increase in spawning stock from historic lows observed during 2000-2001 to average levels, and an increase in availability of mature females to survey gear due to low salinity. Any decline in the index of SSB would be especially troubling given (1) the potential influence of spawning stock on subsequent recruitment detected for North Carolina (Figs. 28, 29, 30); (2) a concurrent decrease in the mean size of mature females over time (Fig. 25, 26b); and (3) the pattern of exploitation of mature females in North Carolina, which are targeted by the peeler fishery, have no size protection in the hard crab fishery, nor any protection as

sponge crabs.

Estimates of annual MSY from all surplus production models ranged widely from 26.3-51.7 million pounds (Tables 12, 13). Average landings were near or above the maximum estimated MSY of 51.7 million pounds from 1994 – 1999 (e.g., 65 million pounds in 1996). The models suggest that since 1996, biomass has declined steadily while fishing mortality has increased sharply (Figs. 32, 35). Relative fishing mortality rates above 1 result in annual yields less than MSY, and current fishing mortality rates are estimated to generally be above this threshold (e.g., F in 2002 = 0.87 – 6.45 times F_{MSY}, Tables 12, 13). Our estimates of relative F_{MSY} and B_{MSY} suggest that the stock is currently overfished and at low stock size (e.g. $B_{2002} < B_{MSY}$), and that the fishery has operated near or above F_{MSY} since 1996 (Figs. 32, 35). Results from the biomass-based model incorporating both fishery-independent (P195 June and September crabs > 127 CW indices of abundance) and fishery-dependent (NC DMF commercial pot CPUE) suggest that while population biomass is remains low, it has stopped declining following low landings (mean landings 2000-2002 = 34.6 million lbs.) in recent years and may be increasing (Figs. 39, 40).

YPR modeling suggests that current fishing mortality rates in North Carolina exceed the conservative fishery benchmark, $F_{0.1}$, and exceed F_{MAX} under reasonable assumptions for M. Helser and Kahn (1999) advocate a target F between $F_{0.1}$ and F_{MAX} for the Delaware Bay fishery. Current Fs exceed values of $F_{30\%}$, but not $F_{20\%}$ for North Carolina (Table 15), indicating conservation of the spawning stock in NC is critical. Given the uncertain status of the blue crab spawning stock in North Carolina, however, a reduction of fishing pressure on mature females is suggested. Further, non-parametric

stock-recruit models estimate that levels of recruitment are generally greater when spawning stock abundance is above the median value. With the exception of 2003, relative SSB has been below the median since 1999. Key management recommendations should include conservation of the spawning stock as an urgent and critical goal.

Numerous biological patterns identified in this study should be considered in terms of effort management for the blue crab fishery in North Carolina, and include: (1) a general lack of coherence among survey indices of abundance resulting in considerable uncertainty regarding current stock status; (2) current spawning stock size has been extremely low in recent years, but appears to be at average levels in 2003; (3) a significant spawning stock-recruitment relationship with some indices of recruitment; (4) generally increased recruitment at levels of relative SSB above the median value; (5) females are harvested at the beginning of their sexual maturity (peeler fishery) and mature females have neither size protection, nor protection as sponge crabs in the hard crab fishery; (6) a decreasing size of mature females and increasing proportion of small (< 100 mm CW) females with a resultant decrease in fecundity; (7) the range of best estimates of MSY for the blue crab in North Carolina was 27.9 to 51.7, and landings were at or above this level from 1994-1999; (8) steadily decreasing biomass and sharply increasing fishing mortality rates, the latter of which are ~ 0.87-3.01 times levels at MSY; (9) predicted numbers of legal-sized crabs from C-S modeling were higher in the early 1990s, then generally declined from 1992 through 2002, concurrent with a generally increasing exploitation rate over time the same period; and (10) biological reference points from YPR and SSBR that suggest a reduction in fishing mortality may be warranted due to growth and recruitment overfishing concerns.

XII. RECOMMENDATIONS

A. Data Collection

1. Of the two NC DMF fishery-independent research survey programs (P120 and 195), P195 provides the most useful information in terms of tracking population trends and estimating population and stock assessment parameters for the blue crab. The timing and deep-water sampling protocol of the P195 survey permitted us to successfully fit spawning stock-recruit, C-S models, and to a lesser extent, biomass-based stock assessment models to the fishery-independent data. Moreover, P120 was biased against sampling female crabs because of the up-estuary nature of the sampling stations. Data generated from P120, however, may be useful in examining historical relationships between water quality in primary nursery habitats and relative abundance of Age 0 blue crabs (e.g., Neuse and Pamlico Rivers), as well as environmentally-driven recruitment variation in Age 0 crabs. Given the length-frequency of blue crabs captured in P120, this survey appears to track recruitment of a cohort spawned in early spring (small crabs < 20 mm CW), as well as larger crabs (40-80 mm CW) that were likely spawned in the fall of the previous year. To the extent possible, NC DMF should consider re-initiating P120 sampling in the fall (October or November) to observe annual recruitment of the fall spawn to juvenile habitats prior to overwintering. For example, consideration of replacing the current sampling protocol of NC DMF P120 from May, June and July to sampling in April, July, and October to better measure recruitment and abundance of early juveniles. If only two months can be effectively sampled due to budgetary or time constraints, the NC DMF may consider sampling in May and October. The NC DMF

should re-initiate sampling in Albemarle Sound by P195 because this region represents a significant percentage (25% of hard crab landings from 1994-2001) of annual landings in NC. If a redirection in current research survey effort was required to resume sampling in Albemarle Sound due to budgetary constraints, then one viable option would be to reduce the number of stations in P195 by treating the Outer Banks, Northwest Pamlico Sound and Southwest Pamlico Sound as a single water body, and redirecting this effort to Albemarle Sound.

2. All crabs captured in each tow should be measured and sexed to facilitate more straightforward data reduction and decreased uncertainty in estimates from trawl catches that were sub-sampled. Moreover, gear efficiency studies should be conducted to assess potential habitat-specific gear biases. Such information would aid in using CPUE survey data to make inferences concerning juvenile habitat requirements.

3. We re-emphasize the critical need for reliable catch and effort data for commercial landings, and catch and effort data for the soft crab and recreational fishery. Currently, the impact of the peeler fishery on the blue crab population may be underestimated, as many crabs that die in shedding operations are not sold to dealers and therefore not reported in landings data. This information is even more critical given the targeting of pre-pubertal females by this fishery; these females are captured just prior to entering the spawning stock. Reliable data for effort and catch for the recreational fishery is currently lacking in NC, and the magnitude of the recreational catch is unknown. The impact of the recreational fishery may be significant. For example, the recreational component of the Chesapeake Bay fishery accounted for 11.5 to 41.2 million lbs in the three years (1983, 1988, 1990) for which data was available (Rugolo et al. 1997). Further, estimates

of the Maryland recreational harvest of blue crabs in 1990 were 11.5 million pounds, whereas the commercial harvest was approximately 30 million pounds (Rugolo et al. 1997). Data on all components of the blue crab fishery in NC may allow for more effective modeling of the fishery, and will increase confidence in fishery model outputs.

4. Environmental variation due to rainfall, hurricanes, wind-stress and temperature appear to play a major role in annual postlarval recruitment of the blue crab, as well as crab availability to fishery-independent trawl surveys, and vulnerability to fishing. It is critical that fishery-independent trawl surveys continue to collect abiotic data, and that future stock assessments and investigations of blue crab population dynamics in NC assess the relative importance of abiotic variation and fishing pressure on the population.

5. Critical data on the spatial and temporal abundance of mature females within North Carolina is lacking. Information of the spatial dynamics of the spawning stock of blue crabs in NC is urgently needed to aid management in rebuilding the potentially depleted spawning stock.

B. Conservation of the spawning stock

1. Although each of the major inlets in NC (ORG, HATT, OCR, DRUM) serves as a spawning sanctuary for the blue crab, declines in fishery-independent index of SSB from 2000-2002 show that these sanctuaries may fail to maintain the spawning stock at a level that ensures sufficient recruitment under intense fishing pressure. Further, based on tagging and telemetry data, Medici (2004) concluded that due to the small size of the current sanctuaries in NC relative to the movement patterns of mature females, the sanctuaries offer minimal protection to the spawning stock as implemented. Possible solutions may be found in current management practices in Chesapeake Bay. The blue

crab spawning stock in Chesapeake Bay has also declined precipitously since 1992, prompting the following management actions: (1) creation of a marine protected area and corridor (MPAC) that covers an area of 935 mi^2 and primarily in water > 10 m deep from June 1 - September 15, which allows females to migrate to the bay mouth to spawn; (2) 8 hour fishing day (dawn-2PM); (3) 3 inch size limit on peelers; (4) protection of dark sponge crabs (brown to black sponge); (5) 5 ¼ inch size limit on hard crabs, and (6) pot limits. If NC considers implementing a MPAC, then it is critical that future research quantify mature female and sponge crab distribution and abundance patterns over time to select the best places and times to establish no take zones. Alternative methods to conserve the spawning stock in NC, which may find a greater chance of being approved by the NC Marine Fisheries Commission and NC legislature include: (1) an upper size limit on mature females; and (2) increasing the size of current inlet spawning sanctuaries and enforcing the sanctuary boundaries.

2. Establish upper size limit on females: The fecundity of female blue crabs increases in a linear, statistically significant manner with carapace width (Prager et al. 1990). For example, an 180 mm CW female blue crab produces broods 3 times as large as a 120 mm CW crab does. The first benefit of establishing an upper size limit would be a sharp increase in egg/larval production per crab. The second benefit would be to allow large females the opportunity to produce multiple broods over their lifetime. Presently, fishing mortality rates on legal-sized crabs are so high that their overall lifetime fecundity must be greatly reduced compared to the relatively small mature females, which escape fishing mortality through cull rings or the crab pot wire. The third benefit to an upper size limit is that it would help conserve a "natural" size-at-age. For example, increasing the

lifetime fecundity of relatively large females would help ensure that their genes are maintained in the population. The fourth benefit is that an upper size limit on females has a much lower economic impact to crabbers than an upper size limit to males. For example, a size of 6.5 inch and greater male blue crabs sell for ~$4.75/crab compared to ~$1.83 for similar sized females (http://www.angelfire.com/f14/overtoncrabcompany1 /bluecrab.html). Thus, since mature female blue crabs are generally not graded by size, protection of large females has less economic impacts than an upper size limit for males. The current system of harvesting most of the large females before they reproduce or after they reproduce once, and allowing an increasing proportional of relatively small mature females to reproduce, may partially explain the observed decline in the mean size of mature female blue crabs in NC and Chesapeake Bay.

To protect large mature females, the NC DMF has recommended that a maximum size limit of 6 ¾" (172 mm) CW be implemented for mature female blue crabs captured in the hard crab fishery from September - April. We support this recommendation as a step toward increased conservation of the blue crab spawning stock in North Carolina, although year round protection would afford greater protection to the spawning stock given the heavy exploitation rates of the fishery during (May-August). Maximum size limits for mature females in NC have been recommended by Medici (2004). Conservation of these large females may buffer the population from a potential decrease in size-at-age from genetic selection occurring as the result of the implementation of cull rings leading to an increasing proportion of escapement from crab pots by small females (< 127 mm CW; see section: V. INDEX OF SPAWNING STOCK BIOMASS, Trends in spawning stock biomass). Although this regulation would offer protection to only small

fraction of the spawning stock, it would preserve larger, more fecund (Prager et al. 1990) individuals. Further, because the regulation protects a small fraction of the total biomass available to the fishery, a minimal impact is expected to the fishery. For example, trawl surveys at all of the inlet spawning sanctuaries in NC in 2002 (Eggleston 2003, see section: INDEX OF SPAWNING STOCK BIOMASS, Relative abundance of mature females on spawning sanctuaries) indicate that mature females > 6 ¾" (172 mm) CW compose less than 1% (Table 16) of the total number of legal hard crabs (crabs > 127 mm CW + mature females) captured within ~ 5 km distance of the sanctuaries. Similarly, P195 trawls in 2002 suggest that mature females > 6 ¾" comprise less than 1% (Table 18) of the fishable population in Pamlico Sound. The percentage of mature females > 6 ¾" in trawls surveys in the Cape Fear River and surrounding waters in 2002, however, composed 16.3% (Table 18) of the legal hard crabs, and suggest that the magnitude of the impact on the fishery may vary regionally. Mature female blue crabs in the Cape Fear River estuary were 22% larger (152.23 vs. 124.36 mm CW) than those in Pamlico Sound in 2002. The smaller size of mature females in Pamlico Sound may be due to regional differences in salinity, or a result of heavier exploitation rates in Pamlico Sound. Although data from 2002 was highlighted because of the large spatial coverage of the sampling in that year, the percentage of mature females > 6 ¾" in the P195 trawl survey between 1987-2002 was never greater than 2% of the total number of legal hard crabs captured in the P195 trawl surveys. (Table 16).

3. Increase the area of the spawning sanctuaries and enforce the boundaries: Unpublished FRG data from Balance & Balance (2002), Eggleston (2003), and Medici (2004) indicate that mature, egg-bearing females are present on the spawning grounds

from spring-fall. Eggleston's trawl surveys at all of the inlet spawning sanctuaries in NC in 2002 indicated equal numbers of mature females within the sanctuary versus an area 5 km outside of the sanctuary (inshore & offshore) from June-September. Similarly, Medici (2004) and Balance & Balance (2002) found that mature females tagged in the Ocracoke Inlet sanctuary are consistently caught in crab pots up to 4 km surrounding the sanctuary. The benefit of this management recommendation is that for inseminated females that manage to migrate successfully to inlet sanctuaries, it would provide a more effective sanctuary to release multiple broods than the present system, particularly if is enforced. For example, over a 6 d period in 2003, Medici (2004) reported up to 176 illegal crab pots within the Ocracoke Inlet spawning sanctuary that were actively being fished.

XIII. ACKNOWLEDGMENTS

We are extremely grateful to S. McKenna, D. Taylor, K. West, L. Henry, L. Sabo, T. Moore and NC DMF staff for their efforts in the collection and distribution of data from NC DMF Program 120 and 195, and Capt. Mike Guthrie of the "RV Coastal Carolina". This report benefited from discussions with J. Gilliam, D. Hewitt, R. Hilborn, R. Lipcius, S. McKenna, J. Miller, T. Miller, and D. Secor, D. Wolcott, and T. Wolcott. Funding for this project was provided by the NC Blue Crab Research Program (99-FEG-10 and 00-FEG-11) administered through NC Sea Grant. We thank B. Hines, M. Turano and S. Rebach for their enthusiastic administration of this project. Additional support for this research was provided to D. Eggleston by the National Science Foundation (OCE 97-34472; OCE-0221086), North Carolina Sea Grant (NA46RG0087), the NC Blue Crab

Research Program (02-POP-04), the Z. Smith Reynolds Foundation, South Eastern Regional Vision of Education, and North Carolina State University.

XIV. LITERATURE CITED

Akaike, H. (1973). 2nd International Symposium on Information Theory, Chapter Information theory and an extension of maximum likelihood principle, pp. 267-281. Budapest: Akademia Kiado.

Ballance, E. S. and E. E. Ballance. (2002). Blue crab sampling near Hatteras and Ocracoke Inlets using crab pots. Report for NC FRG Project 01-POP-04.

Bertelsen, R. D., and C. Cox. (2001). Sanctuary roles in population and reproductive dynamics of Caribbean spiny lobster. Pages 591-605 in Kruse, GH, N. Bez, A. Booth, M. W. Dorn, S Hills, R. N. Lipcius, D. Pelletier, C. Roy, S.J. Smith, and D. Weatherall (Eds) Spatial Processes and Management of marine Populations. Anchorage, AK October 27-30, 1999.

Beverton, R. J. H. and S. J. Holt. (1957). On the dynamics of exploited fish populations. Fisheries Investment Series 2, Vol. 19, U. K. Ministry of Agriculture and Fisheries, London.

Cadman, L. R. and M.P. Weinstein. 1988. Effects of temperature and salinity on the growth of laboratory-reared juvenile blue crabs *Callinectes sapidu*s Rathbun. J Exp Mar Biol Ecol 121:193-207.

Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones and B. A. Menge. (1996). Recruitment and the local dynamics of open marine populations. 27:477-500.

Chaves, J. C, and D. B. Eggleston. (2003). Biotic and operational factors causing mortality in North Carolina's soft shell blue crab industry. J. Shellfish Res. (in press).

Collie, J. S., and M. P. Sissenwine. (1983). Estimating population size from relative abundance data measured with error. Can. J. Fish. Aquat. Sci. 40:1871-1879.

Dittel, A., A. Hines, G. Ruiz, and K. Ruffin. (1995) Effects of shallow water refuge on behaviour and density-dependent mortality of juvenile crabs in Chesapeake Bay. Bull Mar. Sci. 57:902-916.

Dudley, D. L. and M. H. Judy. (1971). Occurrence of larval, juvenile, and mature crabs in the vicinity of Beaufort Inlet, North Carolina. NOAA Tech. Report NMFS SSRF-637.

Eggleston, D. B. and D. A. Armstrong. (1995). Pre- and post-settlement determinants of estuarine Dungeness crab recruitment. Ecol. Monogr. 65:191-254.

Eggleston, D. B. and S. McKenna. (1996). Evaluation of fisheries resource data collection, analysis and availability: an example protocol using the blue crab. UNC-Sea Grant-96-01, 23 p.

Eggleston, D. B. (1998). Population dynamics of blue crab in North Carolina: Statistical analyses of fisheries survey data. Final Report for Contract M-6053, NC Dept. of Environ. health and Nat. Resources, Division of Mar. Fisheries 70 p.

Etherington, L. L. and D. B. Eggleston. (2000). Large-scale blue crab recruitment: linking postlarval transport, post-settlement planktonic dispersal, and multiple nursery habitats. Mar. Ecol. Prog. Ser. 204:179-198.

Eggleston, D. (2003). Field Assessment of Spawning Sanctuaries and Possible Migration Corridors for the Blue Crab Spawning Stock in North Carolina. Interim Report for NC FRG Project 01-POP-08, January 2003.

Etherington, L. L. and D. B. Eggleston. (2003). Spatial dynamics of large-scale, multi-stage crab (*Callinectes sapidus*) dispersal: determinants and consequences for recruitment. Can. J. Fish. Aquat. Sci. 60:873-887.

Fischler, K. J. (1965). The use of catch-effort, catch sampling, and tagging data to estimate populations of blue crabs. Trans. Am. Fish. Soc. 99:80-88.

Fisher, M. R. (1999) Effect of temperature and salinity on size at maturity of female blue crabs. Trans. Am. Fish. Soc. 128:499-506.

Fogarty, M. J., M. P. Sissenwine and E. B. Cohen. (1991). Recruitment variability and the dynamics of exploited marine populations. Trends in Ecology and Evolution 6:241-246.

Freckleton, R. P. (2002). On the misuse of residuals in ecology: regression of residuals vs. multiple regression. J. of Animal Ecology 71:542-545.

Garcia-Berthou, E. (2001). On the misuse of residuals in ecology: testing regression residuals vs. the analysis of covariance. J. of Animal ecology 70:708-711.

Gray, E. H. and C. L. Newcombe (1938). Studies of moulting in *Callinectes sapidus* Rathbun. Growth 2:285:296.

Gulland, J. A. and L. K. Boerema. (1973). Scientific advice of catch levels. Fish. Bull. U. S. 71(2):325-335.

Helser, T. E. and D. M. Kahn. (1999). Stock Assessment of Delaware Bay Blue Crab (*Callinectes sapidus*) for 1999. Dept. of Natural Resources & environmental Control. Delaware Division of Fish and Wildlife. 99 pp.

Helser, T. E., and D. M. Kahn. (2001). Stock assessment of Delaware Bay blue crab (*Callinectes sapidus*) for 2001. Delaware Division of Fish and Wildlife, Dover, DE.

Hewitt, D. and J. M. Hoenig (In review). Comparison of two approaches for estimating natural mortality based on longevity (submitted to Fish. Bull.)

Hilborn, R. and C. J. Walters. (1992). Quantitative Fisheries Stock Assessment: Choice, Dynamics & Uncertainty. Chapman & Hall, Inc. New York. 570 pp.

Hines, A. H. and G. M. Ruiz. (1995). Temporal variation in juvenile blue crab mortality: Nearshore shallows and cannibalism in Chesapeake Bay. Bull. Mar. Sci. 57(3):884-901.

Hoenig, J. M. (1983). Empirical use of longevity data to estimate mortality rates. Fish. Bull. 81:898-903.

Hoenig, J. M. (1987). Estimation of growth and mortality parameters for use in length-structured stock production models. Pages 121-128 in D. Pauley and G. R. Morgan (eds.), Length-based Methods in Fisheries Research. Int. Center for Living Aquatic Resource Management. ICLARM Conference Proceedings 13, 468 p.

Ju, S-J, D. H. Secor, and H. R. Harvey. (2003) Demographic assessment of the blue crab (*Callinectes sapidus*) in Chespaeake Bay using extractable lipofuscins as age markers. Fish. Bull. 101:312-320.

Ju, S. J., D. H. Secor, and H. R. Harvey. (2001). Growth rate variability and lipofuscin accumulation rates in the blue crab Callinectes sapidus. Mar. Ecol. Prog. Ser. 224:197-205.

Ju, S-J, D. Secor, and H. R. Harvey. (1999). The use of extractable lipofuscin for age determination of the blue crab, *Callinectes sapidus*. Mar. Ecol. Prog. Ser. 185:171-179.

Kirkwood, G. P., R. Aukland, and S. J. Zara. (2001). Length Frequency Distribution Analysis (LDFA), Version 5.0. MRAG Ltd, London, UK.

Lipcius, R.N. and Stockhausen, W.T. (2002). Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. Mar. Ecol. Prog. Ser. 226: 45-61.

Lipcius, R. N., W. T. Stockhausen, R. D. Seitz and P. J. Geer. (2003). Spatial dynamics and value of a marine protected area and corridor for the blue crab spawning stock in Chesapeake Bay. Bull. Mar. Sci. 72:453-469.

Lipcius, R. and W. A. Van Engel. (1990). Blue crab population dynamics in Chesapeake Bay: variation in abundance (York River, 1972-1988) and stock-recruit functions. Bull. Mar. Sci. 46:180-194.

Mangel, M., Marinovic, B., Pomeroy, C., and D. Croll. (2002). Requiem for Ricker: Unpacking MSY. Bull. Mar. Sci. 70: 763-781.

McConaugha, J. R., D. F. Johnson, A. J. Provenzano and R. C. Maris. (1983). Seasonal distribution of larvae of Callinectes sapidus (Crustacea: decapoda) in waters adjacent to Chesapeake Bay. J. Crust. Biol. 3:582-591.

McConaugha, J. R. (1991). Tag-recapture study of the spawning stock of the Chesapeake Bay blue crabs. College of Sciences, Old Dominion University, Norfolk, Virgina. Technical Report. 91-1. 2 pp.

McKenna, S. and J. T. Camp. (1992). An examination of the blue crab fishery in the Pamlico River estuary. Report No. 92-08, NC Dept. of Environ. Health and Nat. Resources, Division of Mar. Fish., 92 p.

McKenna, S., L. T. Henry, and S. Diaby. (1998). North Carolina Fishery Management Plan – Blue Crab. NC Dept. of Environ. Health and Nat. Resources, Division of Mar. Fish., 171 p.

Medici, D. (2004). Scale-dependent movement and protection of female blue crabs. MS thesis, Dept. of MEAS, NC State University.

Miller, T. J. and E. D. Houde. (1998). Blue Crab Target Setting. Final Report for the Living Resources Subcommittee, Chesapeake Bay Program, U.S. EPA. 158 pp.

Muller, R. G., J. H. Hunt, T. R. Matthews and W. C. Sharp. (1997). Evaluation of effort reduction in the Florida Keys spiny lobster, *Panulirus argus*, fishery using an age-structured population analysis. Mar. Freshwater Res. 48:1045-1058.

Myers, R. A. and N. J. Barrowman. (1996). Is fish recruitment related to spawner abundance? Fishery Bulletin 94. 94:707-724.

Newcombe, C. L. F. Campbell, and A. M. Eckstine (1949). A study of the form and growth of the blue crab *Callinectes sapidus* Rathbun. Growth 13:71-96.

North Carolina Fishery Management Plan for the Blue Crab: Draft 2 (2004). North Carolina Department of Environmental Health and Natural Resources, Division of Marine Fisheries, 374 pp.

Pauly, D. (1987) A review of the ELEFAN system for analysis of length-frequency data in fish and aquatic vertebrates. Pages 7-34 in Pauly, D. and Morgan, G. R. (Eds) Length-based methods in fisheries research. ICLARM, Manila, Philippines and KISR, Safat, Kuwait. 468p.

Pile, A. J., R. N. Lipcius, J. Van Montfrans and R. J. Orth. (1996). Density-dependent settler-recruit-juvenile relationships in blue crabs. Ecol. Monogr. 66:277-300.

Prager, M., J. McConaugha, C. Jones, and P. Geer. (1990). Fecundity of the blue crab, *Callinectes sapidus*, in Chesapeake Bay. Bull. Mar. Sci. 46:170:179.

Prager, M. H. (1993). A suite of extensions to a non-equilibrium surplus-production model. Fish. Bull., U.S. 92:374-389.

Prager, M. H. (1994). User's manual for ASPIC: a stock-production model incorporating covariates, program version 3.5.x. U. S. National Marine Fisheries Service, Miami Laboratory, MIA-92-/93-55, Miami, FL.

Prager, M. H., C. P. Goodyear, and G. P. Scott. (1996). Application of a surplus production model to a swordfish-like simulated stock with time-changing gear selectivity. Trans. Am. Fish. Soc. 125:729-740.

Punt, A. E., and R. Hilborn. (1996). Biomass dynamic models. User's manual. FAO Computerized Information Series, No. 10. Fodd and Agricultural Organization of the United Nations. Rome.

Punt, A. E. and R. B. Kennedy. (1997). Population modelling of Tasmanian rock lobster, *Jasus edwardsii*, resources. Mar. Freshwater Res. 48:967-980.

Punt, A. E., R. B. Kennedy and S. D. Frusher. (1997). Estimating the size-transition matrix for Tasmanian rock lobster, *Jasus edwardsii*. Mar. Freshwater Res. 48:981-992.

Ricker, W. E. (1954). Stock and recruitment. J. Fish. Res. Bd. Can. 11:559-623.

Rothschild, B. J., J. S. Ault, G. Smith, H. Li, S. Endo, and L. Baylis. (1991). Abundance estimation, population dynamics, and assessment of the Chesapeake Bay blue crab stock: A report to the Maryland Research Program. Final Report on Contract CB90-002-003. 99 p.

Rugolo, L, K. Knotts, A. Lange, V. Crecco (1998). Stock assessment of the Cheaspeake Bay blue crab (Callinectes sapidus Rathbun). J. of Shell. Res. 17(3):906-930.

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). Maryland Department of Natural Resources, 267 p.

Schaefer, M. B. (1954). Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Bull. Inter-Am. Trop. Tuna Comm. 1:27-56.

Sissenwine, M. P. (1981). An overview of some methods of fish stock assessment. Fisheries 6(6):31-35.

Smith, G. (1997). Models of crustacean growth dynamics. Ph.D. thesis, University of Maryland, College Park. 337 p.

Smith, M. T., and J. T. Addison. (2003). Methods for stock assessment of crustacean fisheries. Fisheries Research 65:231-256.

Speir, H. et al. (1995). Chesapeake Bay blue crab management plan. Maryland Dept. of Nat. Res. 66 p.

Tang, Q. (1985). Modifications of the Ricker stock recruitment model to account for environmentally induced variation in recruitment with particular reference to the blue crab fishery in Chesapeake Bay. Fish. Res. 3:13-21.

Van Montfrans, J., C. Epifanio, D. Knott, R. Lipcius, D. Mense, K. Metcalf, E. Olmi, R. Orth, M. Posey, E. Wenner and T. West. (1995). Settlement of blue crab postlarvae in Western North Atlantic estuaries. Bull. Mar. Sci. 57:834-854.

Von Bertalanffy, L. (1938). A quantitative theory of organic growth. Human Biol. 10:181-213.

Vetter, E. F. (1985) Estimation of natural mortality in fish stocks: A Review. Fish. Bull. U.S. 86(1):25-43.

Table 1. Commercial hard crab, peeler, and soft crab landings (lbs.) for the North Carolina blue crab fishery.

Year	Hard Crab	Peeler	Soft Crab	Total landings
1978	23,558,546	46,826 *		23,605,372
1979	26,623,723	80,367 *		26,704,090
1980	34,322,937	87,482 *		34,410,419
1981	37,927,573	77,748 *		38,005,321
1982	38,206,327	148,364 *		38,354,691
1983	34,689,455	87,570 *		34,777,025
1984	32,490,769	199,771 *		32,690,540
1985	29,329,547	326,978 *		29,656,525
1986	23,159,779	595,468 *		23,755,247
1987	31,760,413	663,191 *		32,423,604
1988	35,136,232	468,191 *		35,604,423
1989	33,935,992	788,681 *		34,724,673
1990	36,985,206	1,085,122 *		38,070,328
1991	41,074,063	755,613 *		41,829,676
1992	40,507,415	560,959 *		41,068,374
1993	42,867,109	805,623 *		43,672,732
1994	52,260,188	642,238	610,769	53,513,195
1995	45,033,543	724,442	685,555	46,443,540
1996	65,682,738	878,382	519,316	67,080,436
1997	54,472,171	1,022,695	713,898	56,208,764
1998	60,397,141	975,781	697,741	62,070,663
1999	55,917,857	923,650	510,363	57,351,870
2000	38,794,370	998,971	750,140	40,543,481
2001	29,938,956	1,319,202	921,693	32,179,851
2002	36,401, 654**	555,532**	718,894**	37,712,571**
Average	39,378,002	935,670	676,184	39,915,287

* Prior to 1994 peeler and soft crab landings were not tabulated separately. Asteris ked values represent the sum of peeler and soft crab landings.

** Landings for 2002 are estimates and subject to change prior to official release.

Table 2. Summary of water bodies, sampling areas, and station numbers of a fisheries-independent trawl survey (i.e., Program 120) of juvenile crabs conducted by the North Carolina Division of Marine Fisheries. Station numbers correspond to those shown on Figure 4.

Water Body	Sampling Area	Station Number
Northwest Pamlico Sound	Stumpy Point Bay	1
	Deep Creek	2
	Pains Bay	3
	Broad Creek	4
	Otter Creek	5
	Far Creek	6
	Middletown Creek	7
	Wysocking Bay	8
	Douglas Bay	9
	Harbor Creek	10
	Northwest Creek	11
	Oyster Creek	12
	Shingle Creek	13
	Striking Bay	14
	Unnamed Western	15
	Tooley Creek	16
	Unnamed North	17
	Box Creek	18
Pamlico and Pungo Rivers	Warner Creek	19
	Wood Creek	20
	Spring Creek	21
	Bradley Gut	22
	East Fork	23
	Mixon Creek	24
	Bath Creek	25
	Porter Creek	26
	Tooley Creek	27
	Jacobs Creek	28
	South Creek	29
	Muddy Creek	30
	East Prong	31
	Betty Creek	32
	Mallard Creek	33

Table 2 (continued).

Water Body	Sampling Area	Station Number
Southwest Pamlico Sound	Long Creek	34
	Clark Creek	35
	Porpoise Creek	36
	Upper Jones Bay	37
	Ditch Creek	38
	Dump Creek	39
	Riggs Creek	40
	Long Creek	41
	Smith Creek	42
	Chapel Creek	43
	Moore Creek	44
	Simpson Creek	45
	Bryan Creek	46
	Dipping Vat Creek	47
	Green Creek	48
	Parson's Creek	57
	Fur Creek	58
	Golden Creek	59
	Codduggen Creek	60
Neuse River	Upper Broad Creek	49
	Bright Creek	50
	Pierce Creek	51
	Kershaw Creek	52
	Clubfoot Creek	53
	Jonaquin Creek	54
	Big Creek	55
	Horton Bay	56
Core and Bogue Sounds	Southwest Prong	61
	Cedar Island Bay	62
	E. Thorofare Creek	63
	Oyster Creek	64
	Great Island Bay	65
	Smyrna Creek	66
	Horsepen Point	67
	Core Banks Area	68
	North River Narrows	69
	North River Below	70
	Cross Rock	71

Table 2 (continued).

Water Body	Sampling Area	Station Number
Southern Area	New River	72
	New River	73
	Northeast Creek	74
	French's Creek	75
	Mill Creek	76
	Snead's Bay	77
	Alligator Bay	78
	Turkey Creek	79
	Spicer's Bay	80
	Permuda Island	81
	Virginia Creek	82
	Smith Creek	83
	Cape Fear River	84
	Toomer's Creek	85
	North of Snow's	86
	North of Snow's	87
	North of Snow's	88
	Shallotte River	89
	Shallotte River	90
	Shallotte River	91
	Shallotte River	92
Outer Banks	Hatteras Island	93
	Hatteras Island	94
	Hatteras Island	95
	Hatteras Island	96
	Blossie Creek	97
Croatan Sound	Broad Creek	96
	Cuttthrough	98
	Roanoke Sound	99
	Dough Creek	101
	Dough Creek	102
	Scarboro Creek	103
	Buzzard Bay	104
	Kitty Hawk Bay	105
	Peter Mashoes	106
	Spencer Creek	107

Table 3. Summary of water bodies, sampling areas, station numbers, and number of sites sampled at each station of a fisheries-independent trawl survey (i.e., Program 195) of adult blue crabs conducted by the North Carolina Division of Marine Fisheries. Station numbers correspond to those shown on Figure 5.

Water Body	Sampling Area	Station Number	Number of Sampling Sites
Albemarle Sound	Camden Pt.	1	8
	Long Shoal Pt.	2	6
	Powell's Pt.	3	3
	Ned Bees Pt.	4	10
Croatan Sound	Caroon Pt.	5	11
	Croatan Sound	6	24
Neuse River	Gum Thicket Shoal	48	3
	Cherry Pt/Wilikninson Pt.	49	11
	Mouth to Cherry Pt.	50	52
	South River	51	2
Northwest Pamlico Sound	Off Stumpy Pt.	8	7
	Off Sandy Pt.	9	1
	Long Shoal	10	5
	Long Shoal River	11	2
	Pingleton Shoal	12	7
	Gibbs Shoal	13	2
	Middleton Anchorage	14	2
	Wysocking Bay	18	3
	Outfall Canal	20	1
	East Bluff Bay	21	2
	Bluff Shoal	22	11
	West Bluff Bay	23	1
	Juniper Bay	36	1
	Great Island	37	9
	Swanquarter Bay	38	2
	Deep Cove	39	1
	Rose Bay	41	3

Table 3 (continued).

Water Body	Sampling Area	Station Number	Number of Sampling Sites
Outer Banks	Gull Island	17	4
	Clam Shoal	26	4
	Offshore Oliver	27	1
	Legged Lump	28	1
	Portsmouth Island	29	1
	Howard Reef	30	3
Pamlico River	Sandy Pt./Old Field Pt.	42	6
	Upstream of Durant	43	5
	Durant/Pungo Pt.	44	8
	Gum Pt./Garrison	45	39
	Upstream of Maules Pt.	46	3
Pamlico Sound	Long Shoal/Rodan.	7	86
	Mauls Pt./Rugged Pt.	15	10
	East of Bluff Shoal	16	341
	Gull Shoal	19	4
	Outer Banks	24	1
	Seven Foot Patch	25	3
	Royal Shoal	31	6
	Lower Middle Grounds	32	1
	Inner Middle Grounds	33	4
	Brant Island Shoal	34	13
	Upper Middle Shoal	35	4
	West of Bluff Shoal	40	198
Southwest Pamlico Sound	Bay River	47	3
	Point of Marsh	52	1
	West Bay	53	2
	West Bay	54	2

Table 4. Maximum likelihood estimates of model parameters from length-based modeling of observed blue crab length frequencies from NC DMF Program 120 trawls in May and June from 1987-2002. Growth was assumed to be described by a single von Bertalanffy growth function (VBGF) for all years. VBGF parameters (t0, Linf and k) and standard deviation (StDev) were constant among all years. The Estimated values for t0 (0.41), Linf (216.90), k (0.51), and StDev (21.25) were generated from length-based modeling (see text for details). The proportion of blue crabs in each age class (Prop Age 0, Prop Age 1) were allowed to vary among years.

	May			June		
Year	*N*	*Prop Age 0*	*Prop Age 1*	*N*	*Prop Age 0*	*Prop Age 1*
1987	987	0.93	0.07	954	0.80	0.20
1988	1230	0.89	0.11	913	0.85	0.15
1989	451	0.80	0.20	472	0.88	0.12
1990	884	0.80	0.20	674	0.70	0.30
1991	594	0.70	0.30	496	0.61	0.39
1992	495	0.78	0.22	415	0.70	0.30
1993	893	0.91	0.09	631	0.84	0.16
1994	903	0.90	0.10	710	0.79	0.21
1995	925	0.89	0.11	698	0.81	0.19
1996	1328	0.92	0.08	1460	0.74	0.26
1997	1097	0.87	0.13	825	0.80	0.20
1998	642	0.81	0.19	3800	0.33	0.67
1999	952	0.85	0.15	1048	0.63	0.37
2000	421	0.69	0.31	494	0.69	0.31
2001	886	0.87	0.13	564	0.73	0.27
2002	958	0.86	0.14	813	0.69	0.31
Mean		0.85	0.15		0.72	0.28

Table 5. Maximum likelihood estimates of model parameters from length-based modeling of observed blue crab length frequencies from NC DMF Program 195 trawls in June and September from 1987-2003. Growth was assumed to be described by a single von Bertalanffy growth function (VBGF) for all years. VBGF parameters (t0, Linf and k) and standard deviation (StDev) were constant among all years. The Estimated values for t0 (0.02), Linf (216.90), k (0.47), and StDev (19.53) were generated from length-based modeling (see text for details). The proportion of blue crabs in each age class (Prop Age 0, Prop Age 1, Prop Age 2) were allowed to vary among years.

	June			September		
Year	*N*	*Prop Age 0*	*Prop Age 1*	*N*	*Prop Age 1*	*Prop Age 2*
1987	3062	0.57	0.43	853	0.57	0.43
1988	737	0.59	0.41	603	0.62	0.38
1989	3300	0.69	0.31	489	0.68	0.32
1990	6239	0.75	0.25	625	0.58	0.42
1991	6810	0.62	0.38	687	0.63	0.37
1992	2019	0.44	0.56	422	0.30	0.70
1993	2301	0.67	0.33	579	0.64	0.36
1994	1244	0.68	0.32	639	0.52	0.48
1995	859	0.57	0.43	226	0.22	0.78
1996	525	0.90	0.10	1450	0.36	0.64
1997	1720	0.74	0.26	560	0.43	0.57
1998	944	0.59	0.41	601	0.32	0.68
1999	1911	0.65	0.35	599	0.58	0.42
2000	796	0.82	0.18	204	0.51	0.49
2001	1540	0.72	0.28	257	0.46	0.54
2002	5179	0.85	0.15	247	0.53	0.47
2003	4140	0.95	0.05	1315	0.14	0.86
Mean		0.69	0.31		0.48	0.52

Table 6. Summary of mean annual trawl survey indices of abundance (catch-per-unit-effort;CPUE) for blue crabs (NC DMF Programs 120 and 195) by age, based on surveys conducted in May, June and September from 1987-2003. CPUE values were generated using the length-based model descibed in the text.

	Program 195				**Program 120**			
	June Age 0	June Age 1	Sept Age 1	Sept Age 2	May Age 0	May Age 1	June Age 0	June Age 1
1987	33.56	25.30	9.42	6.98	7.75	0.70	7.08	1.88
1988	8.48	5.96	7.35	4.47	9.24	1.24	6.97	1.26
1989	45.66	20.31	6.69	3.09	3.05	0.87	3.82	0.55
1990	86.41	29.06	6.75	4.82	5.99	1.70	4.28	1.97
1991	79.12	49.32	8.14	4.83	3.51	1.72	2.78	1.88
1992	16.76	21.32	2.36	5.61	3.31	1.05	2.52	1.12
1993	28.65	13.94	6.82	3.90	7.43	0.77	4.87	0.98
1994	16.03	7.43	6.32	5.73	7.14	0.84	4.76	1.31
1995	9.36	7.16	0.98	3.37	7.26	1.01	4.88	1.20
1996	9.10	0.99	10.08	17.80	10.45	1.04	9.22	3.43
1997	24.12	8.31	4.52	6.04	8.19	1.36	6.08	1.60
1998	10.62	7.52	3.72	7.84	4.60	1.19	11.62	25.00
1999	22.89	12.48	6.41	4.68	7.00	1.39	6.12	3.72
2000	12.38	2.64	1.97	1.88	2.83	1.40	3.53	1.65
2001	20.89	8.15	2.23	2.62	6.57	1.15	3.76	1.46
2002	83.34	14.32	2.49	2.17	7.09	1.25	5.10	2.43
2003	80.19	4.47	3.42	21.38				
Mean	34.56	14.04	5.27	6.31	6.34	1.17	5.46	3.22
s.d.	28.96	12.12	2.77	5.29	2.28	0.30	2.39	5.87
C.V.	0.84	0.86	0.53	0.84	0.36	0.26	0.44	1.83

Table 7. Correlations between mean annual indices of abundance for Age 0, Age 1, and Age 2 crabs from Programs 120 and 195 at appropriate lags. For example, Age 0 crabs in a given year are correlated with Age 1 crabs the following year, and correlated to Age 2 crabs at a lag of two years. Each entry represents the Pearson correlation coefficient, significance level, and the number of observations (N). Significant correlations are shown in bold.

	Program 195				**Program 120**			
	June Age 0	June Age 1	Sept Age 1	Sept Age 2	May Age 0	May Age 1	June Age 0	June Age 1
Program 195								
June Age 0	1.000 . 17	**0.537*** **0.016** **16**	0.076 0.386 17	0.324 0.111 16	-0.243 0.182 16	0.422 0.058 15	-0.373 0.077 16	-0.069 0.403 15
June Age 1		1.000 . 16	0.245 0.180 16	-0.291 0.137 16	-0.305 0.125 16	0.403 0.061 16	-0.232 0.193 16	-0.156 0.289 15
September Age 1			1.000 . 17	-0.384 0.071 16	0.380 0.074 16	0.218 0.218 15	0.285 0.142 16	-0.175 0.266 15
September Age 2				1.000 . 17	0.189 0.242 16	-0.152 0.287 16	-0.016 0.476 16	0.257 0.178 15
Program 120								
May Age 0					1.000 . 16	-0.043 0.440 15	**0.485*** **0.028** **16**	0.206 0.231 15
May Age 1						1.000 . 16	0.218 0.218 15	0.403 0.061 15
June Age 0							1.000 . 16	0.120 0.335 15
June Age 1								1.000 . 16

Table 8. Correlations between mean annual indices of abundance for Age 0, Age 1, and Age 2 crabs from Programs 120 and 195 within years. Each entry represents the Pearson correlation coeffcient, significance level, and the number of observations (N). Significant correlations are shown in bold.

	Program 195				**Program 120**			
	June Age 0	June Age 1	Sept Age 1	Sept Age 2	May Age 0	May Age 1	June Age 0	June Age 1
Program 195								
June Age 0	1.000 . 17	**0.581*** **0.007** **17**	0.076 0.386 17	0.125 0.316 17	-0.243 0.182 16	**0.478*** **0.031** **16**	-0.373 0.077 16	-0.191 0.239 16
June Age 1		1.000 . 17	0.346 0.087 17	-0.275 0.143 17	-0.413 0.056 16	0.403 0.061 16	**-0.435*** **0.046** **16**	-0.166 0.270 16
September Age 1			1.000 . 17	0.251 0.017 17	0.380 0.740 16	-0.099 0.358 16	0.285 0.142 16	-0.113 0.339 16
September Age 2				1.000 . 17	**0.486*** **0.028** **16**	-0.152 0.287 16	**0.621*** **0.005** **16**	0.248 0.177 16
Program 120								
May Age 0					1.000 . 16	-0.244 0.181 16	**0.485*** **0.028** **16**	-0.146 0.295 16
May Age 1						1.000 . 16	-0.175 0.259 16	0.068 0.401 16
June Age 0							1.000 . 16	**0.736*** **0.001** **16**
June Age 1								1.000 . 16

Table 9. Correlations between mean annual indices of abundance for Age 0 and Age 1 crabs from Program 120 and commercial hard crab landings within years and at various annual lags. For example, each index in a given year is correlated to landings in the same year (t), the following year (t + 1). Each entry represents the Pearson correlation coefficient, significance level, and the number of observations (N). Significant correlations are shown in bold.

Program 120 May trawls

	Landings	Landings (t + 1)	landings (t + 2)
Age 0	0.311 0.121 16	0.349 0.101 15	0.294 0.154 14
Age 1	0.029 0.457 16	-0.151 0.296 15	-0.271 0.174 14

Program 120 June trawls

	Landings	Landings (t + 1)	landings (t + 2)
Age 0	**0.614*** **0.006** **16**	0.380 0.081 15	-0.059 0.420 14
Age 1	**0.479*** **0.030** **16**	0.296 0.142 15	-0.191 0.257 14

Table 10. Correlations between mean annual indices of abundance for Age 0, Age 1, and Age 2 crabs from Program 195 and commercial hard crab landings within years and at various annual lags. For example, each index in a given year is correlated to landings in the same year (t), the following year (t + 1),. Each entry represents the Pearson correlation coefficient, significance level, and the number of observation (N). Significant correlations are shown in bold.

Program 195 June trawls

	Landings	Landings (t + 1)	landings (t + 2)
Age 0	-0.393 0.066 16	-0.246 0.188 15	-0.247 0.197 14
Age 1	-0.380 0.074 16	-0.262 0.173 15	-0.266 0.179 14

Program 195 September trawls

	Landings	Landings (t + 1)	landings (t + 2)
Age 1	0.167 0.268 16	-0.187 0.252 15	-0.095 0.373 14
Age 2	**0.679*** **0.002** **16**	0.358 0.095 15	0.407 0.075 14

Table 11. Summary of length-based estimates of blue crab mortality (Z) for sexes combined from NC DMF Program 195 using the Hoenig (1987) approach with three previously published growth trajectories (Rugolo et al. 1998, Helser and Kahn 1998), and two growth trajectories generated from length-based modeling in the present study.

			Total Instantaneous mortality (Z)				
			Previous growth estimates			Present Assessment	
Year	N	Mean CW (mm)	K = 0.59 L_{inf} = 262.5	K = 0.93 L_{inf} = 200.3	K = 0.75 L_{inf} = 235.7	K = 0.47 L_{inf} = 216.9	Average
1987	1081	142.70	1.48	1.17	1.42	1.02	1.27
1988	309	143.00	1.47	1.15	1.40	1.01	1.26
1989	643	141.62	1.54	1.23	1.48	1.08	1.33
1990	916	142.56	1.49	1.18	1.43	1.03	1.28
1991	1078	139.19	1.71	1.39	1.64	1.22	1.49
1992	815	141.93	1.53	1.21	1.46	1.06	1.32
1993	545	141.68	1.54	1.23	1.48	1.07	1.33
1994	428	141.51	1.55	1.24	1.49	1.08	1.34
1995	283	141.60	1.55	1.23	1.48	1.08	1.33
1996	800	143.00	1.47	1.15	1.40	1.01	1.26
1997	440	141.84	1.53	1.22	1.47	1.06	1.32
1998	445	144.78	1.37	1.06	1.31	0.92	1.17
1999	324	141.86	1.53	1.22	1.47	1.06	1.32
2000	158	144.95	1.37	1.05	1.30	0.92	1.16
2001	300	144.48	1.39	1.08	1.32	0.94	1.18
2002	468	145.06	1.36	1.05	1.29	0.91	1.15
2003	1036	143.62	1.43	1.12	1.37	0.98	1.22
Mean	1092	142.61	1.49	1.18	1.43	1.03	1.28
s.d.		1.58	0.09	0.09	0.09	0.08	0.09

Table 12. Estimates of carrying capacity (K), first-year biomass (B_1), maximum sustainable yield (MSY), biomass at MSY (B_{MSY}), fishing mortality at MSY (F_{MSY}), and relative biomass (B_{2002}/B_{MSY}), fishing mortality rates (F_{2002}/F_{MSY}) for 2002, and maximum log likelihood (-2ln(L) for the blue crab stock in NC generated from fixing the population growth rate (r) and fitting the remaining model parameters simultaneously to the commercial crab pot CPUE time series from 1953 - 2002. B_1 was constrained to be equal to K.

	r									
	0.2	0.4	0.6	0.8	1.0	1.2	1.4	1.6	1.8	2.0
K	526.60	347.97	263.29	213.19	179.70	155.62	137.40	123.20	111.71	102.29
B_1	526.60	347.97	263.29	213.19	179.70	155.62	137.40	123.20	111.71	102.29
MSY	26.30	34.78	39.49	42.64	44.90	46.69	48.10	49.30	50.27	51.15
B_{MSY}	263.30	173.99	131.64	106.60	89.90	77.82	68.70	61.60	55.86	51.15
F_{MSY}	0.10	0.20	0.3	0.40	0.50	0.60	0.70	0.80	0.90	1.00
F_{2002}/F_{MSY}	6.45	4.36	3.52	3.05	2.74	2.53	2.37	2.25	2.15	2.08
B_{2002}/B_{MSY}	0.21	0.24	0.26	0.28	0.30	0.31	0.32	0.33	0.34	0.34
- 2(ln)L	49.50	51.13	52.08	52.69	53.10	53.43	53.70	53.90	54.01	54.14

Table 13. Estimates of carrying capacity (K), first-year biomass (B_1), maximum sustainable yield (MSY), biomass at MSY (B_{MSY}), fishing mortality at MSY (F_{MSY}), and relative biomass (B_{2002}/B_{MSY}), fishing mortality rates (F_{2002}/F_{MSY}) for 2002, and maximum log likelihood (-2ln(L) for the blue crab stock in NC generated from fixing the population growth rate (r) and fitting the remaining model parameters simultaneously to Program 195 June and September indices (crabs > 127 mm CW; 1987 – 2002) and commercial crab pot CPUE time series (1953 – 2002). B_1 was constrained to be equal to K.

	r									
	0.2	0.4	0.6	0.8	1.0	1.2	1.4	1.6	1.8	2.0
K	557.62	364.57	273.77	220.23	184.61	159.14	140.00	125.10	113.17	103.41
B_1	557.62	364.57	273.77	220.23	184.61	159.14	140.00	125.10	113.17	103.41
MSY	27.88	36.46	41.06	44.05	46.15	47.74	49.00	50.04	50.93	51.71
B_{MSY}	278.81	182.28	136.88	110.12	92.31	79.57	70.00	62.55	56.59	51.71
F_{MSY}	0.10	0.20	0.30	0.40	0.50	0.60	0.70	0.80	0.90	1.00
F_{2002}/F_{MSY}	3.01	1.96	1.56	1.34	1.20	1.09	1.02	0.96	0.91	0.87
B_{2002}/B_{MSY}	0.43	0.51	0.57	0.62	0.66	0.70	0.73	0.76	0.78	0.81
- 2(ln)L	82.48	83.57	84.15	84.46	84.63	84.73	84.80	84.85	84.89	84.94

Table 14. Estimates of absolute recruit (crabs < 127 mm CW) and fishable (crabs > 127 mm CW) abundance in millions , annual harvest rate and fishing mortality for the blue crab stock in North Carolina generated from a Collie-Sissenwine model fit to observed relative abundance data , at varying assumed natural mortality rates (M) of 0.55, 0.87, 1.44.

	M = 0.55				**M = 0.87**				**M = 1.44**			
	Absolute abundance				Absolute abundance				Absolute abundance			
Year	Recruits	Fishable	Harv Rate	Est F	Recruits	Fishable	Harv Rate	Est F	Recruits	Fishable	Harv Rate	Est F
1988	141.6	200.9	0.47	0.63	247.9	360.2	0.34	0.41	1610.9	2446.0	0.08	0.08
1989	779.6	104.8	0.18	0.19	1500.0	169.1	0.12	0.13	10584.4	886.9	0.03	0.03
1990	26.1	420.7	0.38	0.48	43.0	616.6	0.33	0.39	259.5	2646.1	0.11	0.12
1991	649.8	160.1	0.23	0.26	1334.5	186.2	0.16	0.17	8885.8	610.2	0.04	0.04
1992	27.8	358.8	0.48	0.65	46.2	537.0	0.40	0.52	284.5	2163.0	0.15	0.16
1993	332.8	116.1	0.44	0.57	604.6	145.6	0.33	0.40	3906.7	494.3	0.09	0.09
1994	228.6	145.7	0.64	1.02	382.5	209.8	0.51	0.72	2207.0	952.1	0.15	0.16
1995	253.7	77.9	0.62	0.97	411.5	120.7	0.49	0.68	2305.9	638.0	0.14	0.15
1996	252.9	72.4	0.92	2.58	327.1	113.2	0.87	2.03	1236.0	602.3	0.32	0.38
1997	446.8	14.2	0.54	0.78	793.0	24.3	0.39	0.49	5913.3	296.7	0.08	0.08
1998	253.4	122.5	0.74	1.33	390.9	209.9	0.59	0.88	2445.8	1356.4	0.14	0.15
1999	296.2	57.3	0.73	1.30	465.1	104.4	0.57	0.85	2954.1	773.1	0.13	0.14
2000	205.2	55.8	0.68	1.15	329.7	101.9	0.52	0.74	2032.6	764.5	0.12	0.13
2001	187.5	47.9	0.58	0.87	289.4	86.0	0.46	0.62	1439.2	580.5	0.13	0.14
2002		56.8				84.3				415.3		
	Mean (1987-2001)		0.54	0.91			0.43	0.65			0.12	0.13
	Mean (1995-2001)		0.69	1.28			0.56	0.90			0.15	0.17

Table 15. Fishery management benchmarks resulting from YPR and SSBR analyses, and estimates of the average instantaneous total and fishing mortality from Collie-Sissenwine modeling from two time periods (1987-2001 and 1995-2001) for the North Carolina blue crab. The values for F were calculated by subtracting M from Z. Reference points were calculated from a growth trajectory generated from statistical length-based modeling and using three estimates of natural mortality. F values which exceed benchmark values are shown in bold.

		Instantaneous mortality rates (Z and F)			
	Benchmark	Z (1987-2001)	F (1987-2001)	Z (1995-2001)	F (1995-2001)
M = 0.55					
F_{MAX}	0.51	1.46	**0.91**	1.83	**1.28**
$F_{0.1}$	0.36	1.46	**0.91**	1.83	**1.28**
$F_{30\%}$	0.56	1.46	**0.91**	1.83	**1.28**
$F_{20\%}$	0.81	1.46	**0.91**	1.83	**1.28**
		Z (1987-2001)	F (1987-2001)	Z (1995-2001)	F (1995-2001)
M = 0.87					
F_{MAX}	0.64	1.52	**0.65**	1.77	**0.90**
$F_{0.1}$	0.45	1.52	**0.65**	1.77	**0.90**
$F_{30\%}$	0.78	1.52	0.65	1.77	**0.90**
$F_{20\%}$	1.12	1.52	0.65	1.77	0.90
		Z (1987-2001)	F (1987-2001)	Z (1995-2001)	F (1995-2001)
M = 1.44					
F_{MAX}	0.93	1.57	0.13	1.61	0.17
$F_{0.1}$	0.62	1.57	0.13	1.61	0.17
$F_{30\%}$	1.07	1.57	0.13	1.61	0.17
$F_{20\%}$	1.55	1.57	0.13	1.61	0.17

Table 16. Percent of mature females greater than 6 ¾" of the total crabs legal (crabs > 127 mm CW and mature females) to be harvested in the hard crab fishery from P195 trawl surveys between 1987 and 2002, and trawls surveys conducted in the inlet sanctuaries (Barden's, Drum, Hatteras, Ocracoke, Oregon) and Cape Fear River in 2002.

	Program 195		Inlet Sanctuaries		Cape Fear River	
Year	N	%	N	%	N	%
1987	1148	0.52				
1988	316	0.32				
1989	786	0.51				
1990	825	0.49				
1991	944	0.21				
1992	717	0.84				
1993	541	0.74				
1994	376	0.80				
1995	267	1.12				
1996	764	0.65				
1997	412	0.73				
1998	422	1.66				
1999	319	1.57				
2000	150	2.00				
2001	177	1.13				
2002	750	0.67	215	0.93	1179	16.28
Mean		0.87		0.93		16.28

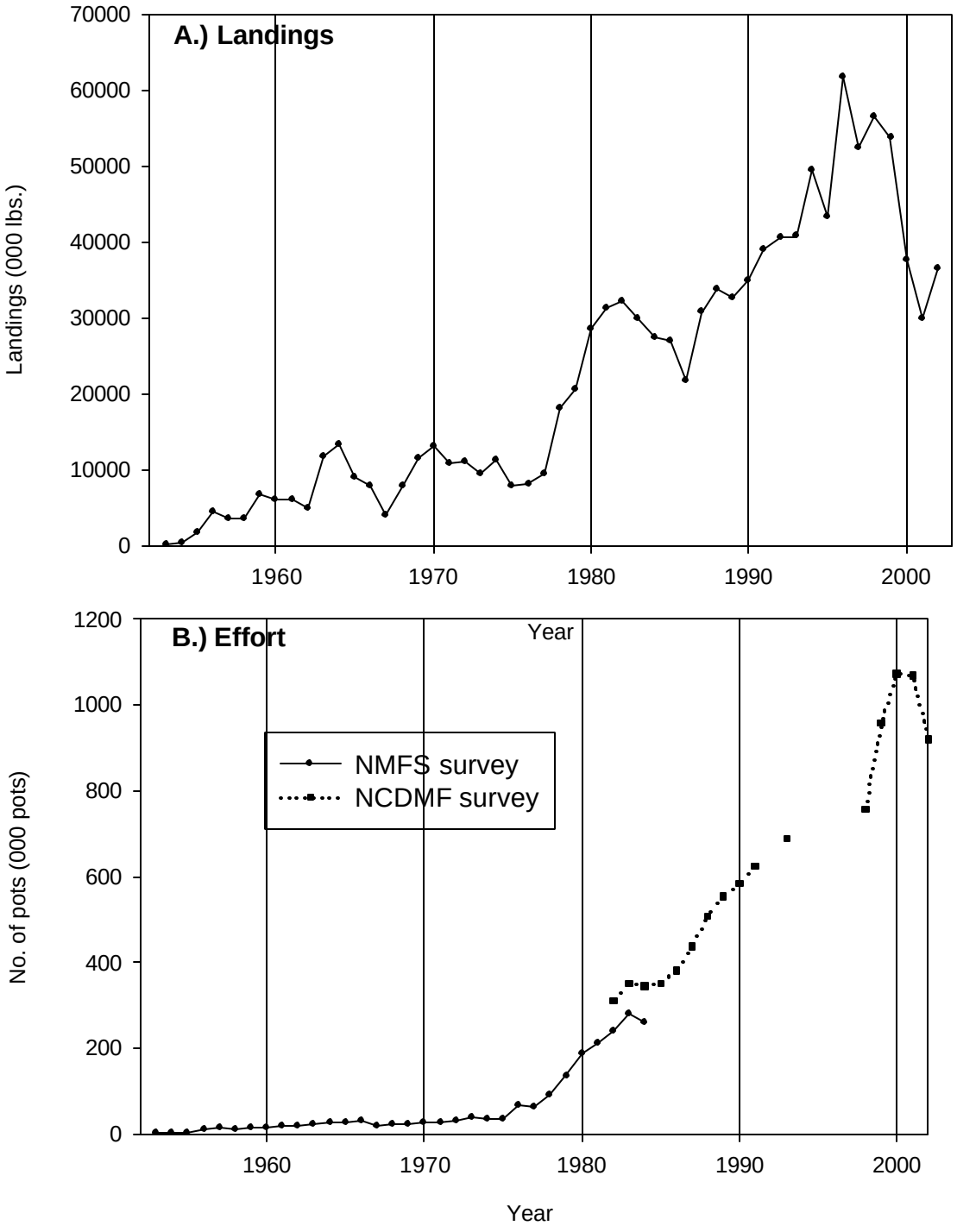


Figure 1. A.) Commercial landings in North Carolina from 1953 - 2002, and B.) National Marine Fisheries Service (NMFS) and North Carolina Division of Marine Fisheries (NC DMF) estimates of effort for the North Carolina Blue Crab pot fishery from 1953 - 2002. Fishing effort from 1994-1997 was removed because of problems with assumed over reporting in response to perceived pot limit legislation (S. McKenna, NC DMF, pers. comm.).

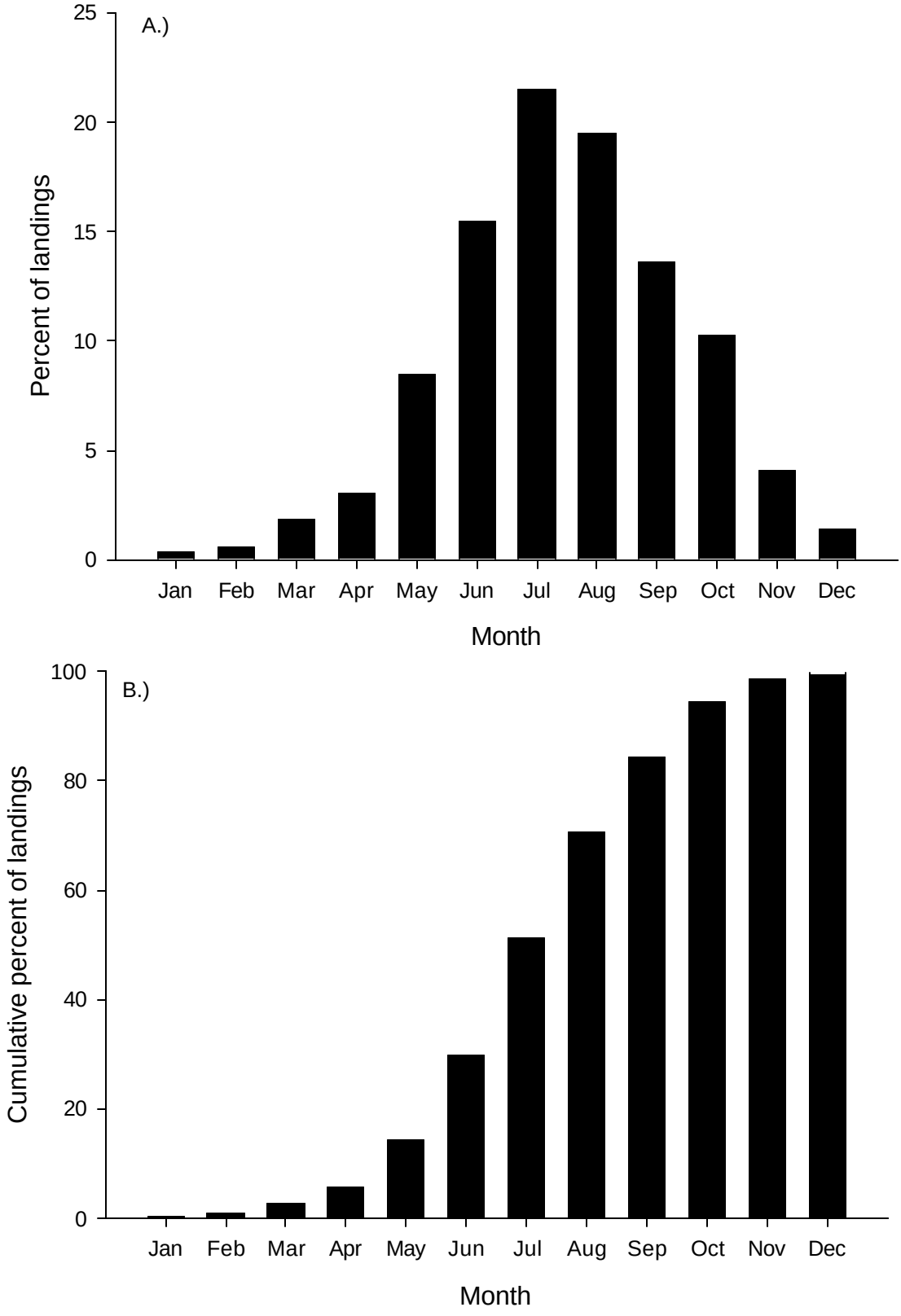


Figure 2. North Carolina commercial landings averaged by month from 1987 - 2002 A.) percentage of landings by month, and B.) cumulative percentage of annual commercial landings.

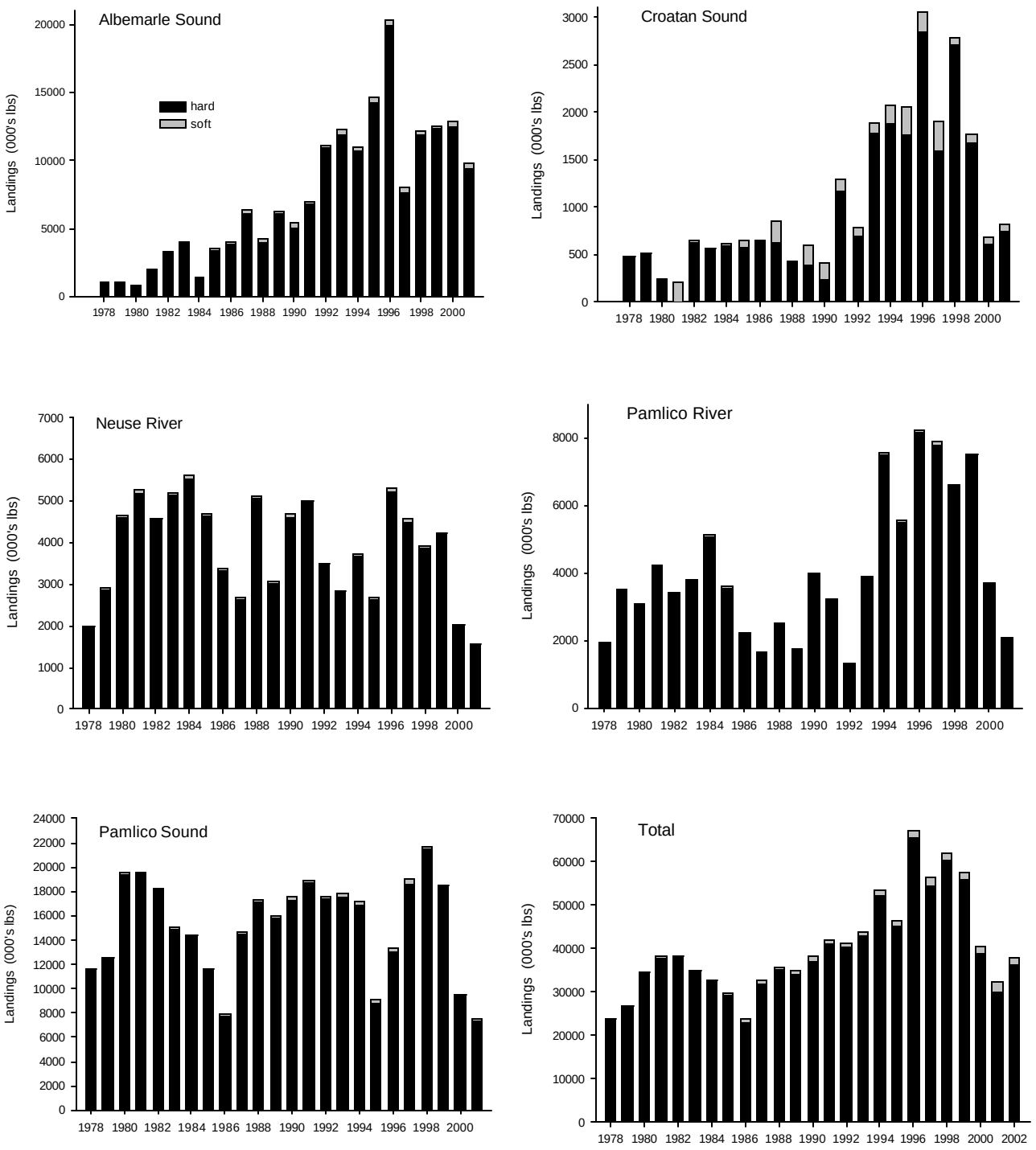


Figure 3. Commercial landings of hard and soft blue crabs in North Carolina by water body and year (1978-2001). These years were chosen as a comparison with blue crab trawl survey data collected by the NC DMF from 1978-2002 (Program 120 and Program 195). The landings for all five water bodies pooled equals total landings.

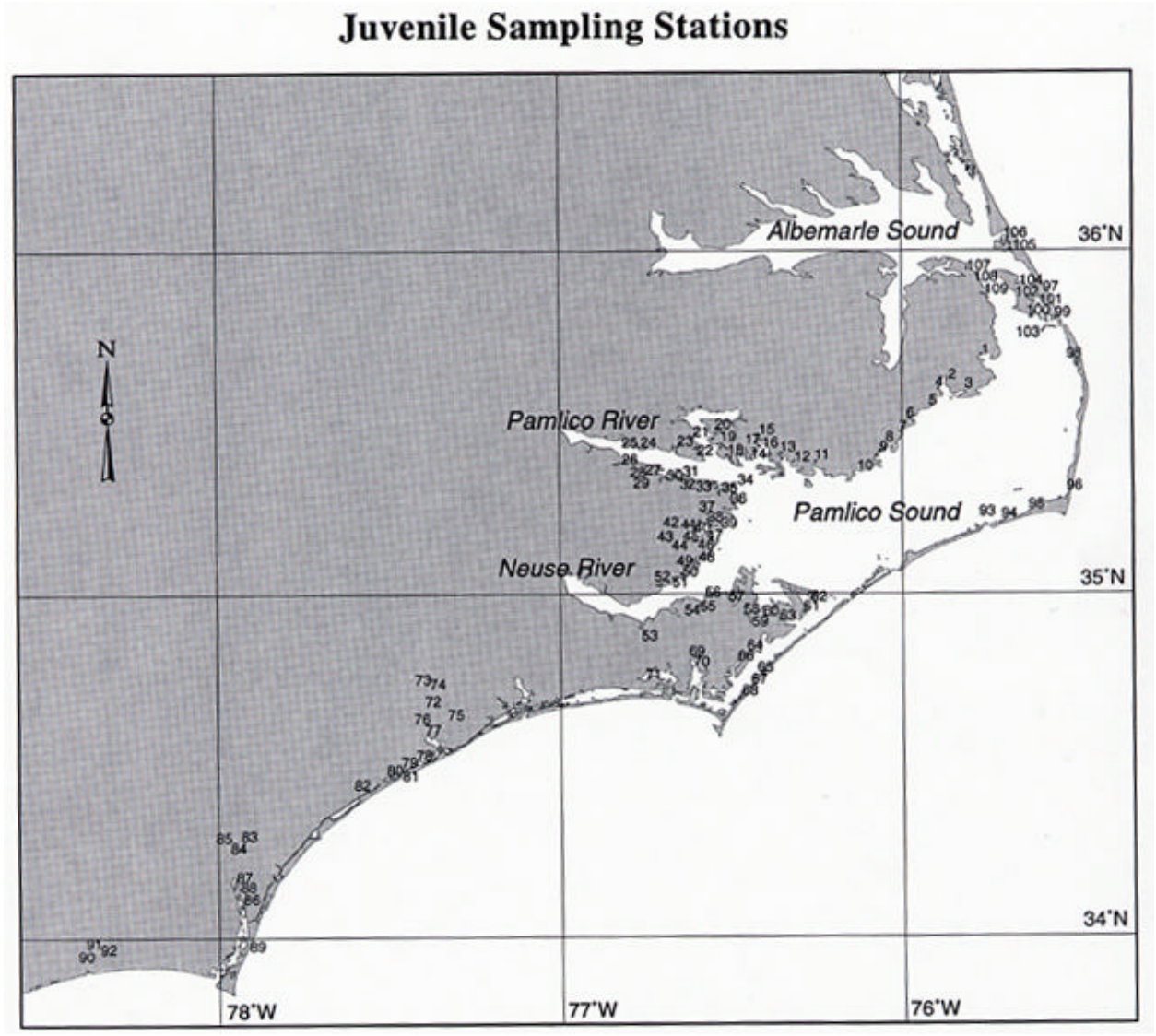


Figure 4. Locations of trawl survey sampling stations for juvenile blue crabs conducted by the North Carolina Division of Marine Fisheries (NC DMF Program 120). See Table 2 for the water body and sampling area for a given station number.

Adult Sampling Stations

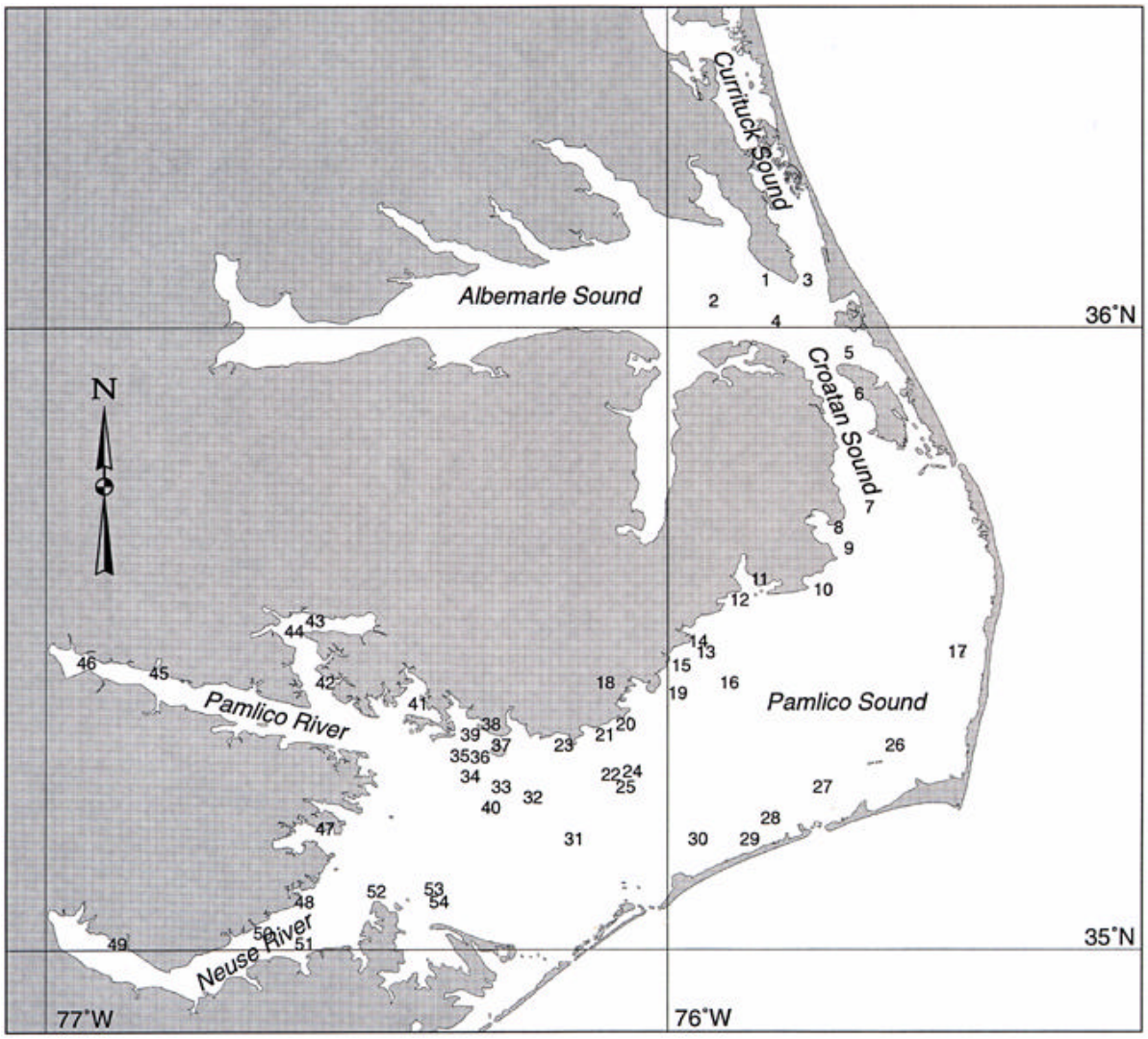


Figure 5. Locations of trawl survey core sampling stations for juvenile blue crabs conducted by the North Carolina Division of Marine Fisheries (NC DMF Program 195). See Table 3 for the water body and sampling area for a given station number.

Adult Sampling Sites within Stations

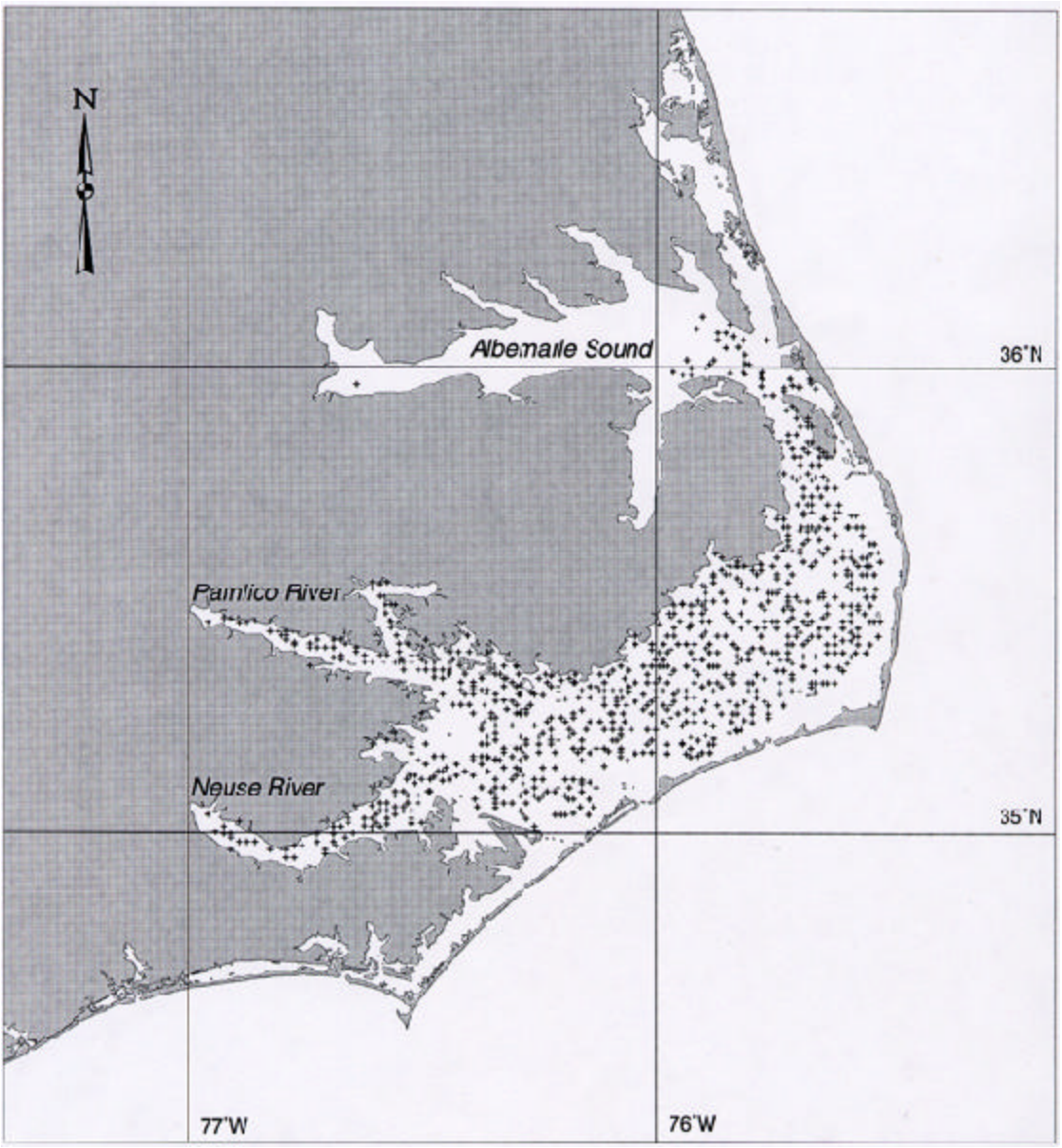


Figure 6. Locations of trawl survey sampling sites within core sampling stations (Fig. 5) for adult blue crabs conducted by the North Carolina Division of Marine Fisheries (NC DMF Program 195).

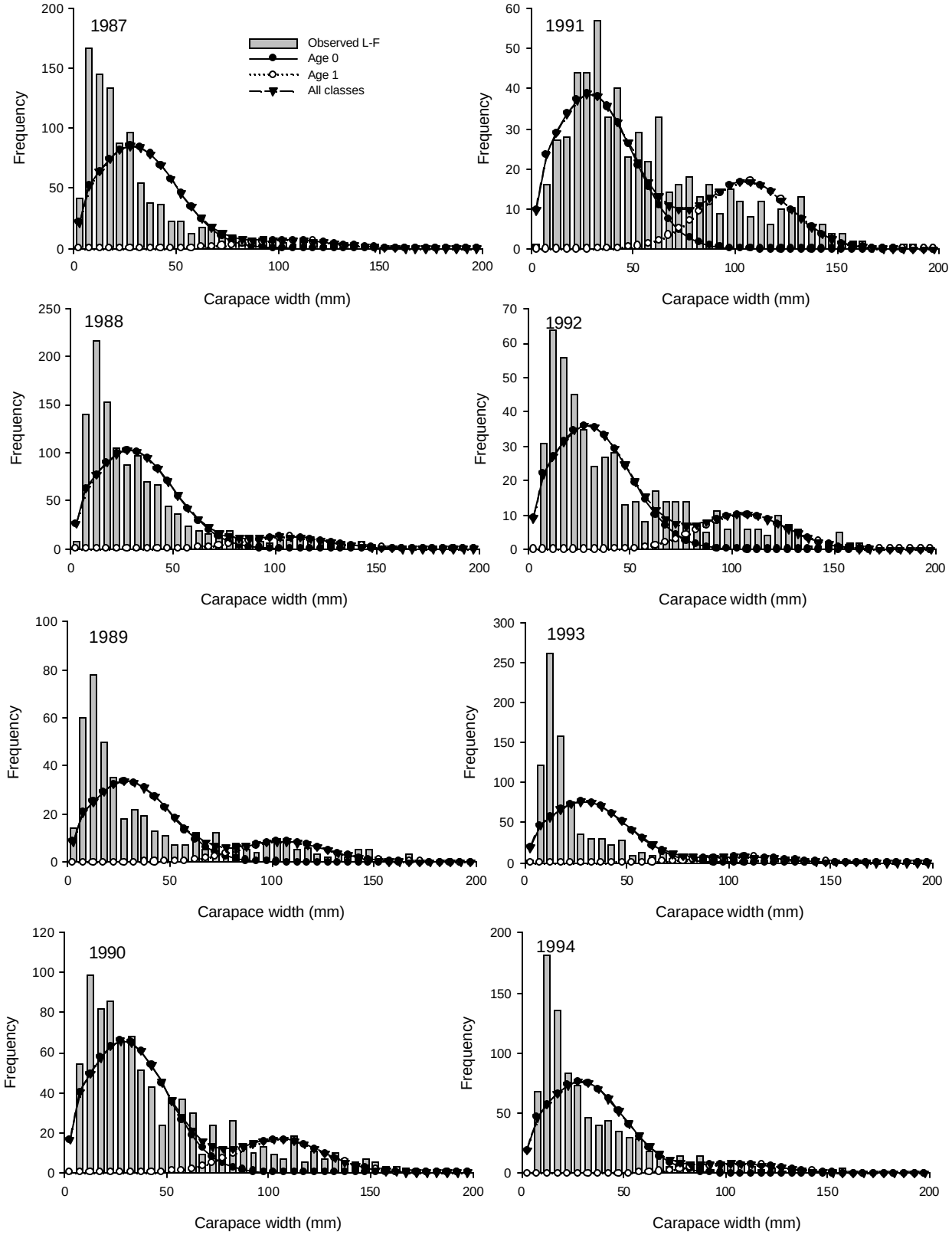


Figure 7. The observed (histograms) and predicted (symbols) size frequency of blue crabs by year collected in NC DMF Program 120 in May from 1987 – 2002 pooled across all water bodies. The predicted fits shown were produced by minimizing the model log likelihood.

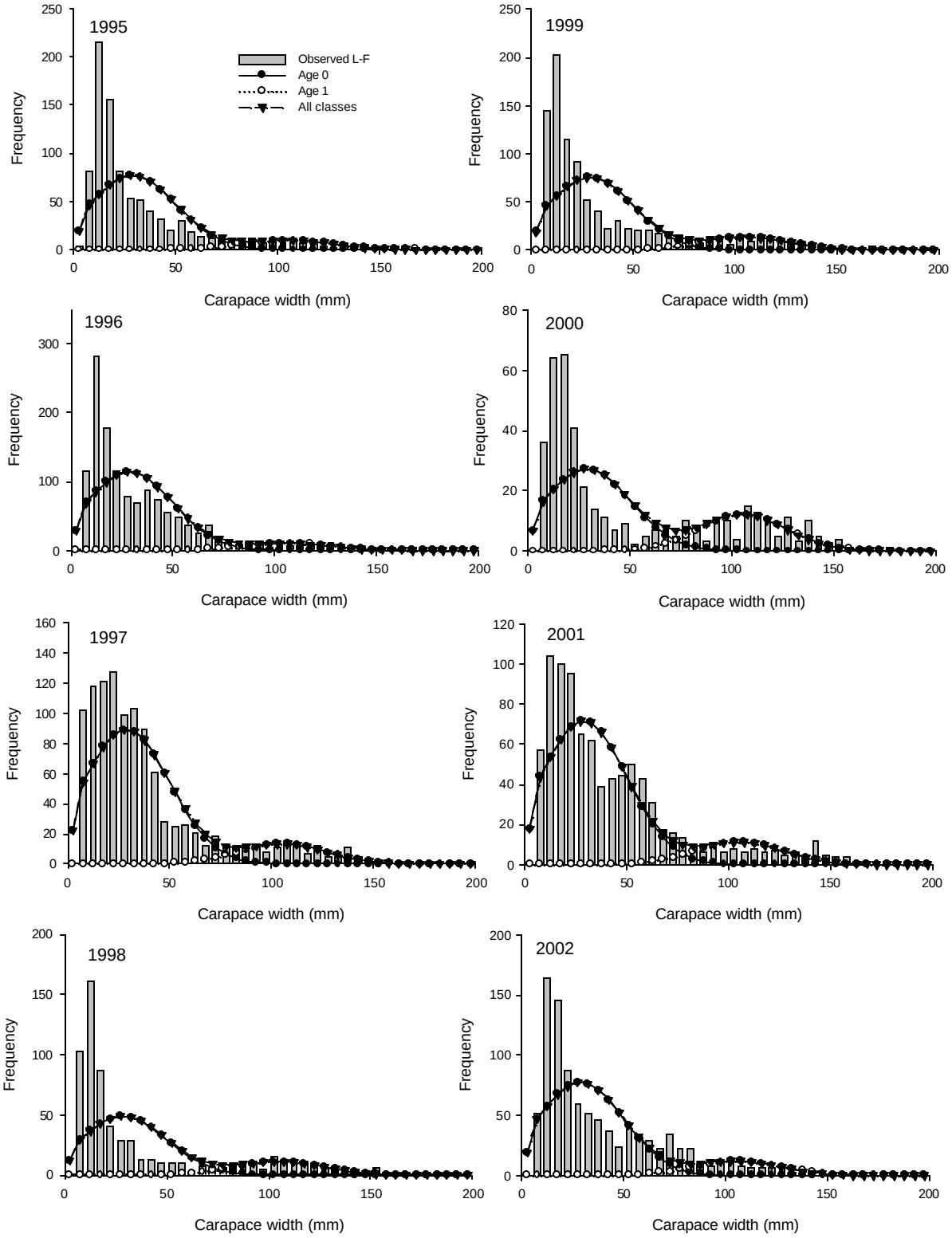


Figure 7 (continued). The observed (histograms) and predicted (symbols) size frequency of blue crabs by year collected in NC DMF Program 120 in May from 1987 – 2002 pooled across all water bodies. The predicted fits shown were produced by minimizing the model log likelihood.

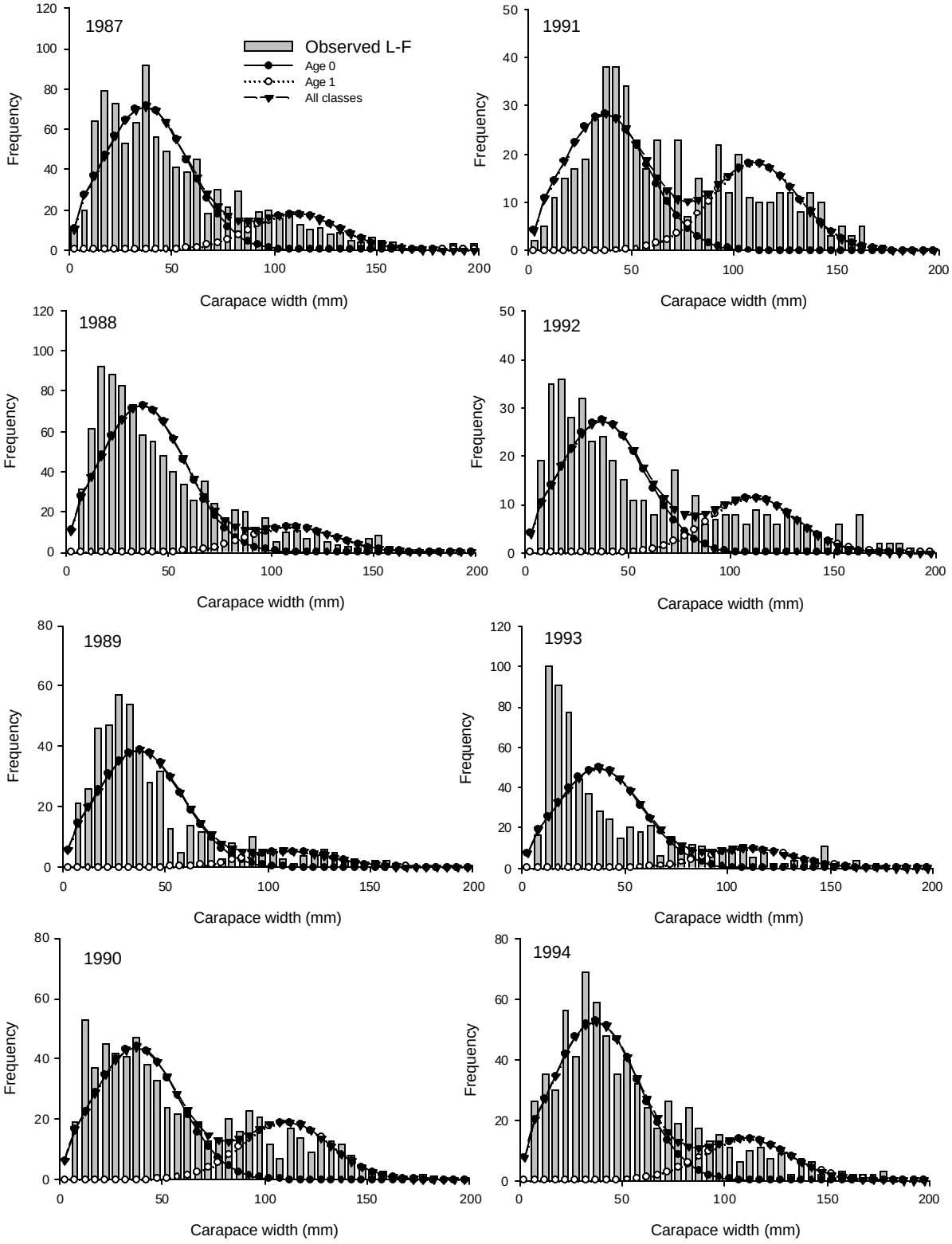


Figure 8. The observed (histograms) and predicted (symbols) size frequency of blue crabs by year collected in NC DMF Program 120 in June from 1987 – 2002 pooled across all water bodies. The predicted fits shown were produced by minimizing the model log likelihood.

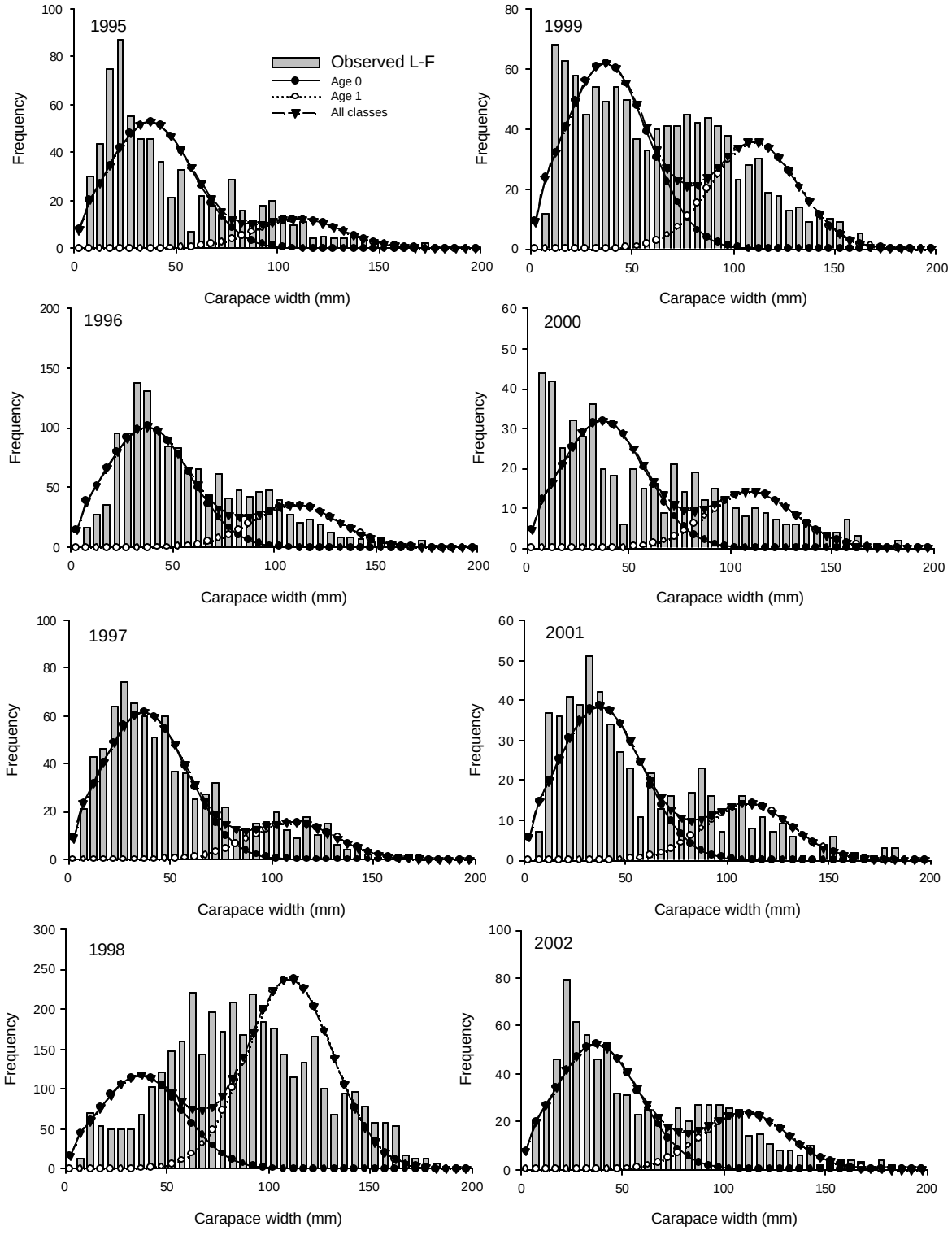


Figure 8 (continued). The observed (histograms) and predicted (symbols) size frequency of blue crabs by year collected in NC DMF Program 120 in June from 1987 – 2002 pooled across all water bodies. The predicted fits shown were produced by minimizing the model log likelihood.

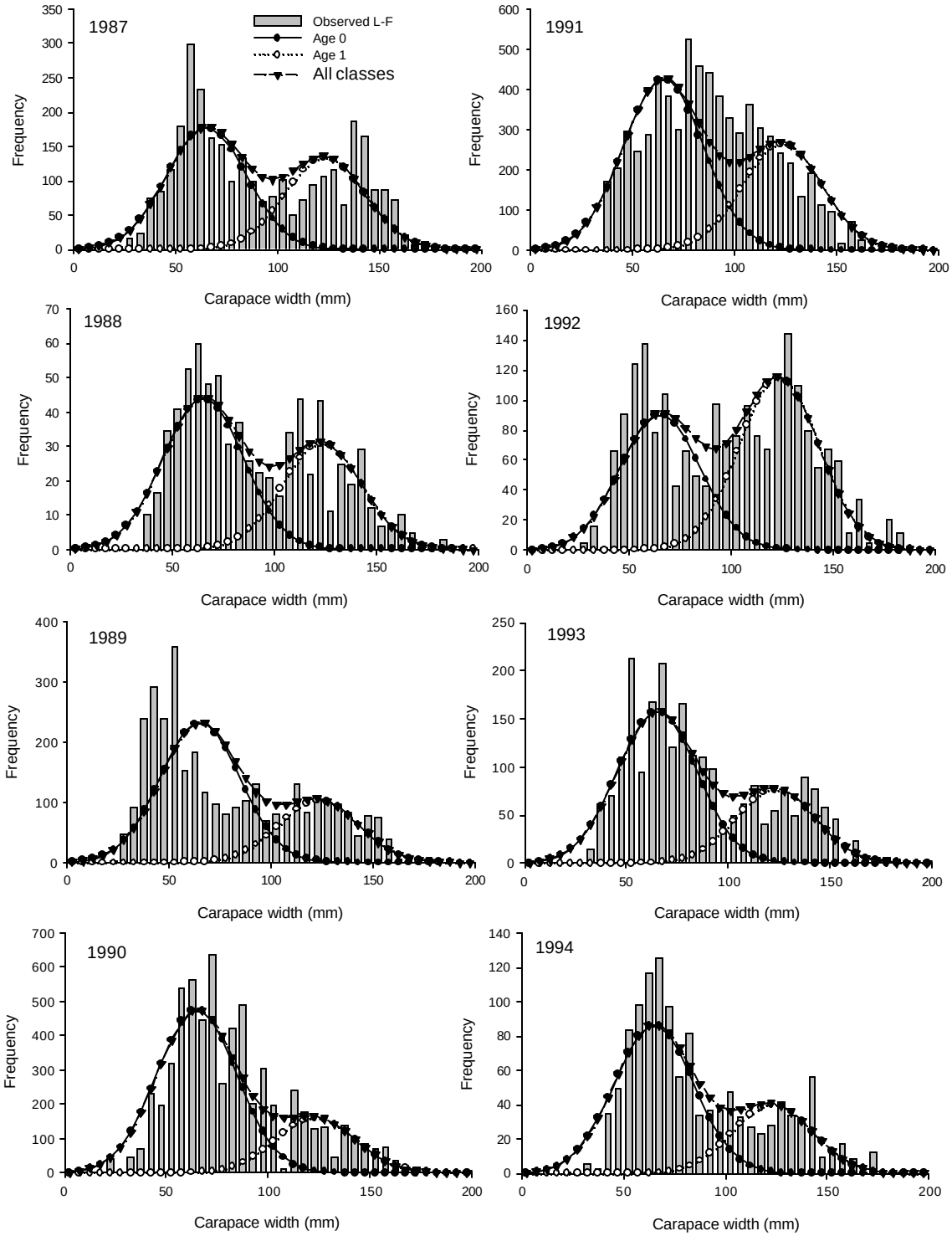


Figure 9. The observed (histograms) and predicted (symbols) size frequency of blue crabs by year collected in NC DMF Program 195 in June from 1987 – 2003 pooled across all water bodies. The predicted fits shown were produced by minimizing the model log likelihood.

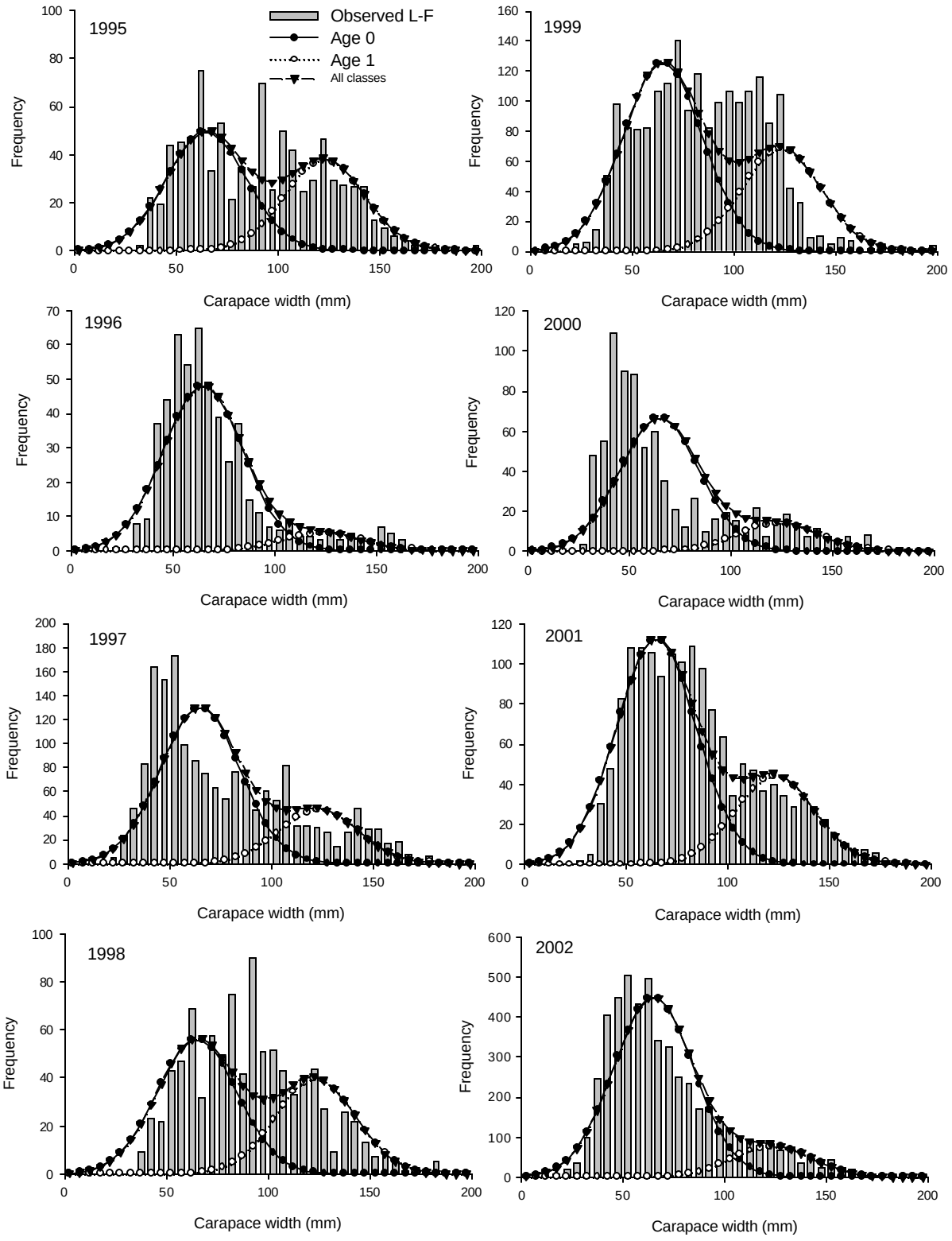


Figure 9 (continued). The observed (histograms) and predicted (symbols) size frequency of blue crabs by year collected in NC DMF Program 195 in June (except 1999 which occurred in July) from 1987 – 2003 pooled across all water bodies. The predicted fits shown were produced by minimizing the model log likelihood.

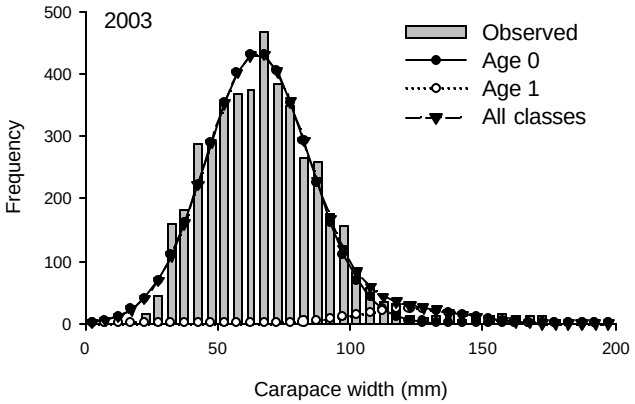


Figure 9 (continued). The observed (histograms) and predicted (symbols) size frequency of blue crabs by year collected in NC DMF Program 195 in June from 1987 – 2003 pooled across all water bodies.

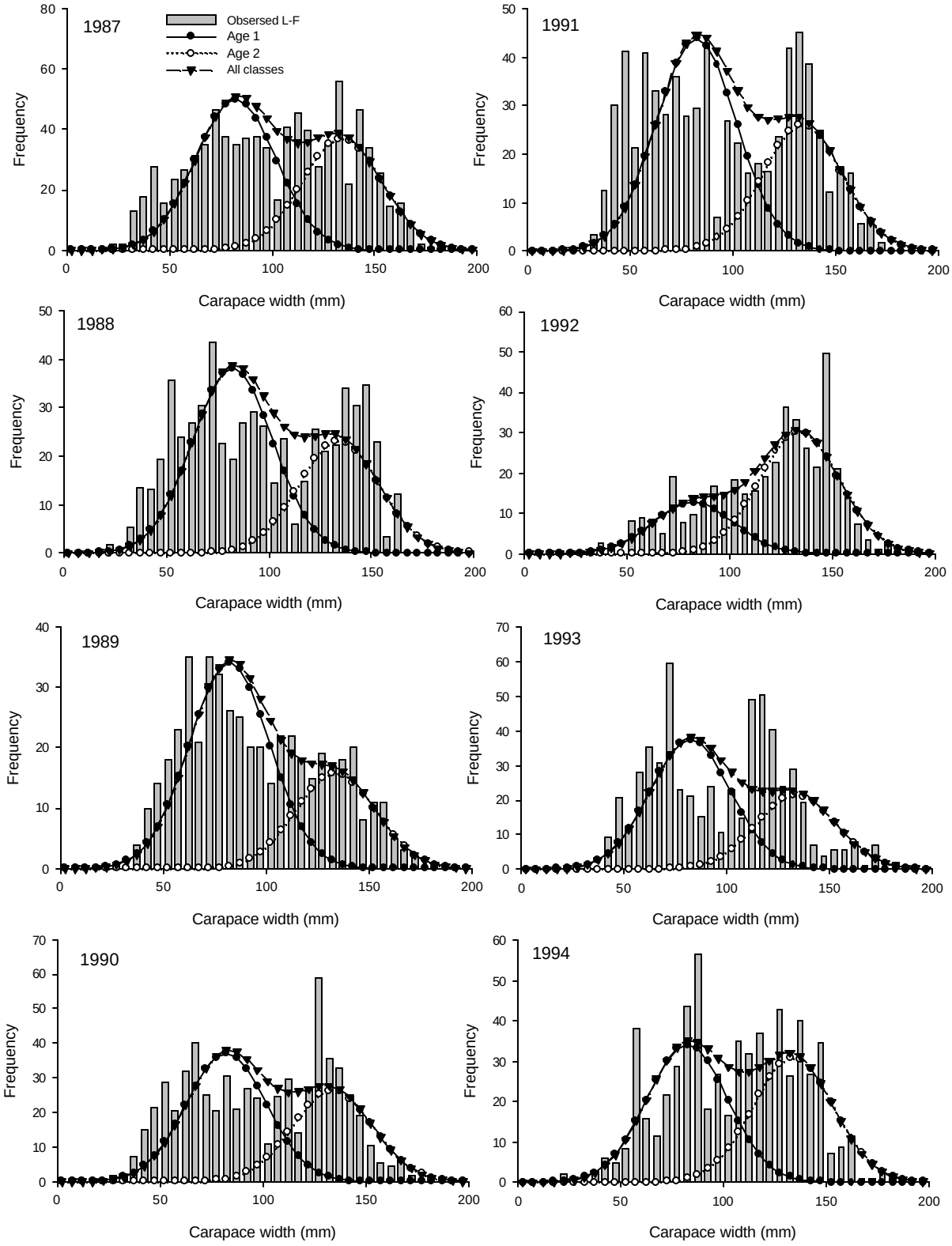


Figure 10. The observed (histograms) and predicted (symbols) size frequency of blue crabs by year collected in NC DMF Program 195 in September from 1987 – 2003 pooled across all water bodies. The predicted fits shown were produced by minimizing the model log likelihood.

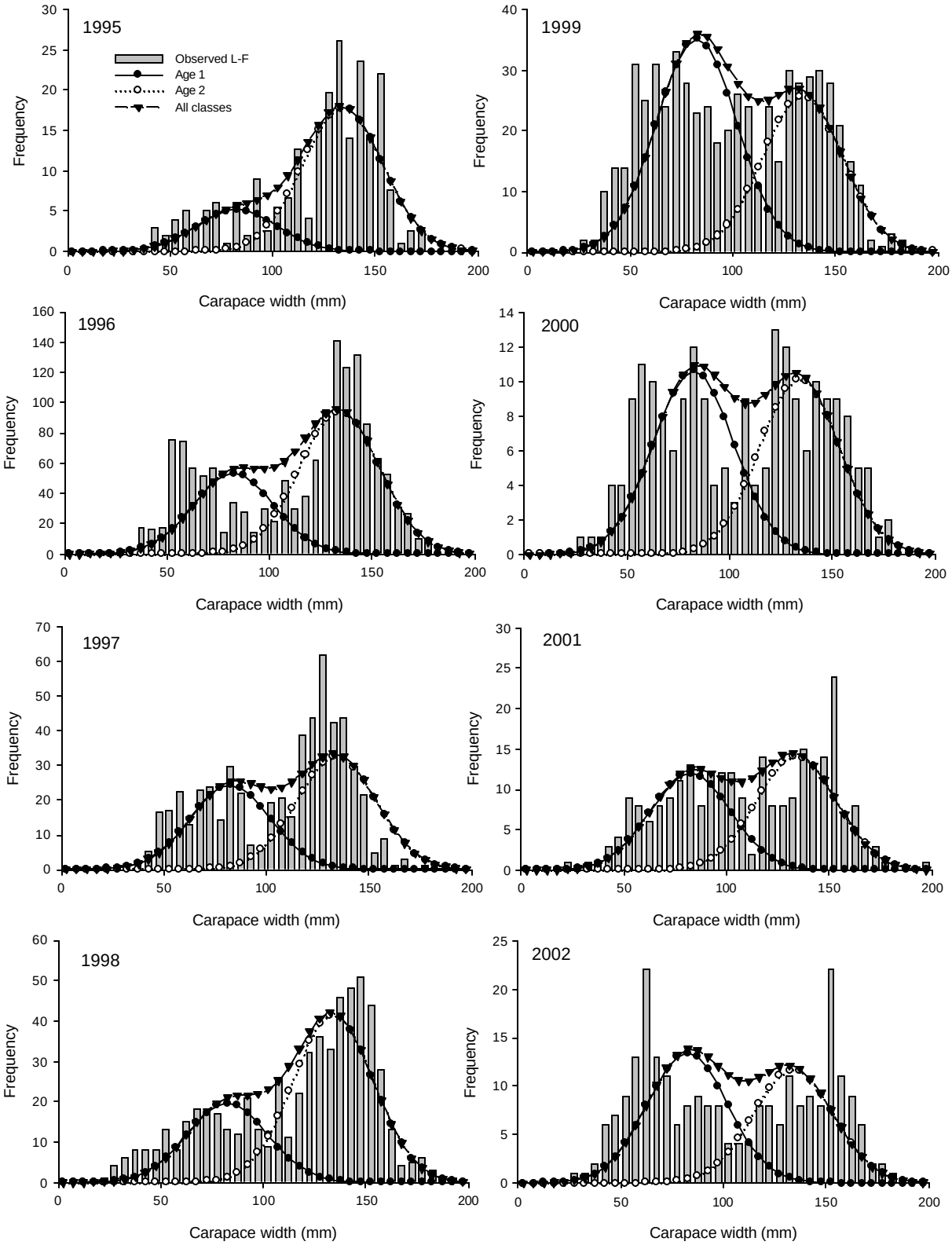


Figure 10 (continued). The observed (histograms) and predicted (symbols) size frequency of blue crabs by year collected in NC DMF Program 195 in September (except 1999 in which surveys were conducted in October) from 1987 – 2003 pooled across all water bodies. The predicted fits shown were produced by minimizing the model log likelihood.

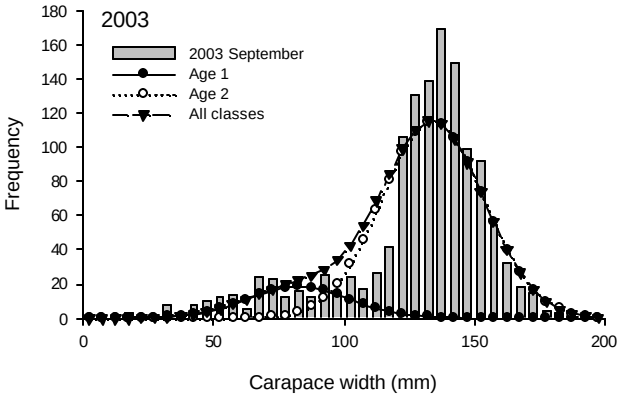


Figure 10 (continued). The observed (histograms) and predicted (symbols) size frequency of blue crabs by year collected in NC DMF Program 195 in September from 1987 – 2003 pooled across all water bodies The predicted fits shown were produced by minimizing the model log likelihood.

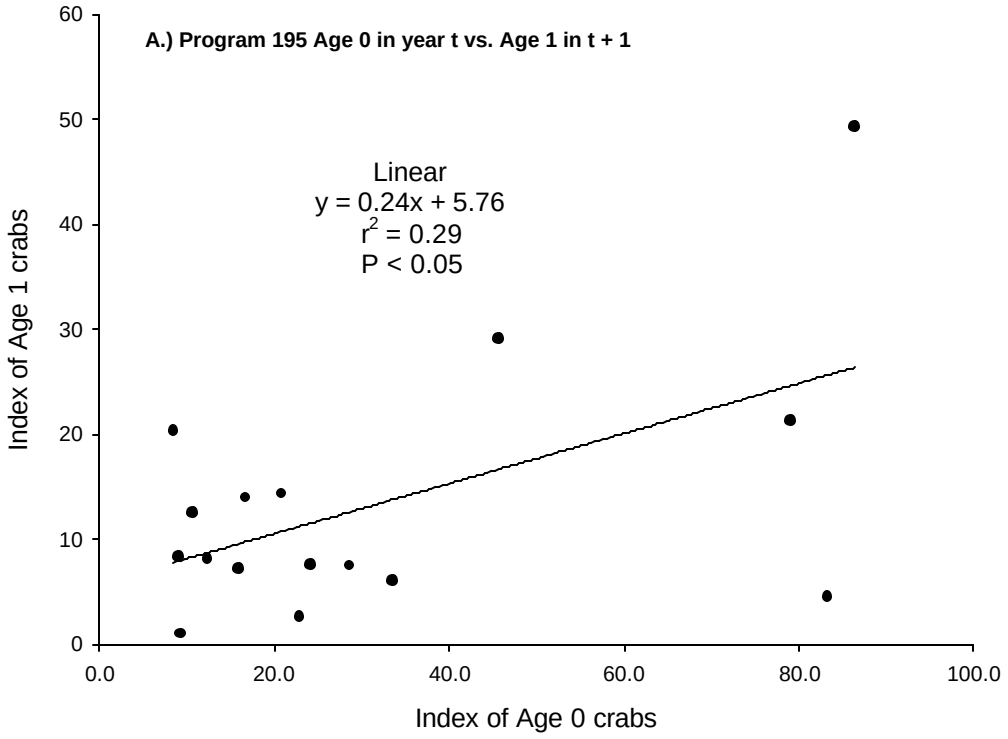


Figure 11. Relationship between mean indices of abundance from NC DMF trawl surveys for A.) Indices of Program 195 June Age 0 crabs in year t and Age 1 crabs in year t + 1.

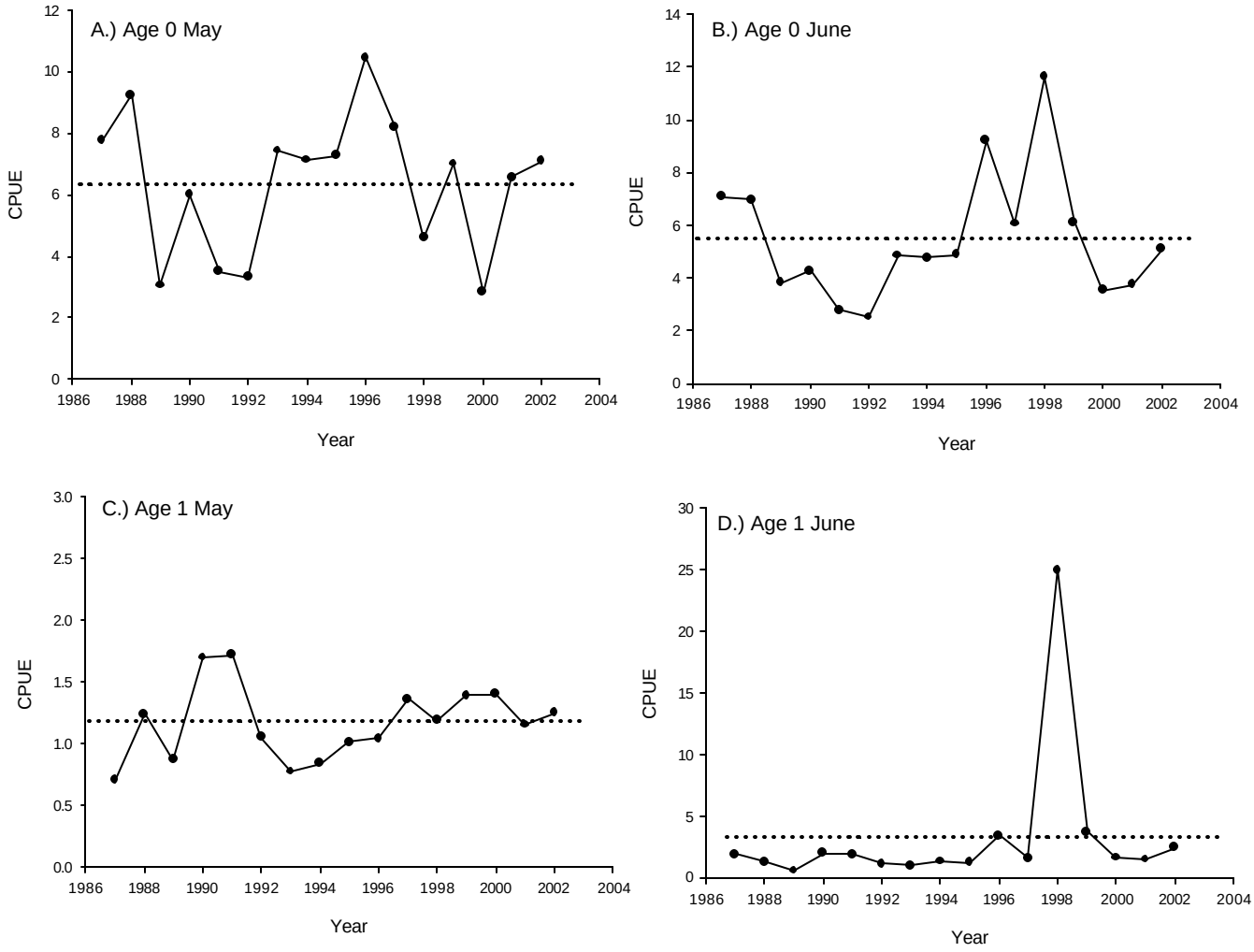


Figure 12. Annual mean trawl survey index of abundance (CPUE) pooled across water bodies in North Carolina collected in Program 120 tows 1987 - 2002 for May (panels A and C) and June (panels B and D). The dotted line indictaes the mean CPUE for the entire time series.

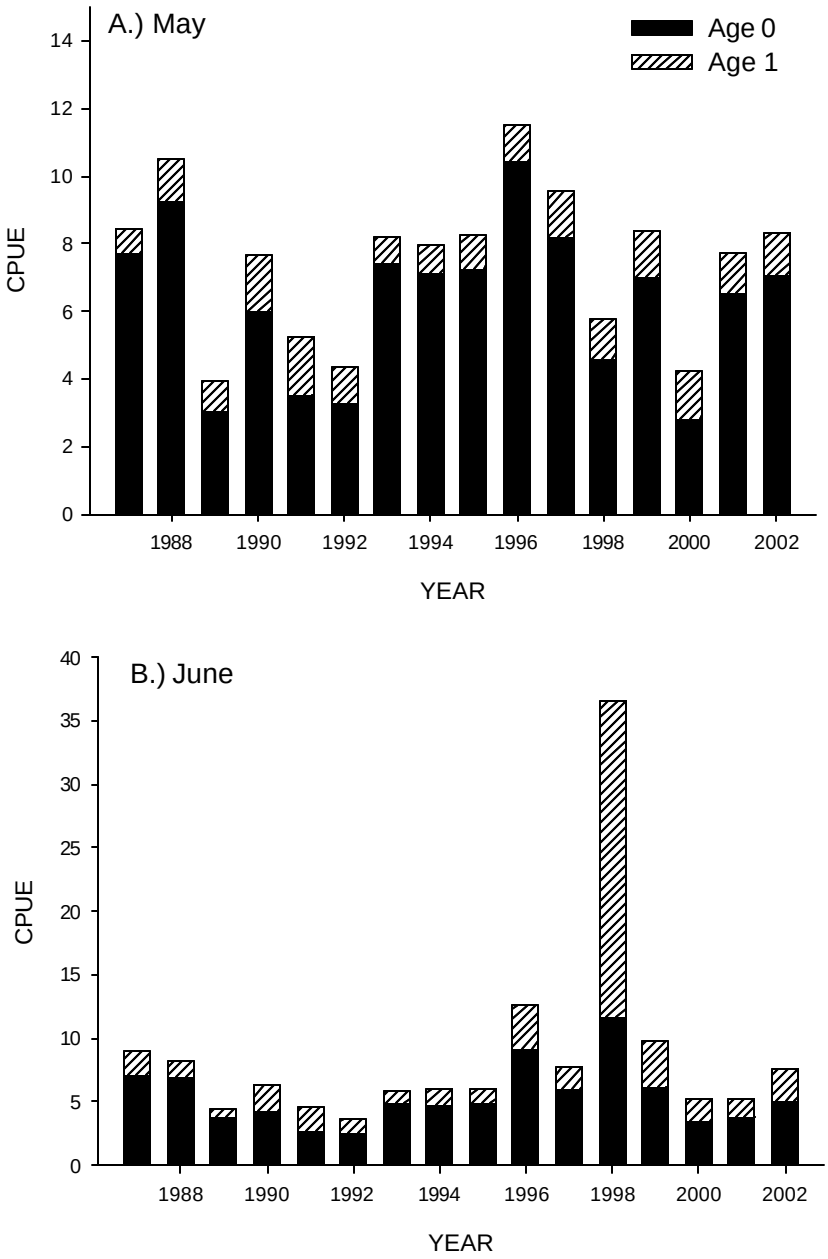


Figure 13. Mean catch-per-unit-effort of blue crabs from Program 120 (May and June) by year, and age class. The CPUE for all eight water bodies pooled equals the total CPUE.

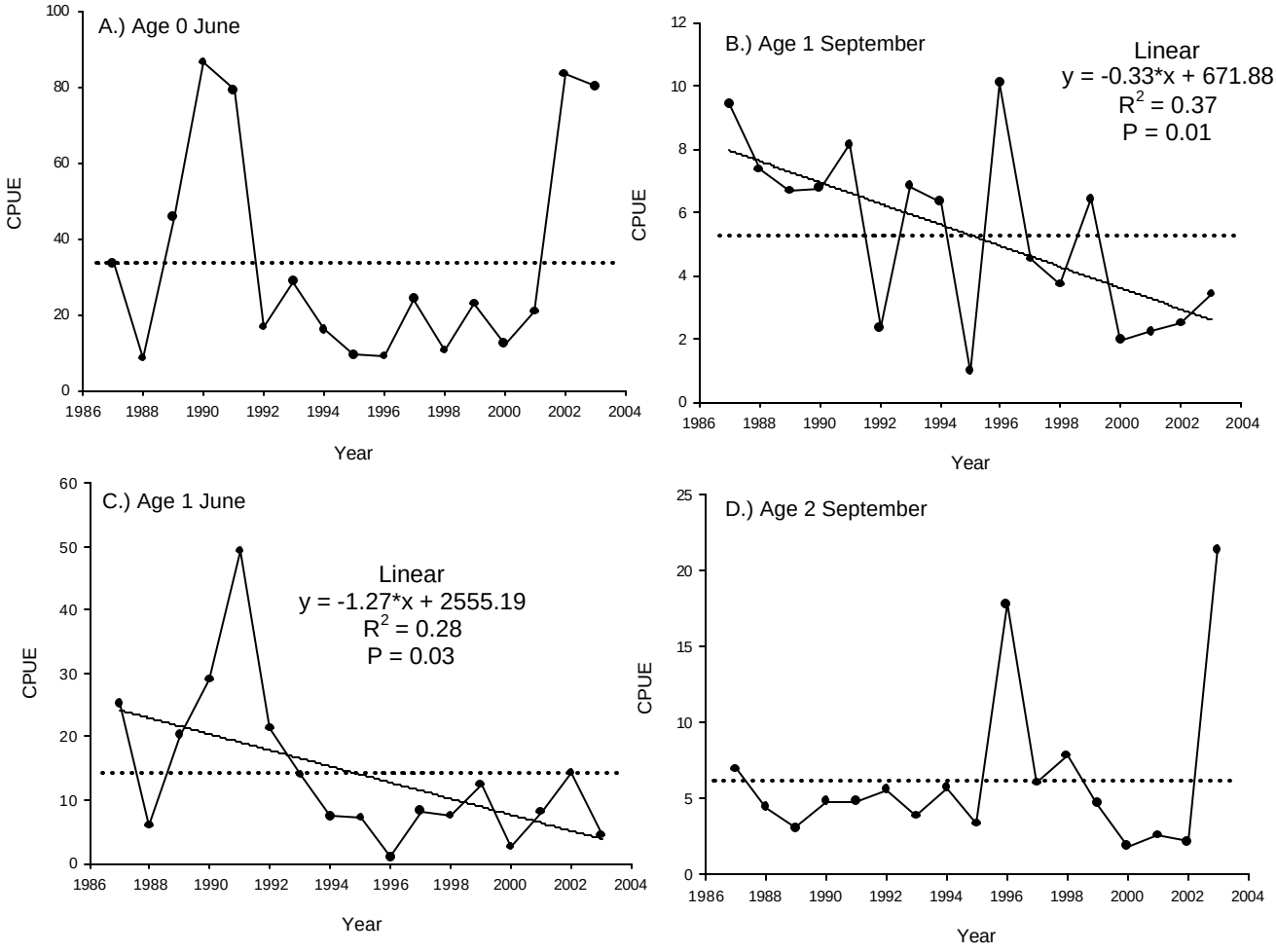


Figure 14. Annual mean trawl survey index of abundance (CPUE) pooled across water bodies in North Carolina collected in Program 195 tows 1987 - 2002. The dotted line indicates the mean CPUE for the entire time series. Linear regression models were fit to the data, and significant regressions are shown. Plots are shown in chronological order and assume a September 15th birth date for a given year class (see text for justification). For example, Age 0 crabs sampled in June are 0.75 years of age, calculated by dividing the 273 days between the assumed birthdate (September 15th) and the timing of sampling assumed to be the mid-point of each sampling month (June 15th), by the 365 days in a calender year. Similarly, Age 1 crabs sampled in September were assumed to be collected on their birthday and be exactly one year old.

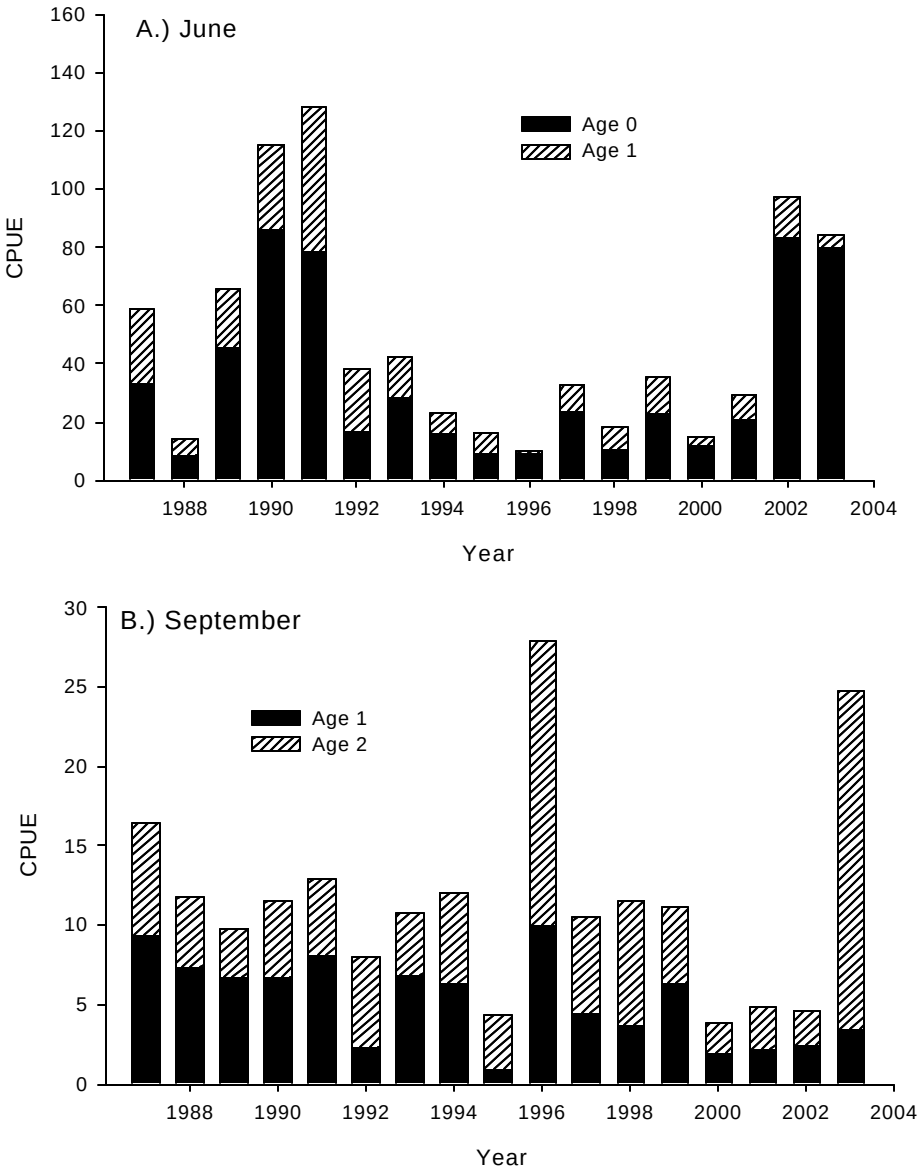


Figure 15. Mean catch-per-unit-effort of blue crabs from Program 195 (June and September) by water body, year, and age class. Note y-axes differ.

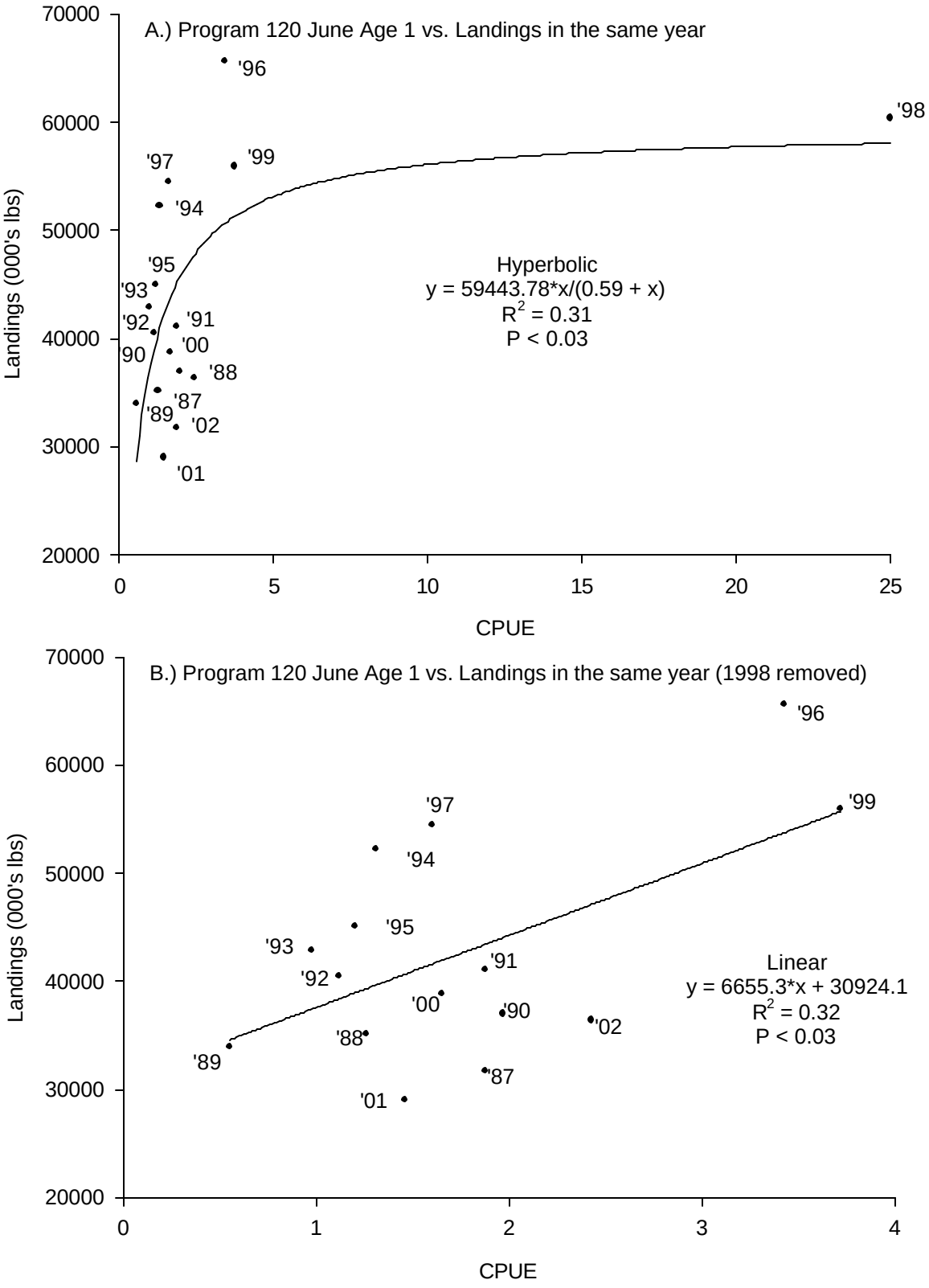


Figure 16. Relationship between A.) mean annual CPUE of Age 1 crabs from Program 120 June and commercial landings from 1987 - 2002, and B.) mean annual CPUE of Age 1 crabs from Program 120 June and commercial landings with 1998 data removed.

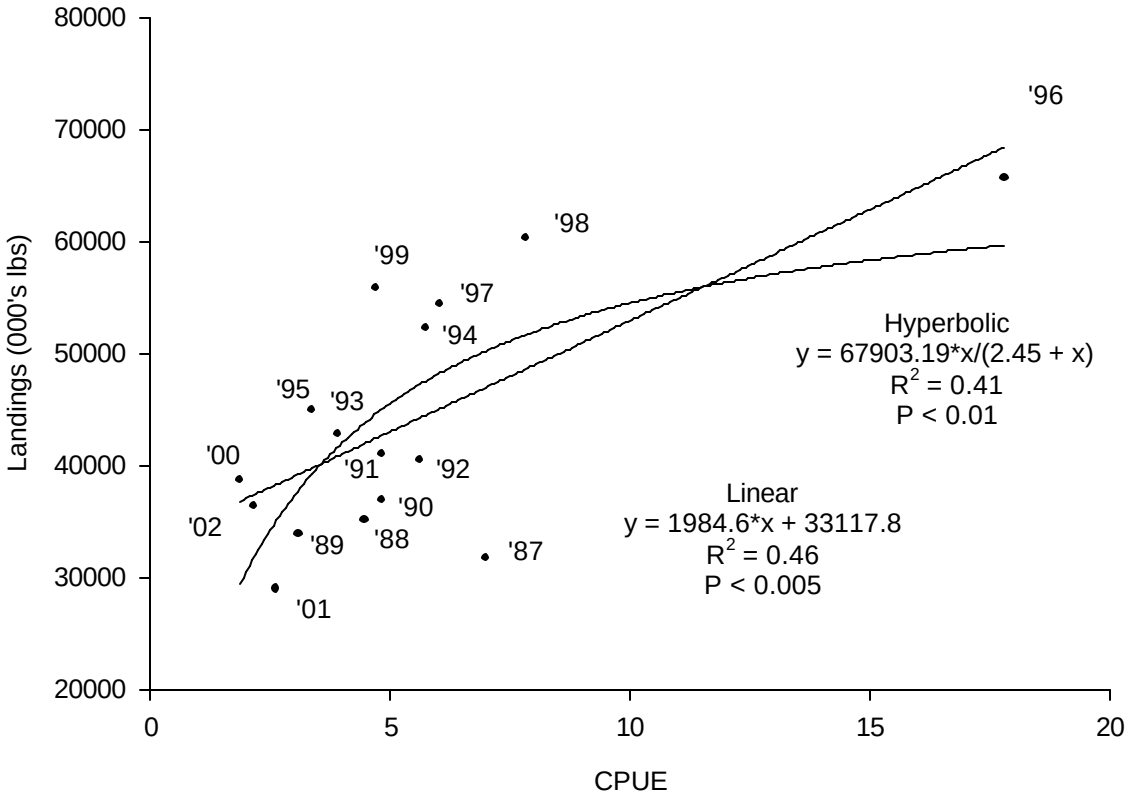


Figure 17. Relationship between mean annual CPUE of Age 2 crabs from Program 195 September and commercial landings from 1987 - 2002.

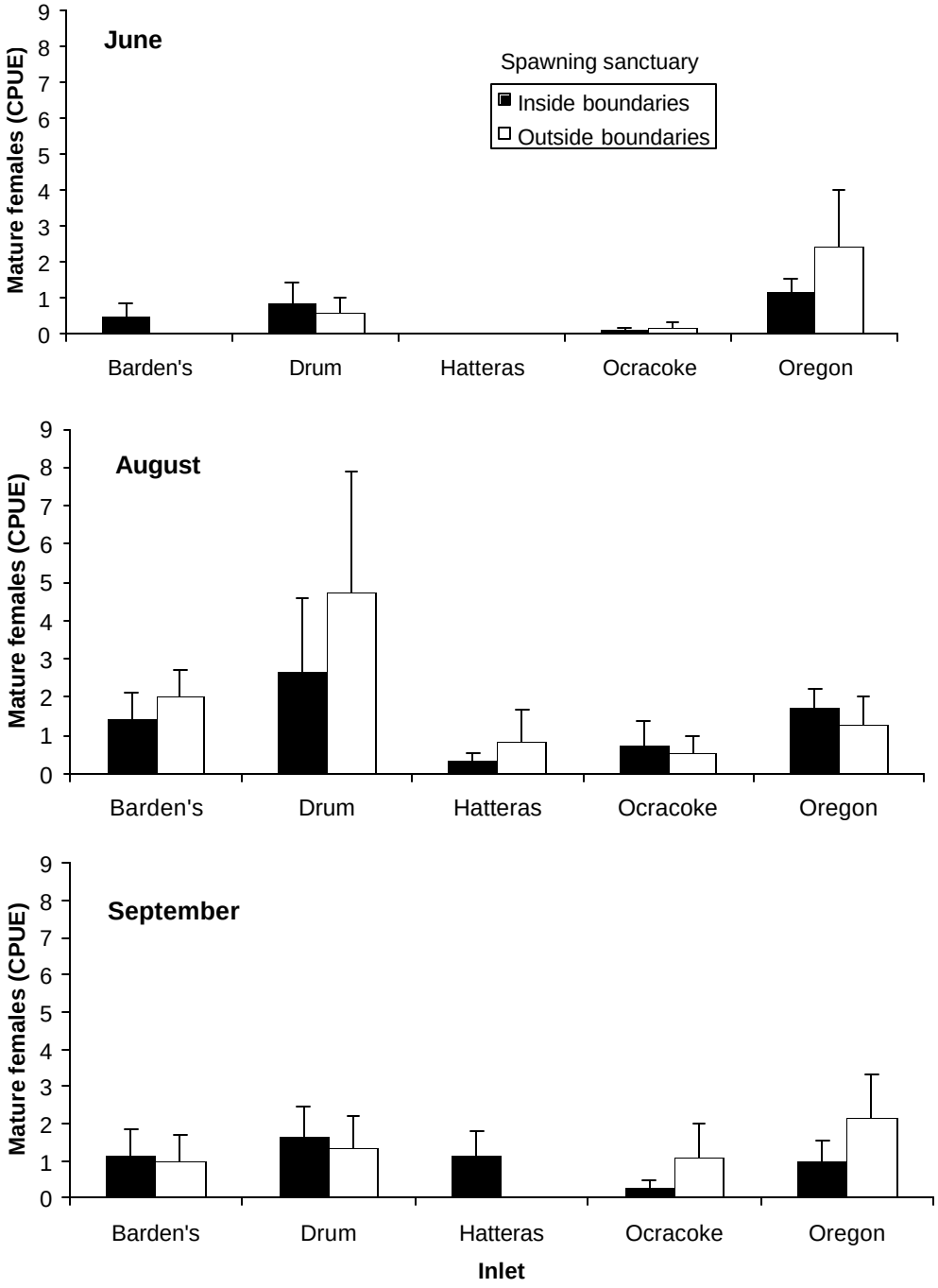


Figure 18. Mean (± SE) catch-per-unit-effort of mature female blue crabs as a function of month (June, August, September), inlet (Barden's, Drum, Hatteras, Ocracoke, Oregon), and within versus outside of blue crab spawning sanctuary boundaries. Statistical analysis of the data indicate that there was no difference in mean crab CPUE within versus outside sanctuary boundaries, higher CPUE in August and September than June, and lowest CPUE in Hatteras and Ocracoke Inlets (adapted from Eggleston 2003).

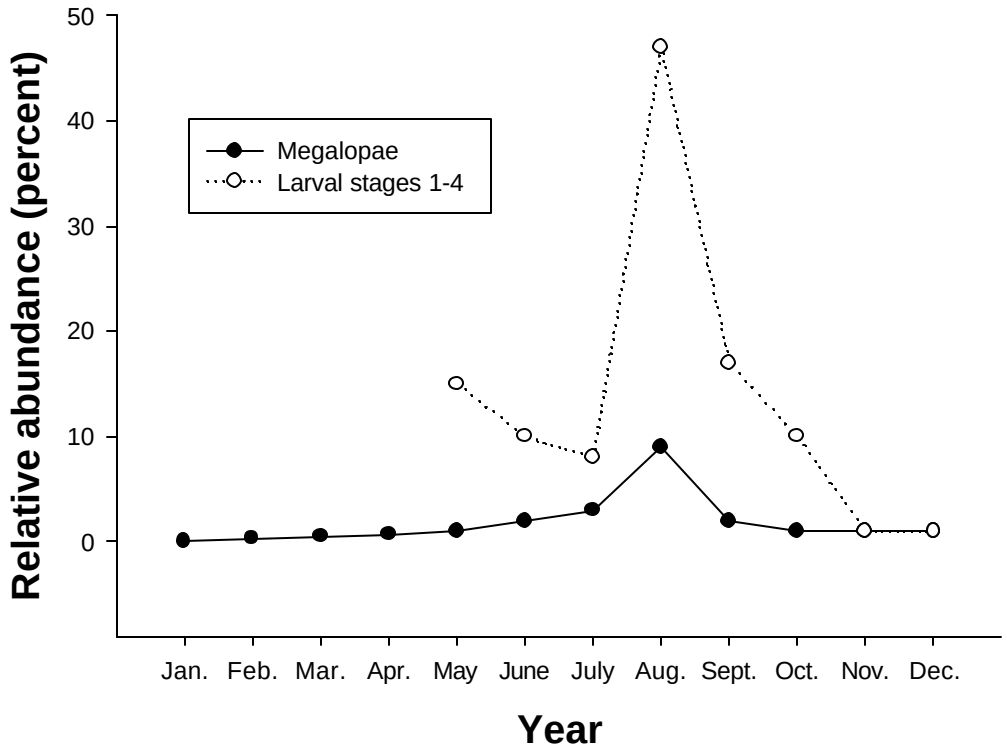


Figure 19. Relative abundance of early stage zoeae and megalopae of the blue crab by month in plankton samples collected on the continental shelf off North and South Carolina during 1953-54 (adapted from Nichols and Keney 1963).

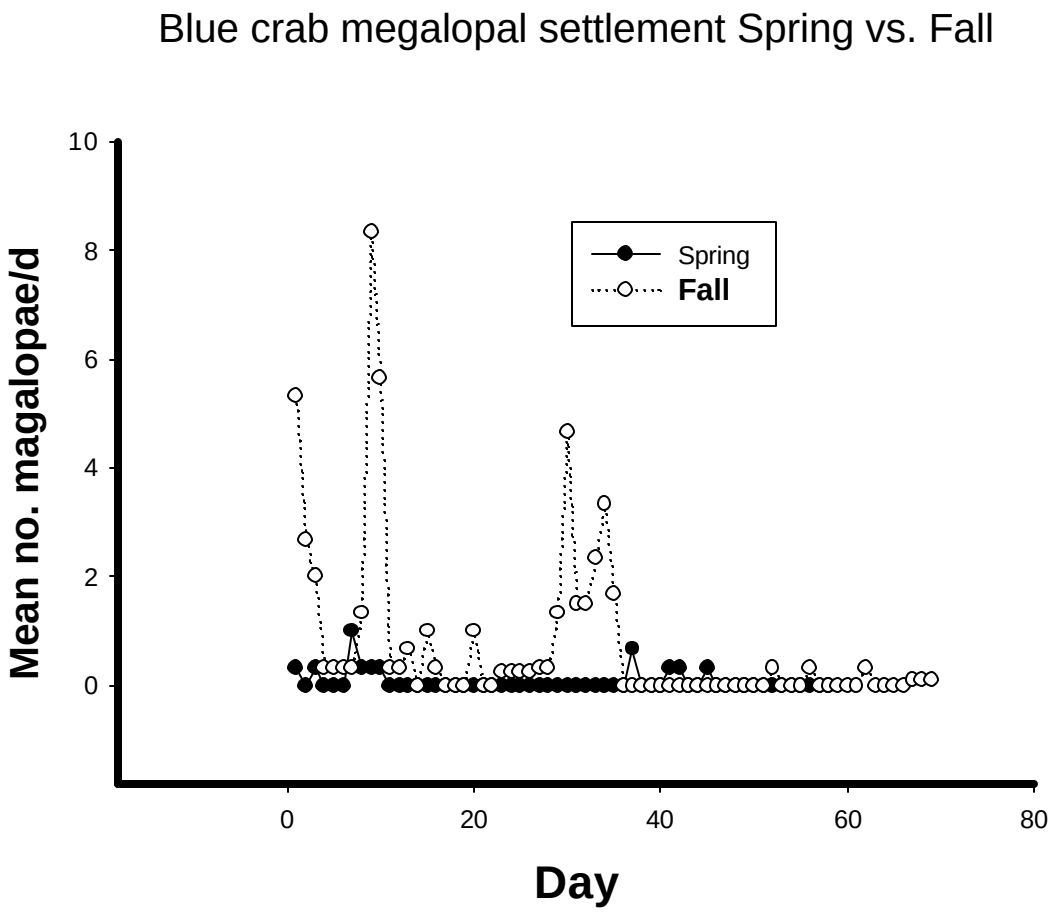


Figure 20. The relative abundance of blue crab megalopae collected on floating, artificial settlement substrates (N = 3) moored on the US Coast Guard dock at Oregon Inlet, NC During Spring, artificial settlement substrates were checked daily from April 8-June 4, 2002. During late summer-early Fall, artificial substrates were checked daily from August 1-October 31, 2002 (from D. Eggleston, unpubl. data).

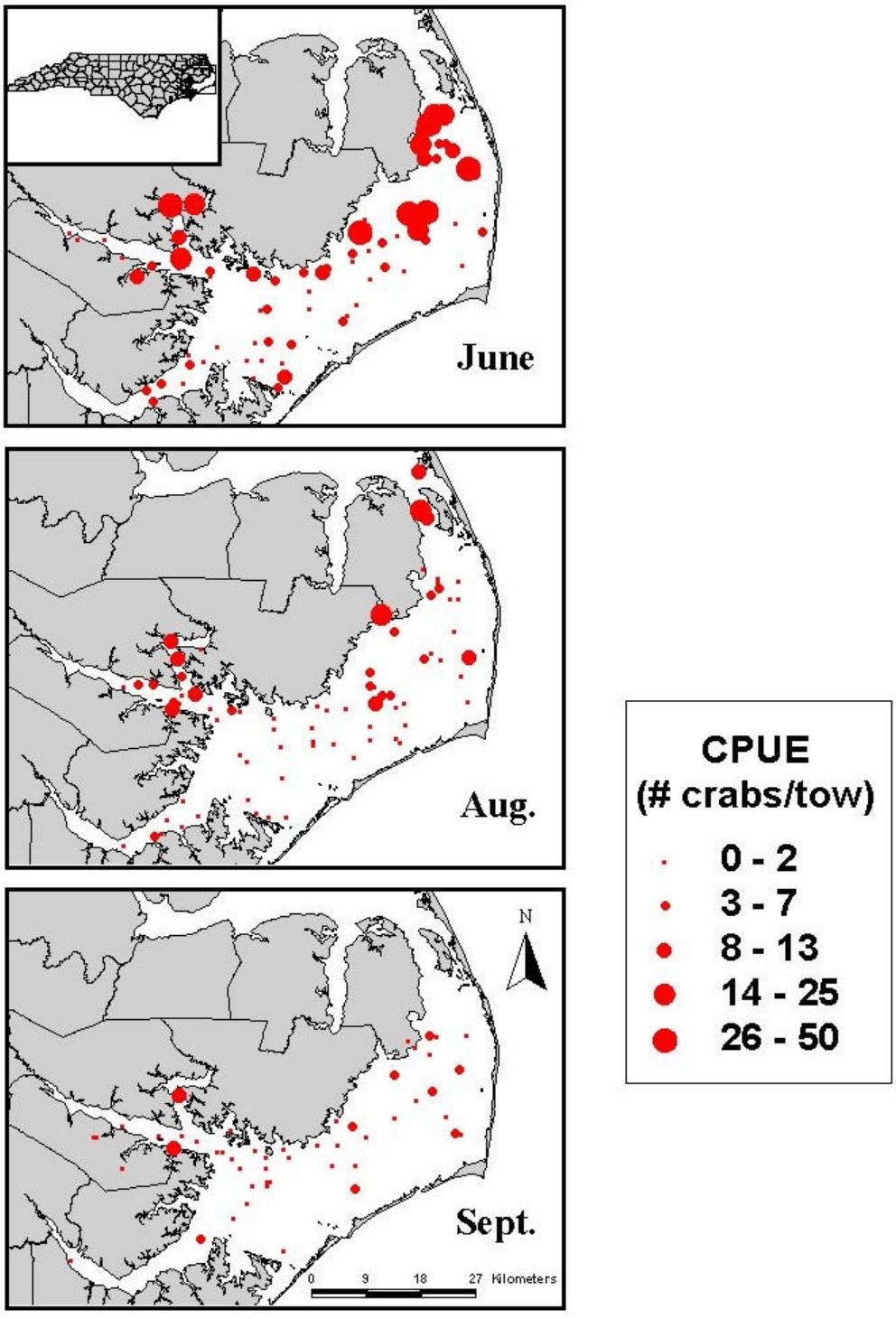


Figure 21. Catch-per-unit-effort of mature female blue crabs from NC DMF Program 195 and supplemental stations (75 stations per month) during 2002. Note decline in relative abundance (CPUE) from June to September (from Eggleston 2003).

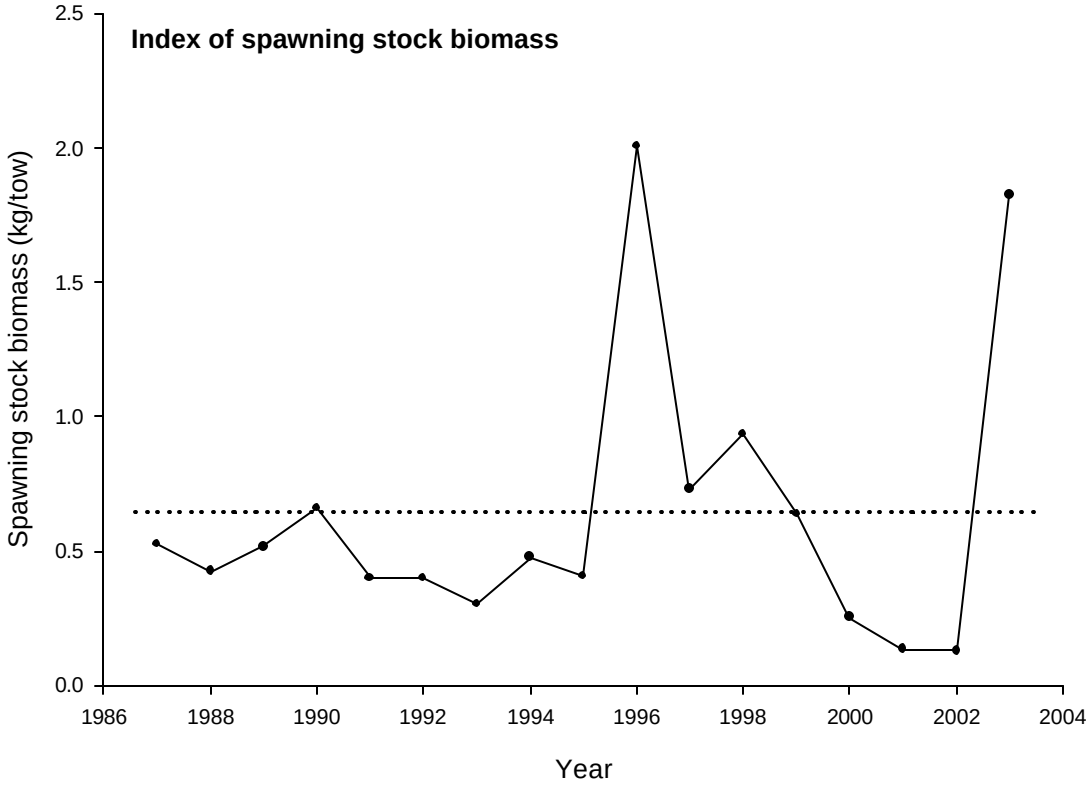


Figure 22. Annual mean trawl survey index of spawning stock biomass (SSB; kg/tow) collected in September from NC DMF Program 195 pooled across water bodies in North Carolina. The dotted line represents the average SSB for the time series.

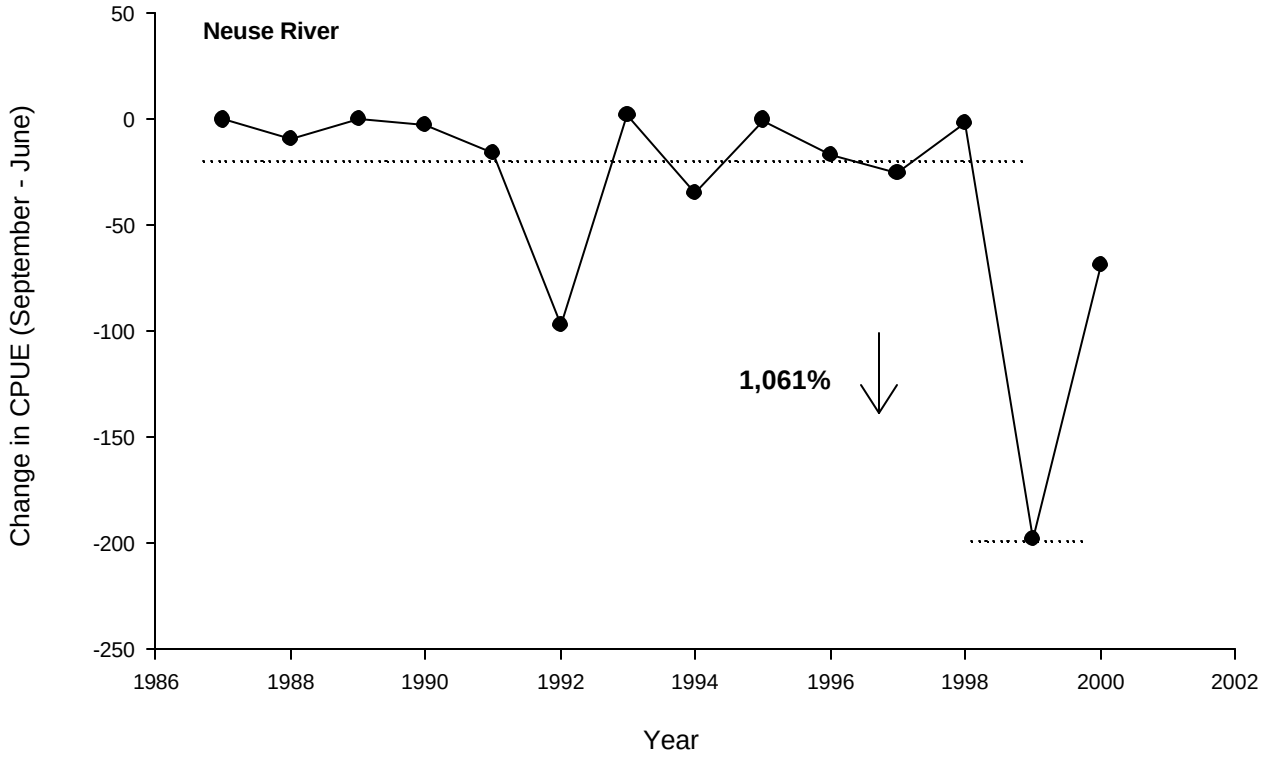


Figure 23. Index of loss of adult blue crabs in the Neuse River, a tributary of Pamlico Sound, calculated by subtracting the June cpue from NC DMF Program 195 from the September cpue. The index of loss should be negative since the abundance of crabs is expected to decline during summer (June-August) due to fishing and natural mortality, as well as migration of inseminated females to seaward inlets to spawn.

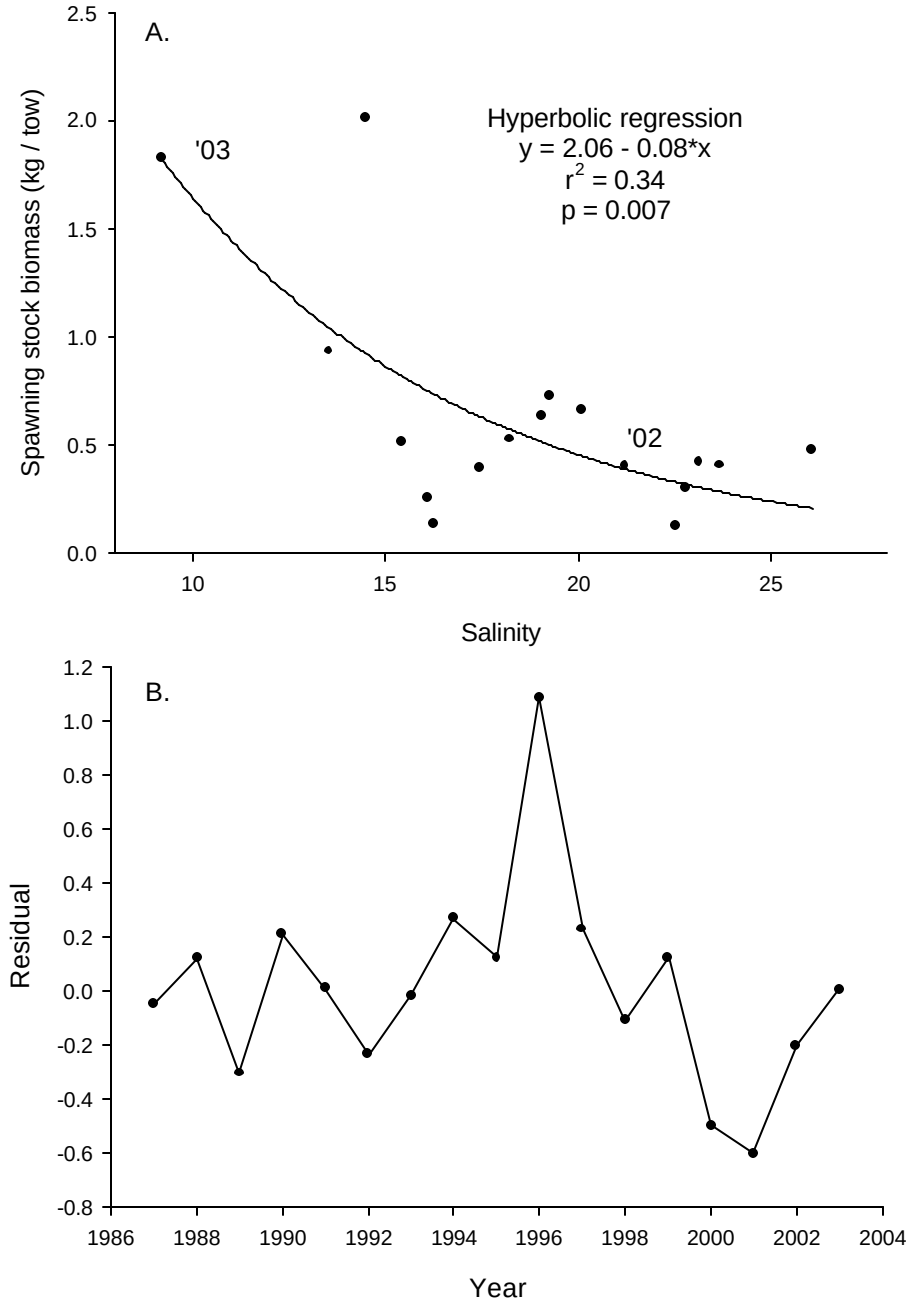


Figure 24. A.) Relationship between the annual mean trawl survey index of spawning stock biomass (SSB; kg/tow) collected in September and mean salinity from NC DMF Program 195 pooled across all water bodies and the mean salinity B.) Residuals from the fit of the regression model (exponential decay) shown in panel A.

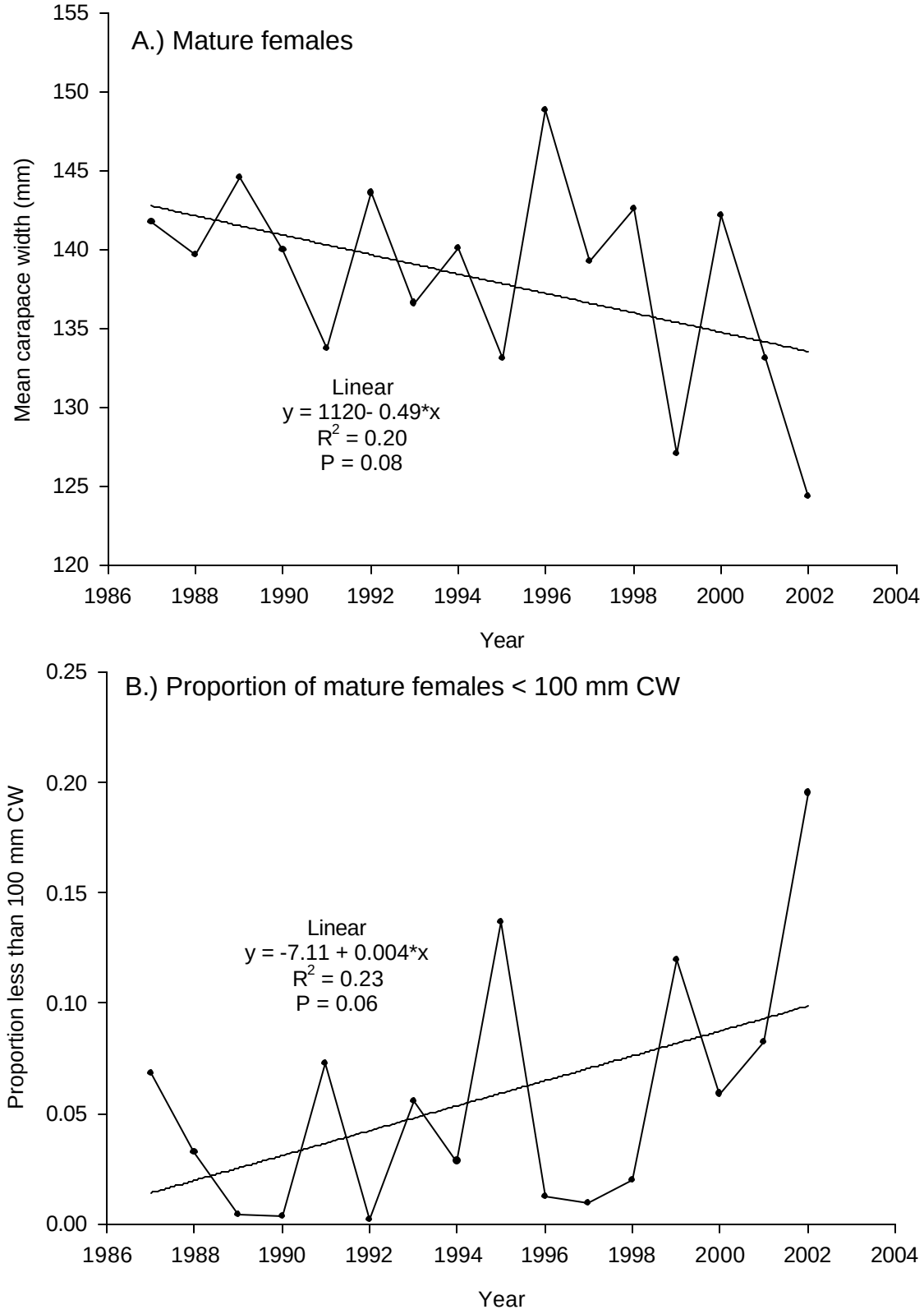


Figure 25. Relationships of mature female size over time A.) mean carapace width of mature females from Program 195 trawl surveys from 1987 - 2003, and B.) annual proportion of mature females less than 100 mm carapace width.

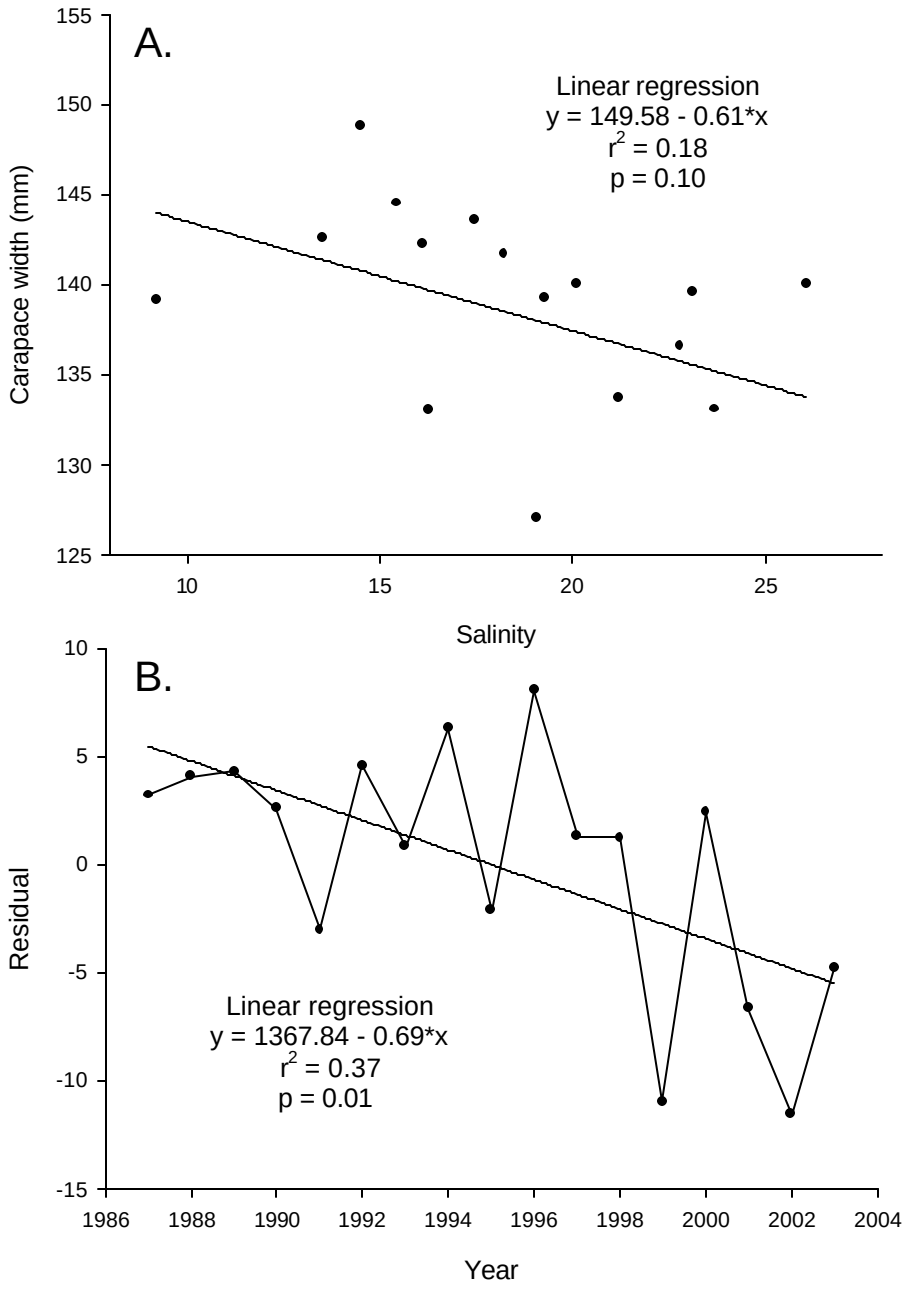


Figure 26. A.) Relationship bewteen annual mean carapace width (mm) of mature females and salinity from NC DMF Program 195 trawl surveys from 1987-2003. B.) residuals from the fit of the linear regression model shown in panel A.

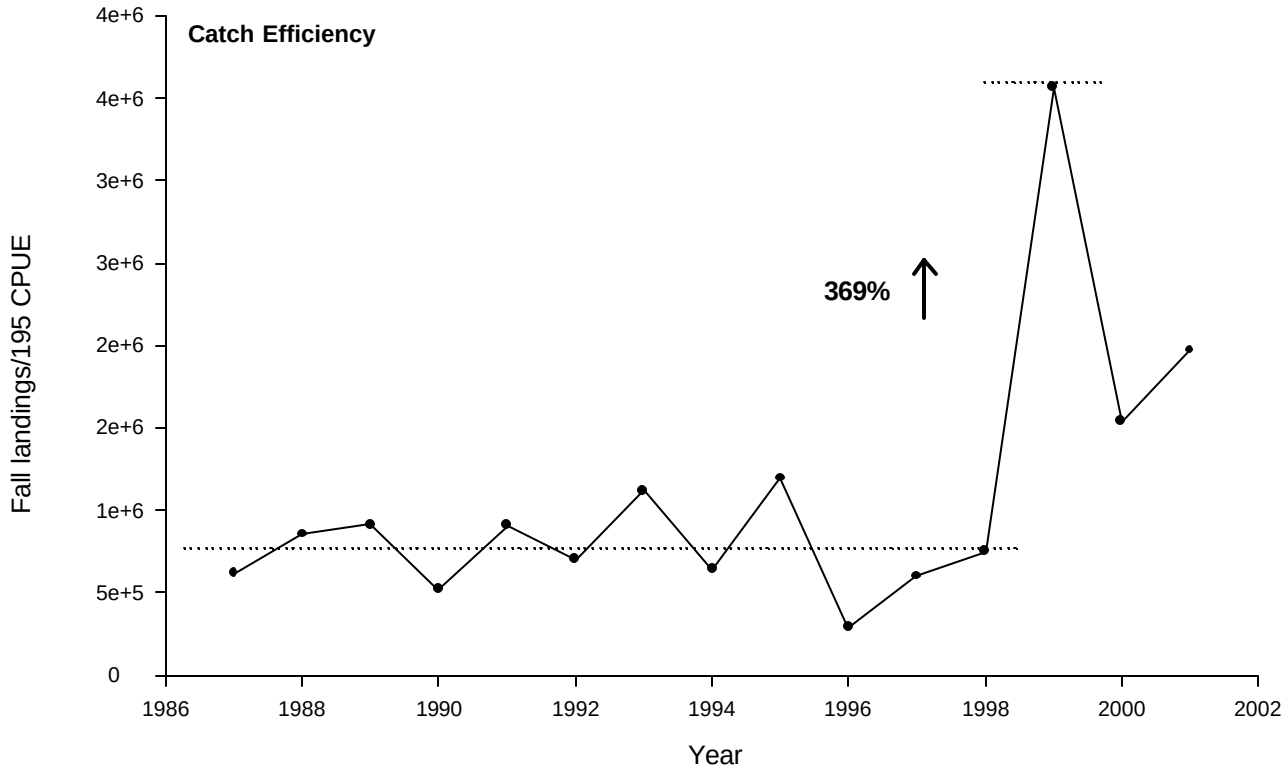


Figure 27. Annual changes in mean catch efficiency, estimated by dividing crab landings from Fall (Sept.-Nov.) each year by the nominal population size determined from index of Age 2 crabs for September from NC DMF Program 195. The horizontal lines represent the average prior to 1999.

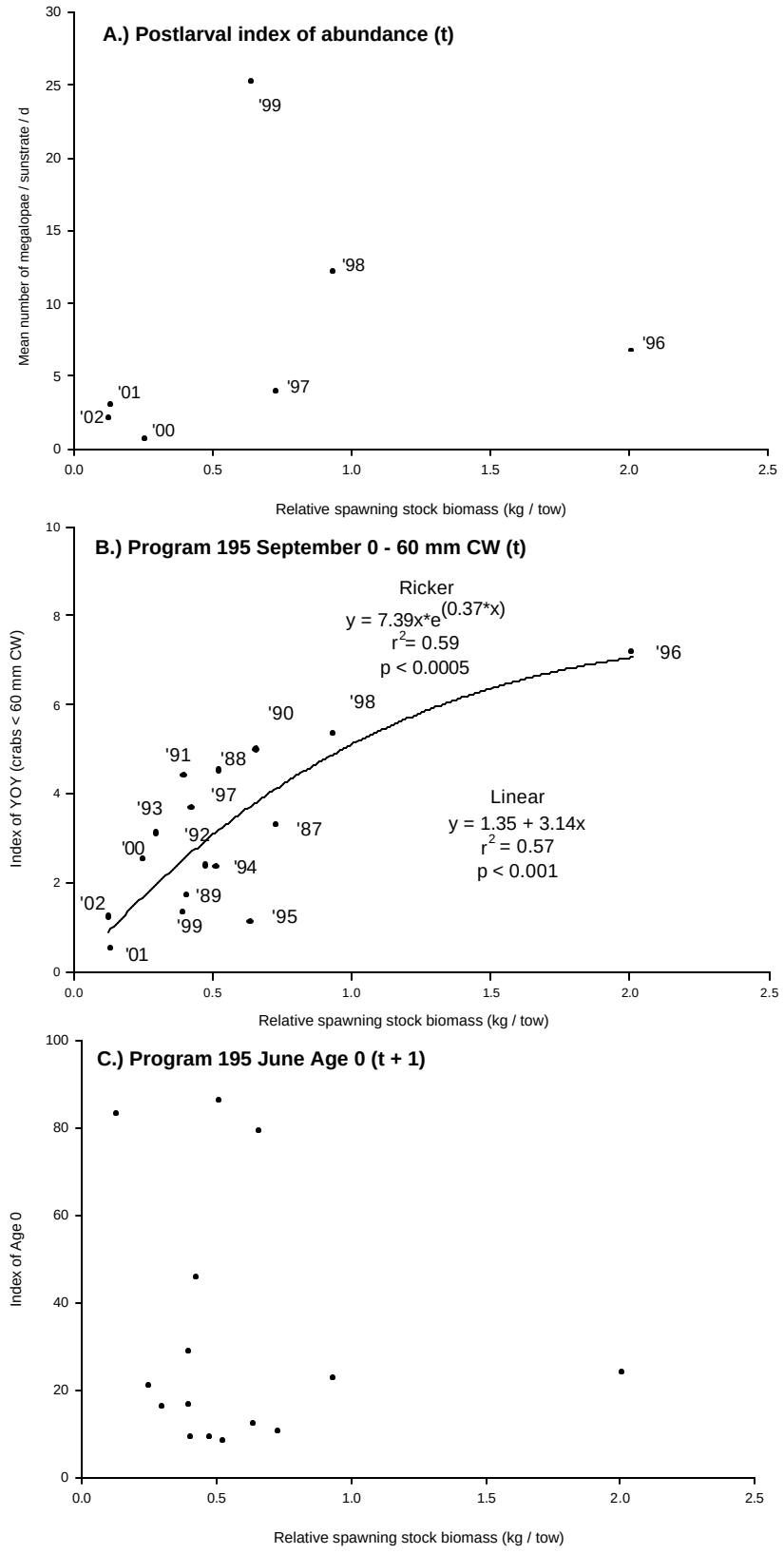


Figure 28. The relationship between the relative spawning stock biomass in September of year t and A.) postlarval settlement (mean number of blue crab megalopae/substrate/d collected from Oregon and Hatteras inlets from August - October) from in year t, B.) Program 195 crabs less than 60 mm CW and C.) Program 195 Age 0 CPUE from trawls in June in year t + 1.

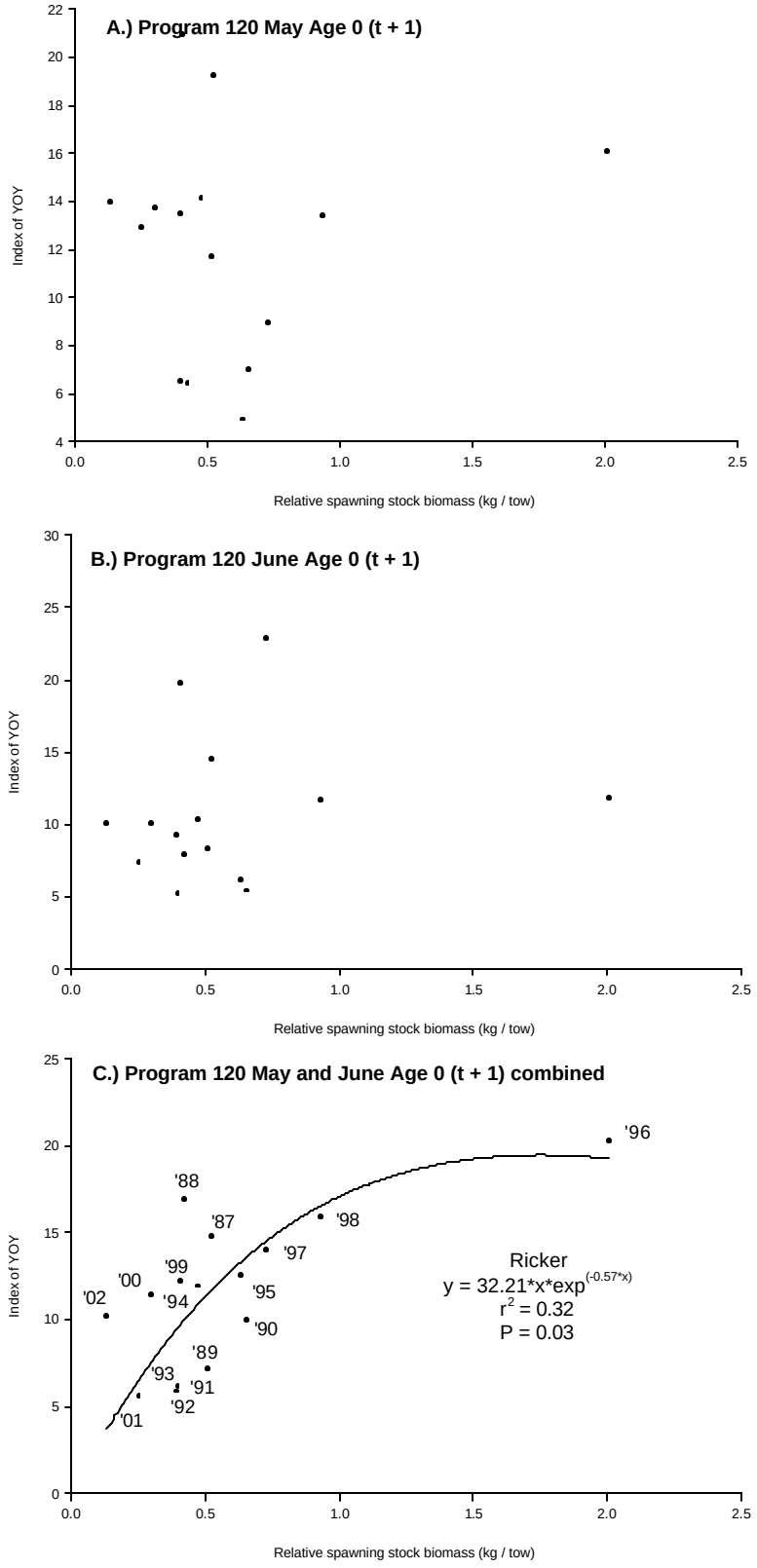


Figure 29. The relationship between the relative spawning stock biomass in September of year t and A.) Program 120 Age 0 CPUE from trawls taken in May of year t + 1, B.) Program 120 Age 0 CPUE from trawls taken in June of year t + 1 and C.) Program 120 Age 0 CPUE from trawls taken in May and June of year t + 1 averaged.

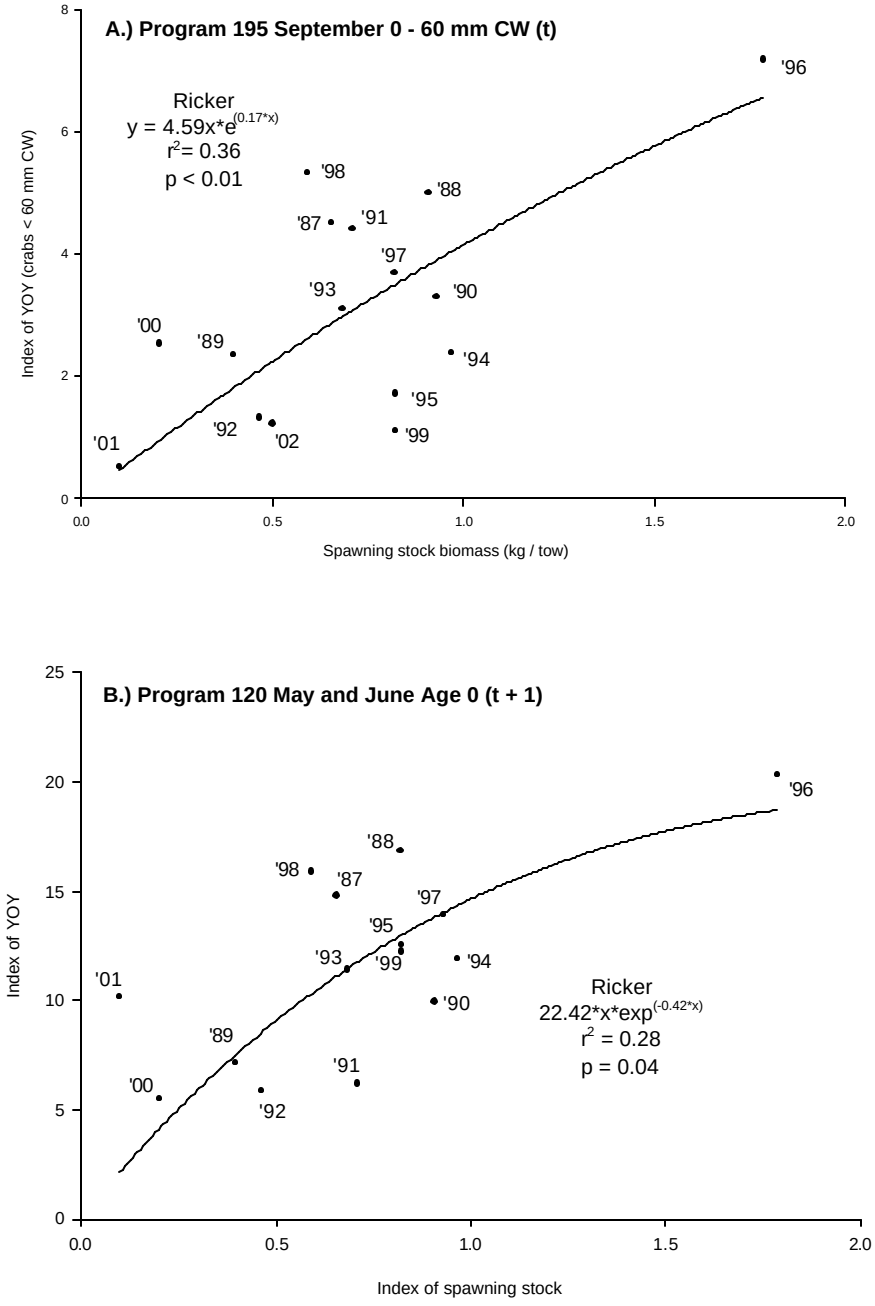


Figure 30. The relationship between the relative spawning stock biomass (SSB; kg/tow) adjusted for mean annual salinity (see figure 23 and text for details) in September of year t and A.) Program 195 crabs less than 60 mm CW in September of year t and B.) Program 120 Age 0 CPUE from trawls in May and June combined in year t + 1.

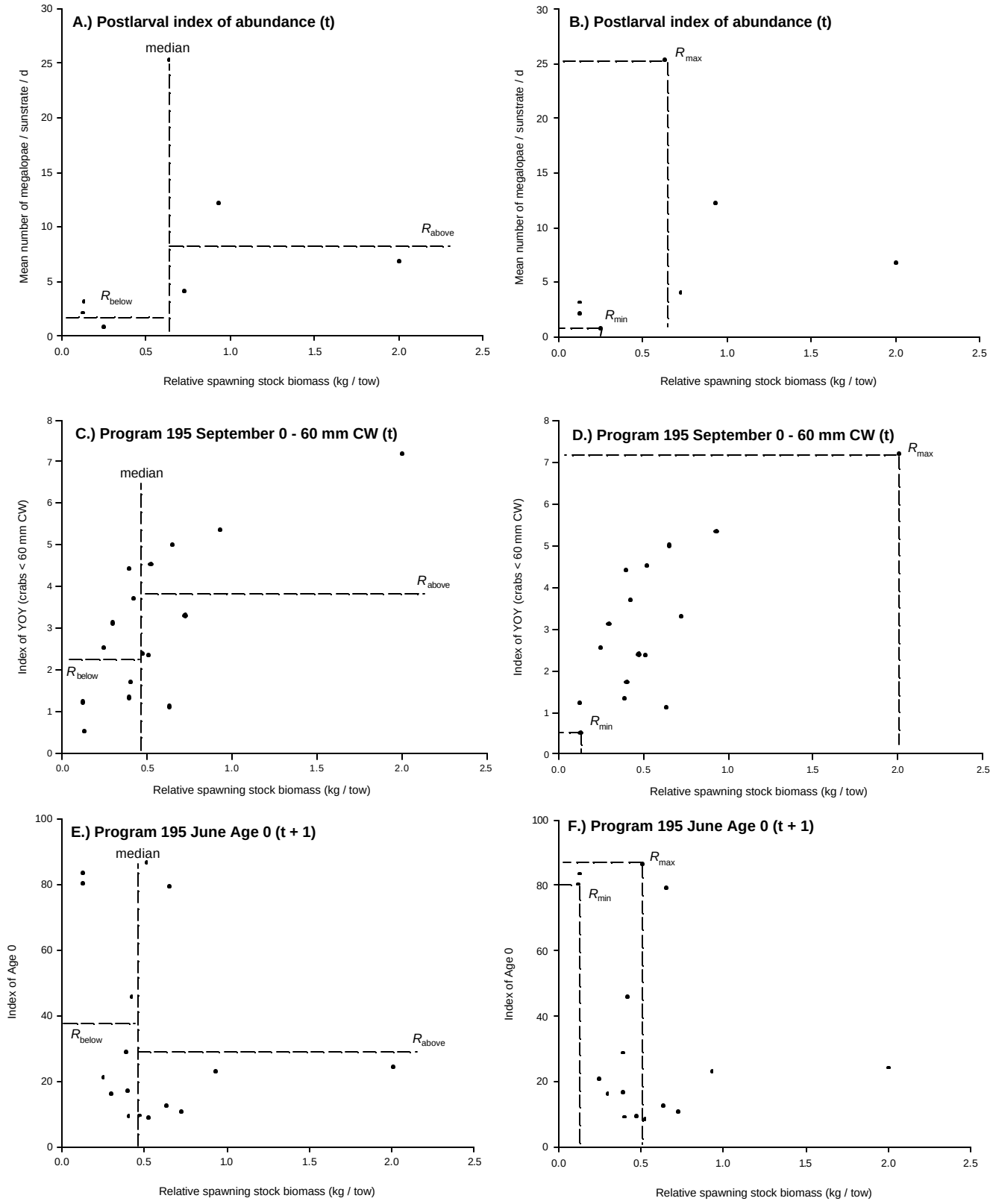


Figure 31. The relationship between the relative spawning stock biomass (mean kg/tow collected Program 195 in September) and various indices of recruit abundance. Non-parametric methods (Myers and Barrowman 1996) were fitted to the data to investigate the strength of the spawner-recruit relationship with postlarval settlement in year t (A and B), Program 195 crabs less than 60 mm CW in year t (C and D), and Program 195 Age 0 crabs in June of year t+1 (E and F). The vertical dashed line represents the median spawner abundance. R_{above} is the mean recruitment for spawner abundance greater than the median and R_{below} is the mean recruitment for spawner abundance lower than the median. r_{max} shows the maximum observed recruitment and the SSB that produced it (this value is associated with the rank

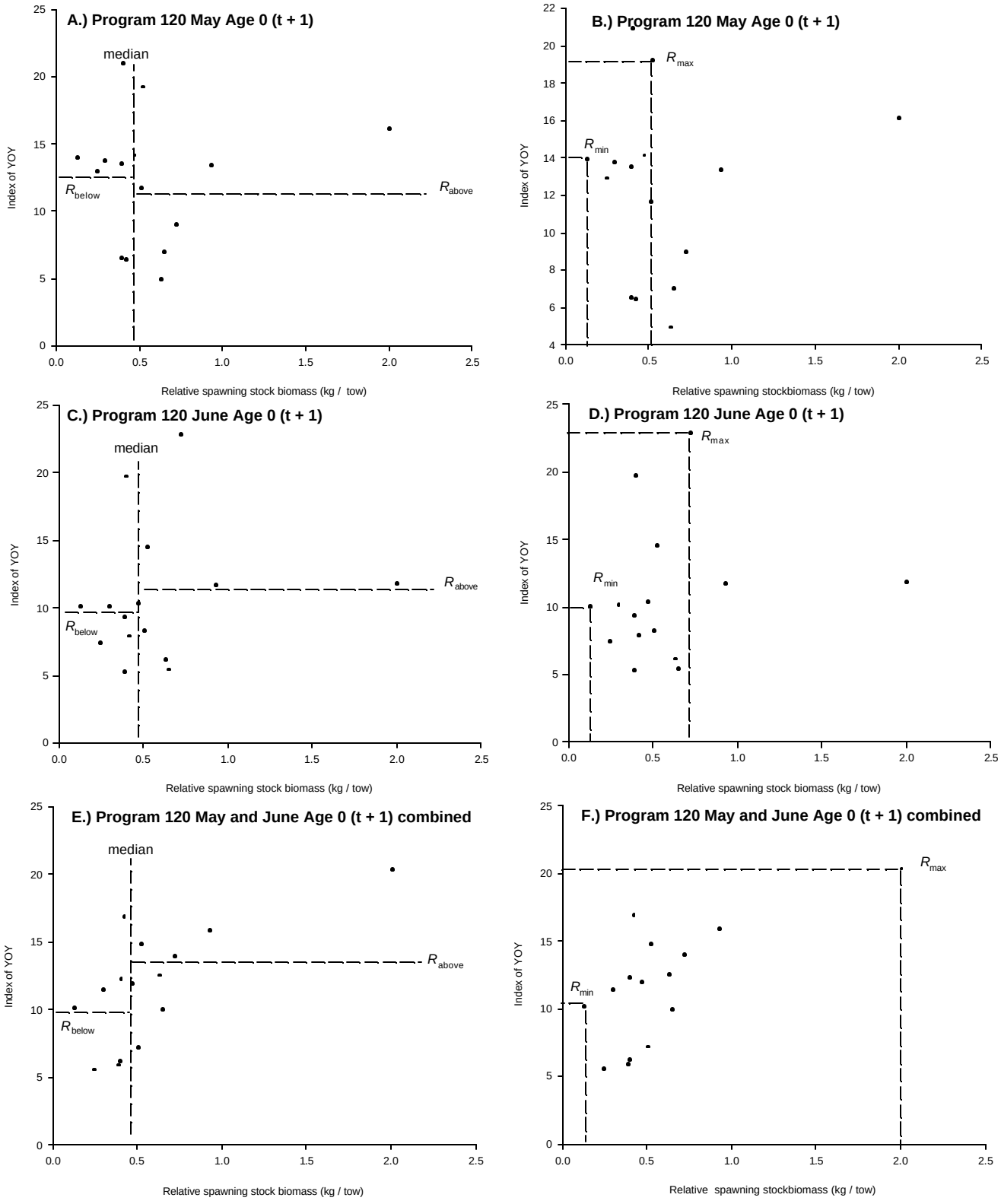


Figure 32. The relationship between the relative spawning stock biomass (mean kg/tow collected Program 195 in September) and various indices of recruit abundance. Non-parametric methods (Myers and Barrowman 1996) were fitted to the data to investigate the strength of the spawner-recruit relationship with Program 120 Age 0 crabs in May of year t + 1 (A and B), Program 120 crabs in June of year t + 1 (C and D), and Program 120 Age 0 crabs in May and June averaged of year t+1 (E and F). The vertical dashed line represents the median spawner abundance. R_{above} is the mean recruitment for spawner abundance greater than the median and R_{below} is the mean recruitment for spawner abundance lower than the median. r_{max} shows the maximum observed recruitment and the SSB that produced it (this value is associated with the rank value R_{max}) and r_{min} is the minimum observed recruitment and the SSB that produced it (this value is associated with the rank value R_{min}).

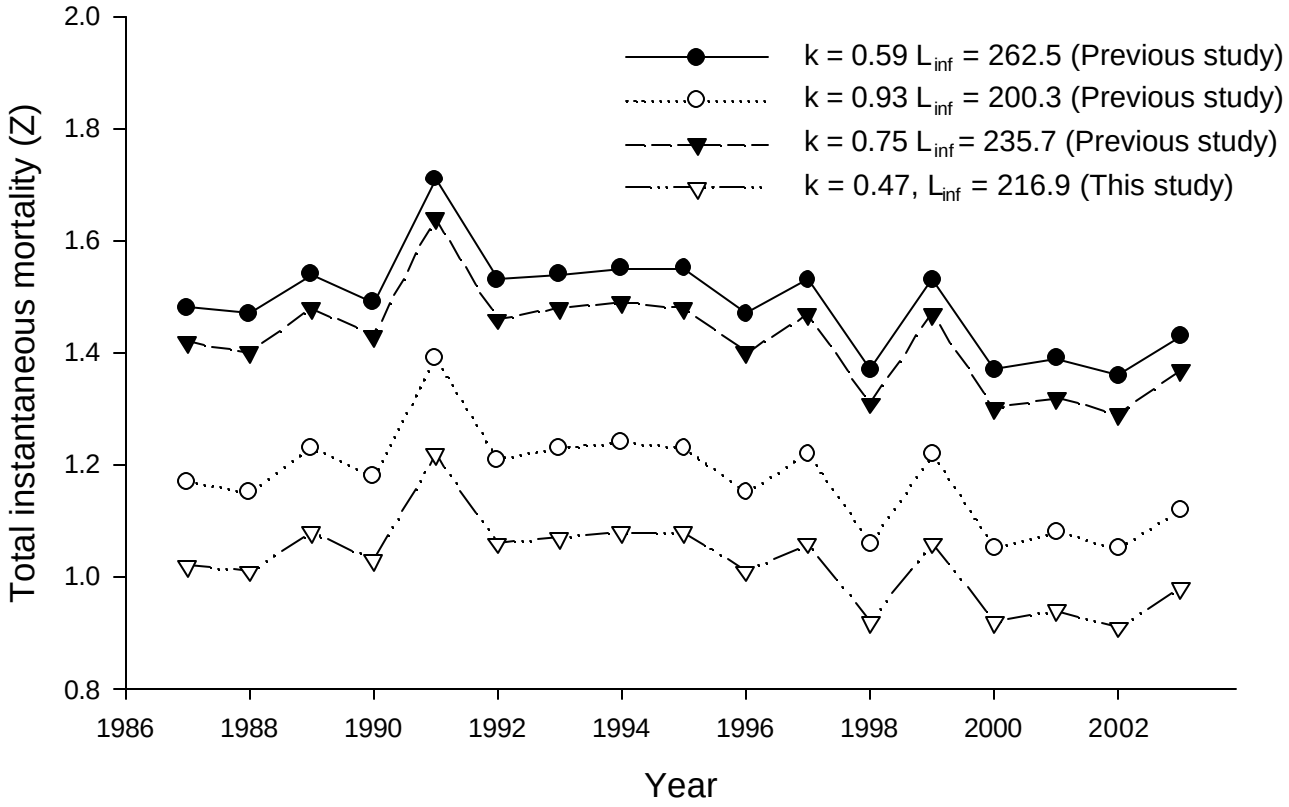


Figure 33. Length-based estimates of blue crab mortality rates (Z) for sexes combined from NC DMF trawl survey data for Program 195 using the approach of Hoenig (1987). Since estimates are highly dependent on growth rate estimates, mortality is shown for five different sets of von Bertalanffy parameters: three from previous published work (see text) and one fit from the present study.

Figure 34. Von Bertalanffy growth trajectories fit to blue crab length frequency data from NC DMF adult (Program 195) trawl survey data from June and September. A length-based model was fit to the observed data (see text for details on model fitting).

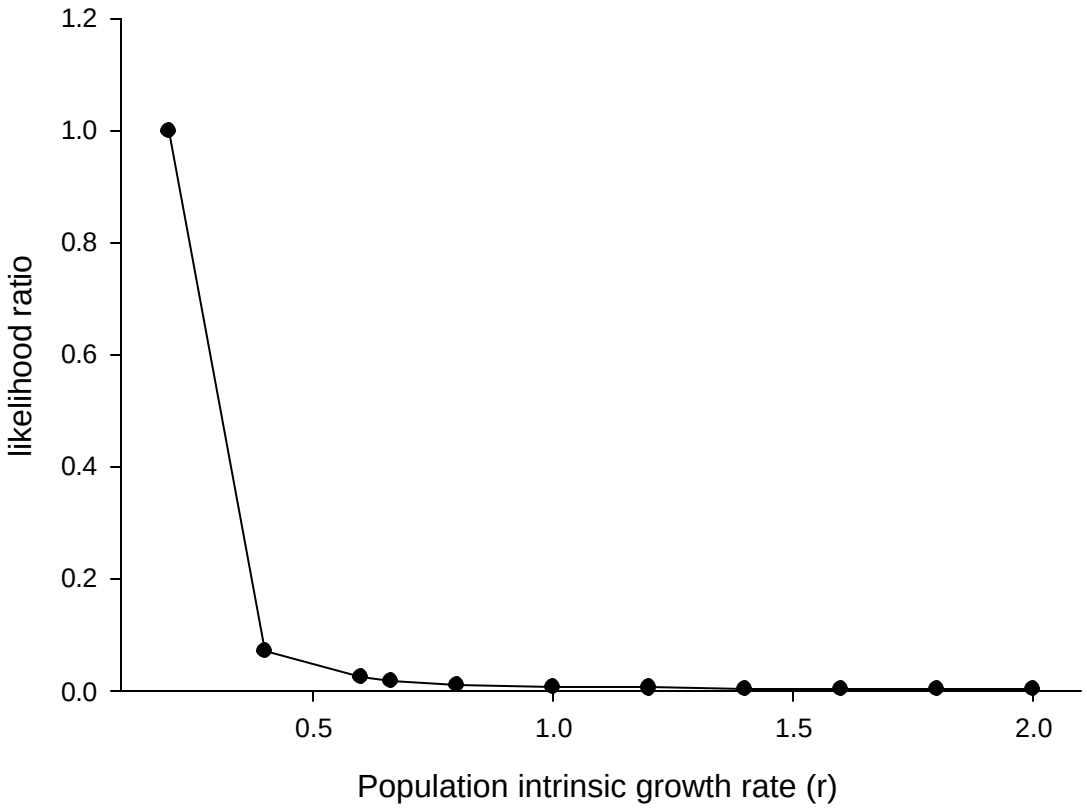


Figure 35. Likelihood profile from a non-equilibrium surplus production model that was fitted to the commercial pot CPUE data series for the period 1953-2002. Values were generated by fixing the intrinsic population growth rate (r) and fitting the remaining model parameters (K) using a maximum likelihood approach B_1 was assumed to be equal to K for model runs. A value of 1.0 indicates the most likely fit, values near 0 indicate poorer fits.

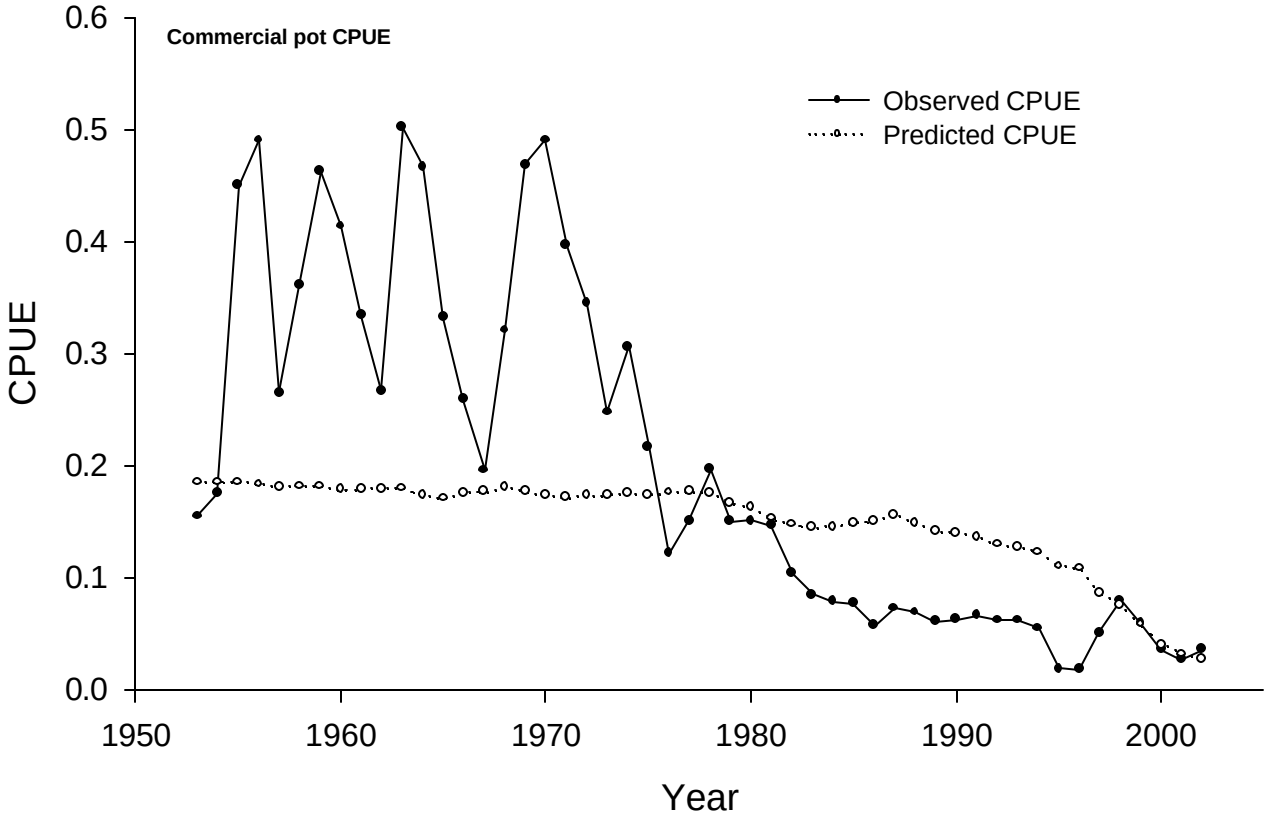


Figure 36. Relationship between observed and predicted mean CPUE from 1953 - 2002 as described by a non-equilibrium surplus production model with mean CPUE of commercial pots. The fit shown was for a fixed r = 1.0.

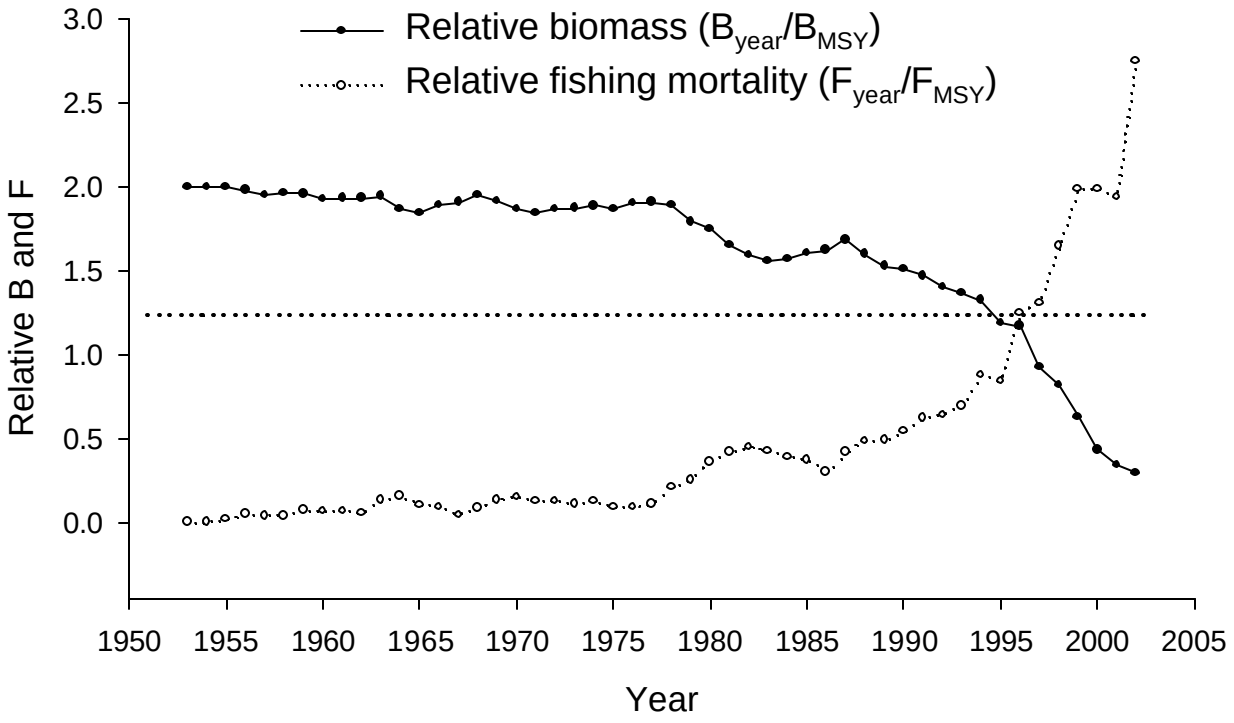


Figure 37. Historical relationship between relative biomass (Relative B = B_{year}/B_{MSY}) and fishing mortality (Relative F = F_{year}/F_{MSY}) generated by a non-equilibrim surplus production model fitted to observed CPUE of crab from commercial pots. The "nearness" index, which ranges from 0 (least reliable) to 1 (most reliable), indicates how closely a modeled stock has approached the biomass level producing B_{MSY}. " Coverage" ranges from 0 (least reliable) to 2 (most reliable), and indicates how widely stock biomass has varied between 0 and K. The rationale for these indices is that MSY will be estimated more reliably if estimated biomass has gone from above B_{MSY} to below (or vice versa). In this case,"nearness" 1 was and "coverage" was 1.73, respectively. The fit shown is for r fixed at 1.0.

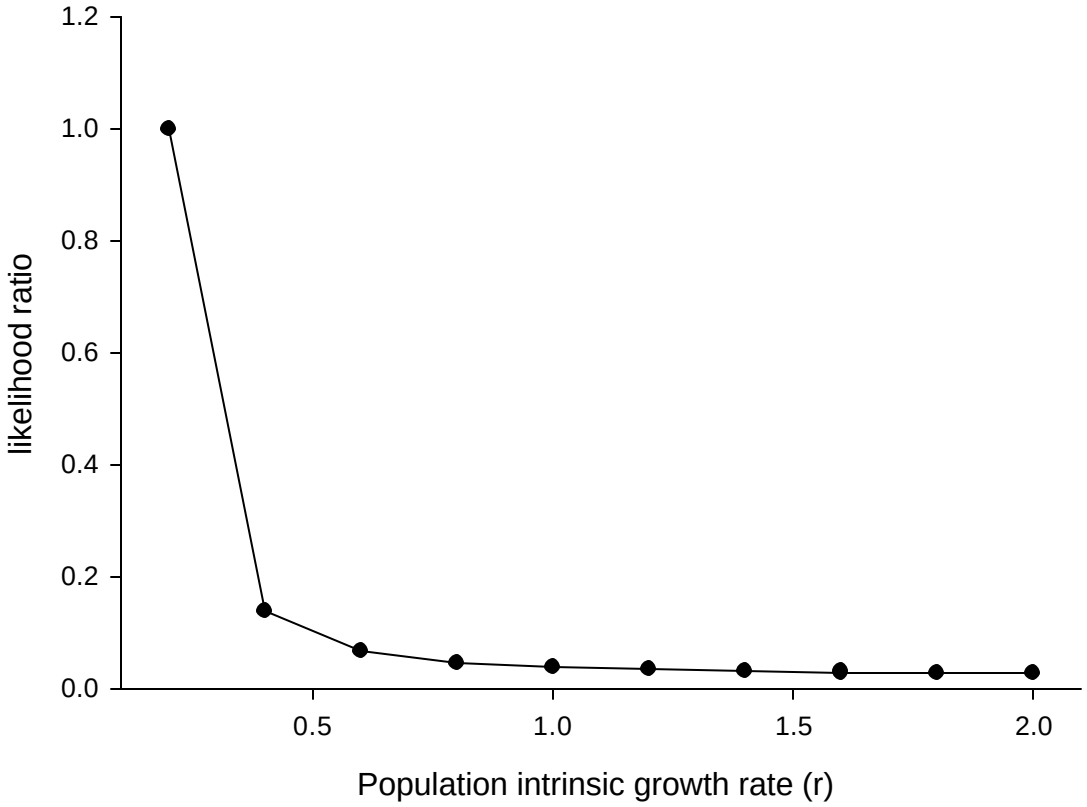


Figure 38. Likelihood profile from a non-equilibrium surplus production model that was fitted to Program 195 June and September indices of abundance (crabs > 127 mm CW) and commercial pot CPUE data series simultaneously. Values were generated by fixing the intrinsic population growth rate (*r*) and fitting the remaining model parameters (*K*) using a maximum likelihood approach. B_1 was assumed to be equal to K for model runs.

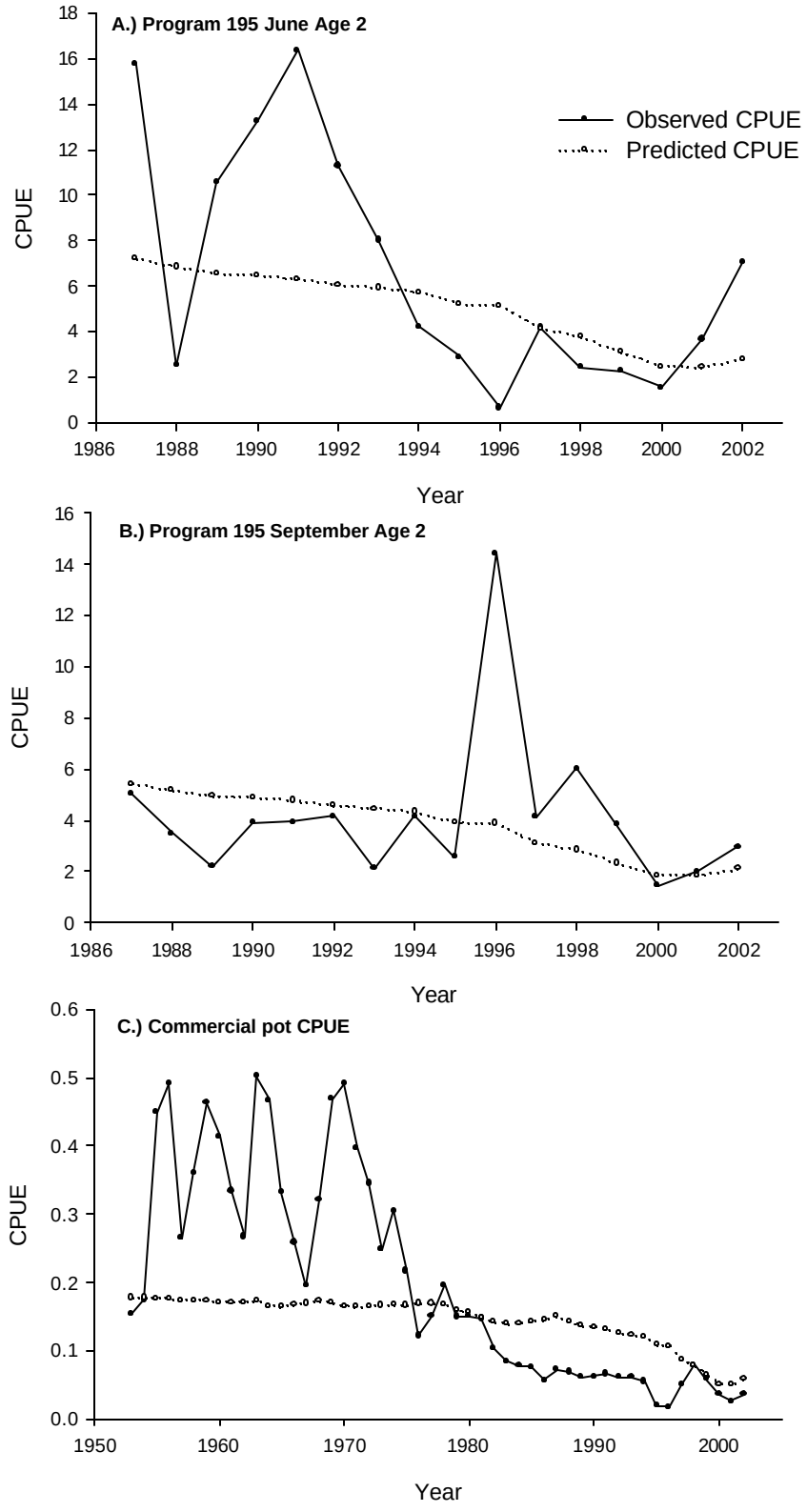


Figure 39. Relationship between observed and predicted mean CPUE from 1953 - 2002 as described by a non-equilibrium surplus production model with A.) Program 195 June index of abundance (crabs > 127 mm CW), B.) Program 195 September index of abundance (crabs > 127 mm CW), and C.) mean CPUE of commercial pots. The model fits shown are for r fixed at 1.

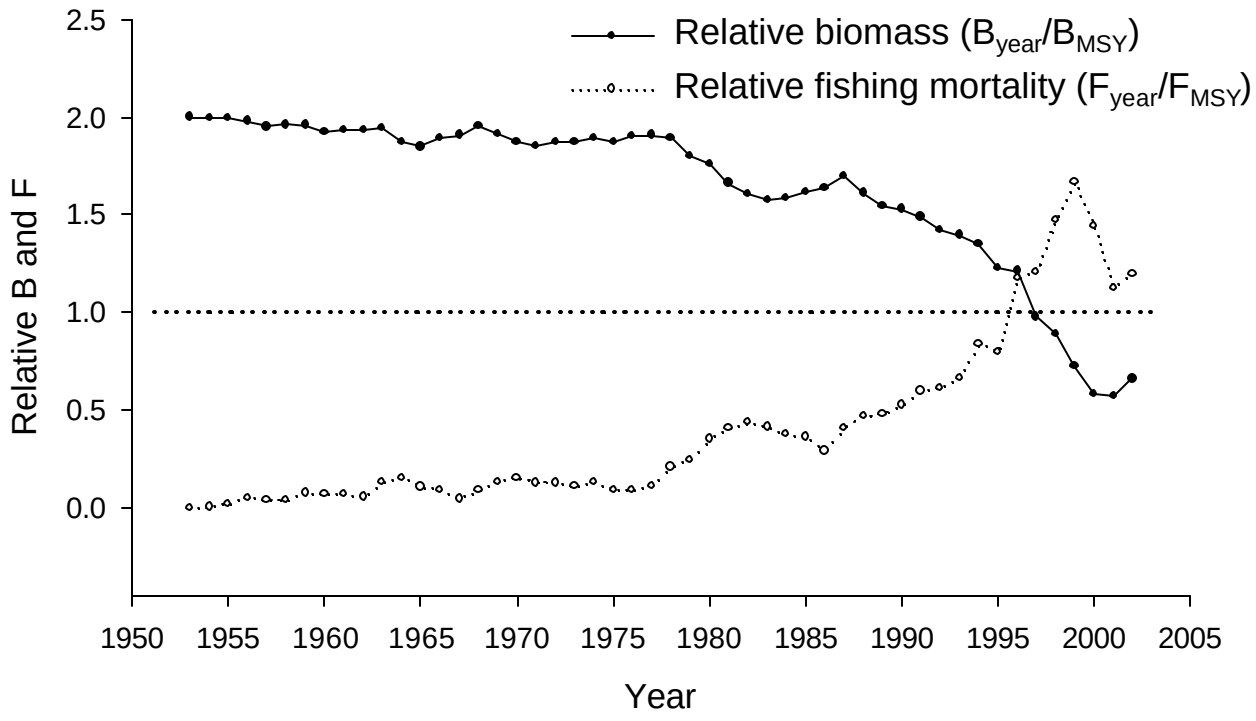


Figure 40. Historical relationship between relative biomass (Relative B = B_{year}/B_{MSY}) and fishing mortality (Relative F = F_{year}/F_{MSY}) generated by a non-equilibrim surplus production model fitted to observed CPUE of crabs > 127 mm CW from Program 195 June and September indices of abundance and commercial pots. The "nearness" index, which ranges from 0 (least reliable) to 1 (most reliable), indicates how closely a modeled stock has approached the biomass level producing B_{MSY}. " Coverage" ranges from 0 (least reliable) to 2 (most reliable), and indicates how widely stock biomass has varied between 0 and K. The rationale for these indices is that MSY will be estimated more reliably if estimated biomass has gone from above B_{MSY} to below (or vice versa). In this case,"nearness" 1 was and "coverage" was 1.44, respectively. The fit shown is for r fixed at 1.0.

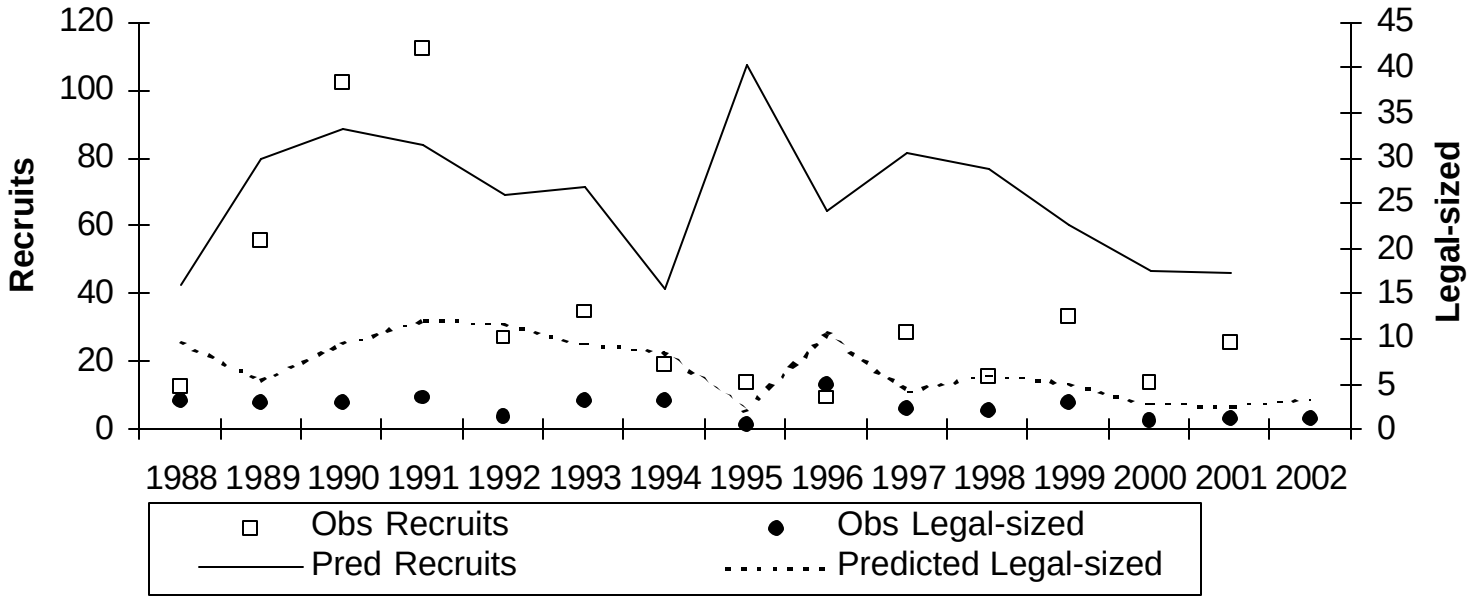
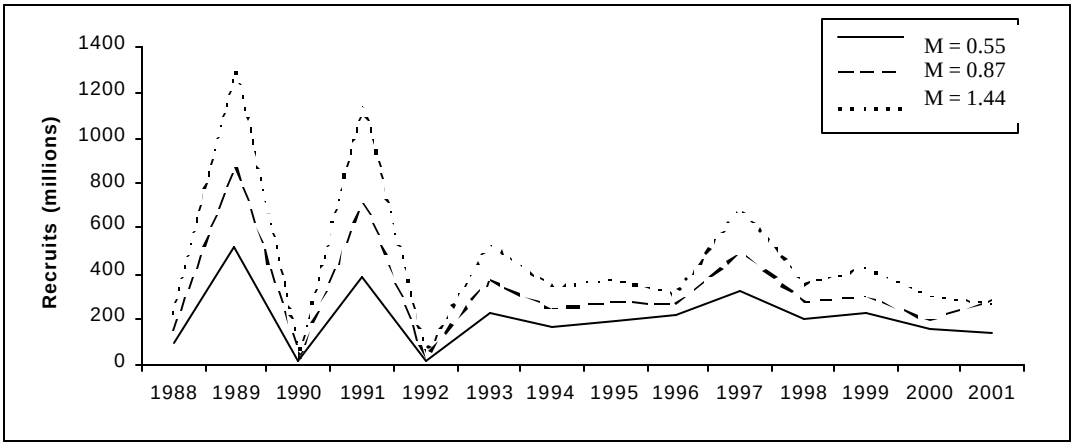


Figure 41. Example of a Collie-Sissenwine model fitted to observed relative abundance data for recruits (<127 mm CW) and legal-sized (127 mm and greater CW) blue crabs, at an assumed natural mortality rate (M) of 0.87. Survey data are from the September P195 surveys



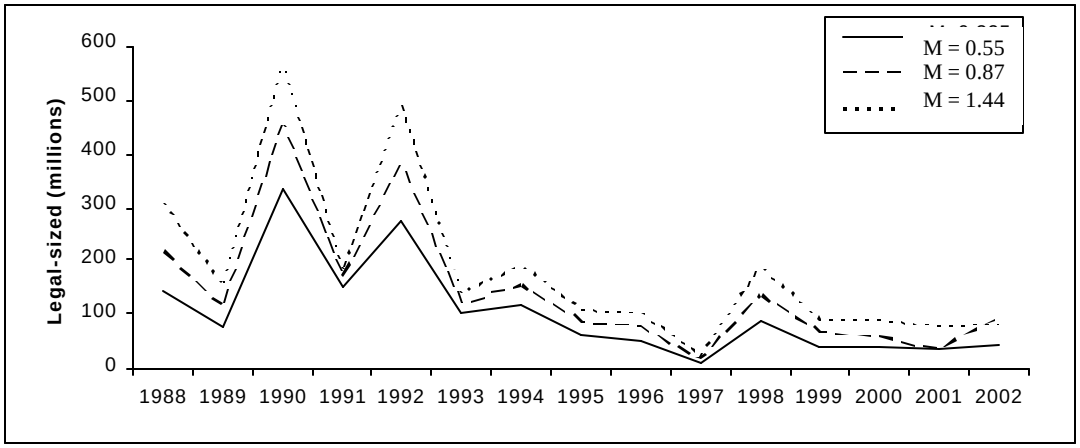


Figure 42. Estimated abundance (number in millions) for recruit (<127 mm CW, upper panel) and legal-sized (127 mm and greater CW, lower panel) blue crabs, based on a Collie-Sissenwine model and one of three assumed natural mortality rates (M).

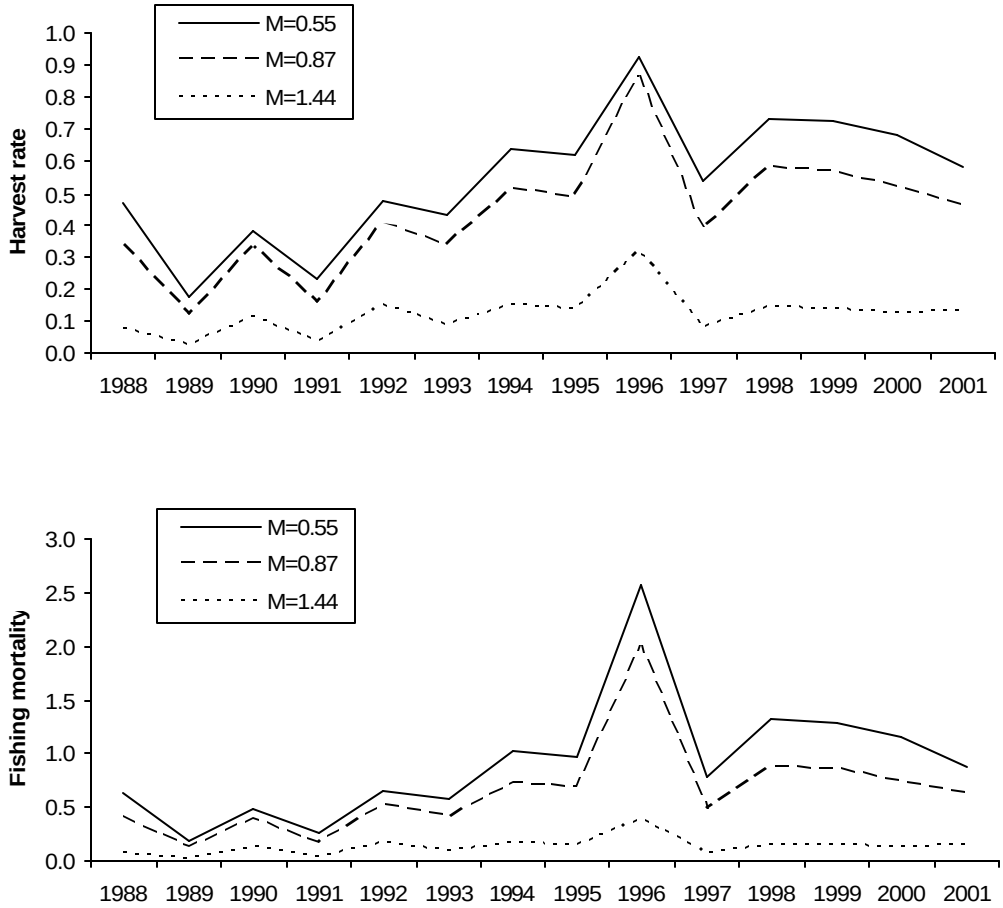


Figure 43. Estimated exploitation rate (upper panel) and instantaneous fishing mortality rate (lower panel), based on a Collie-Sissenwine model and one of three assumed natural mortality rates (M).

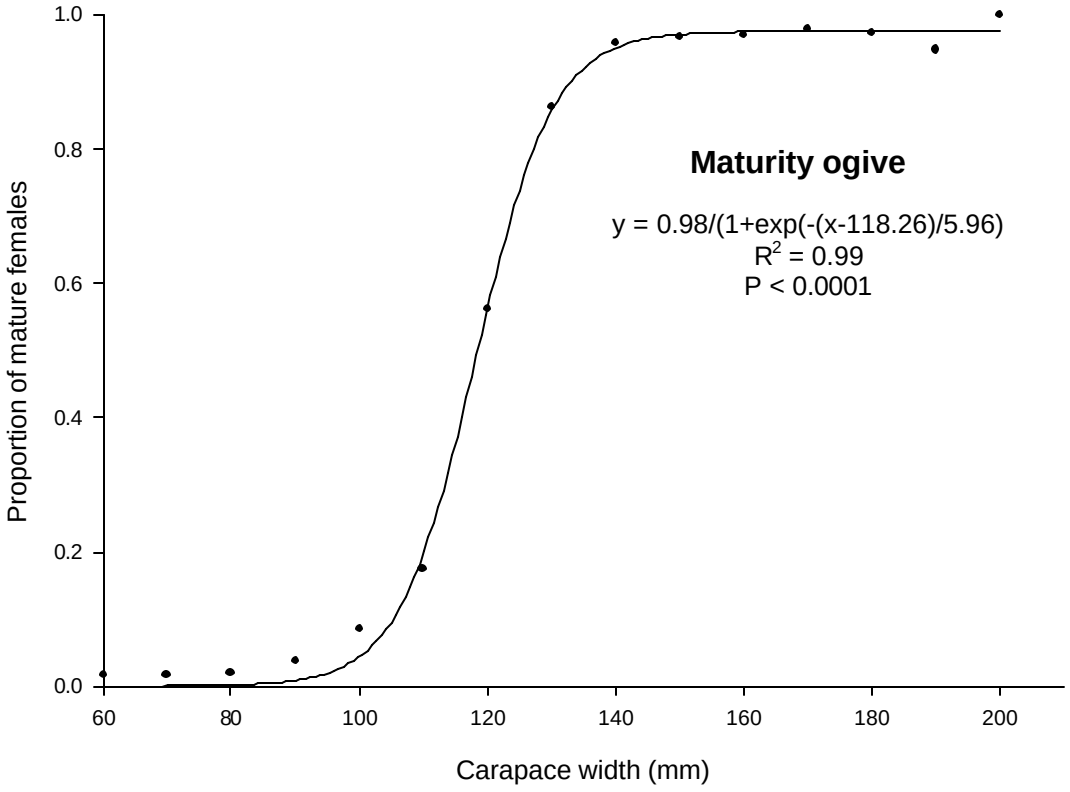


Figure 44. Proportion of mature females by size class from NC DMF Program 195 trawl surveys. A sigmoidal relationship was fitted to the data (n = 16,620 crabs) for the years 1987 - 2002.

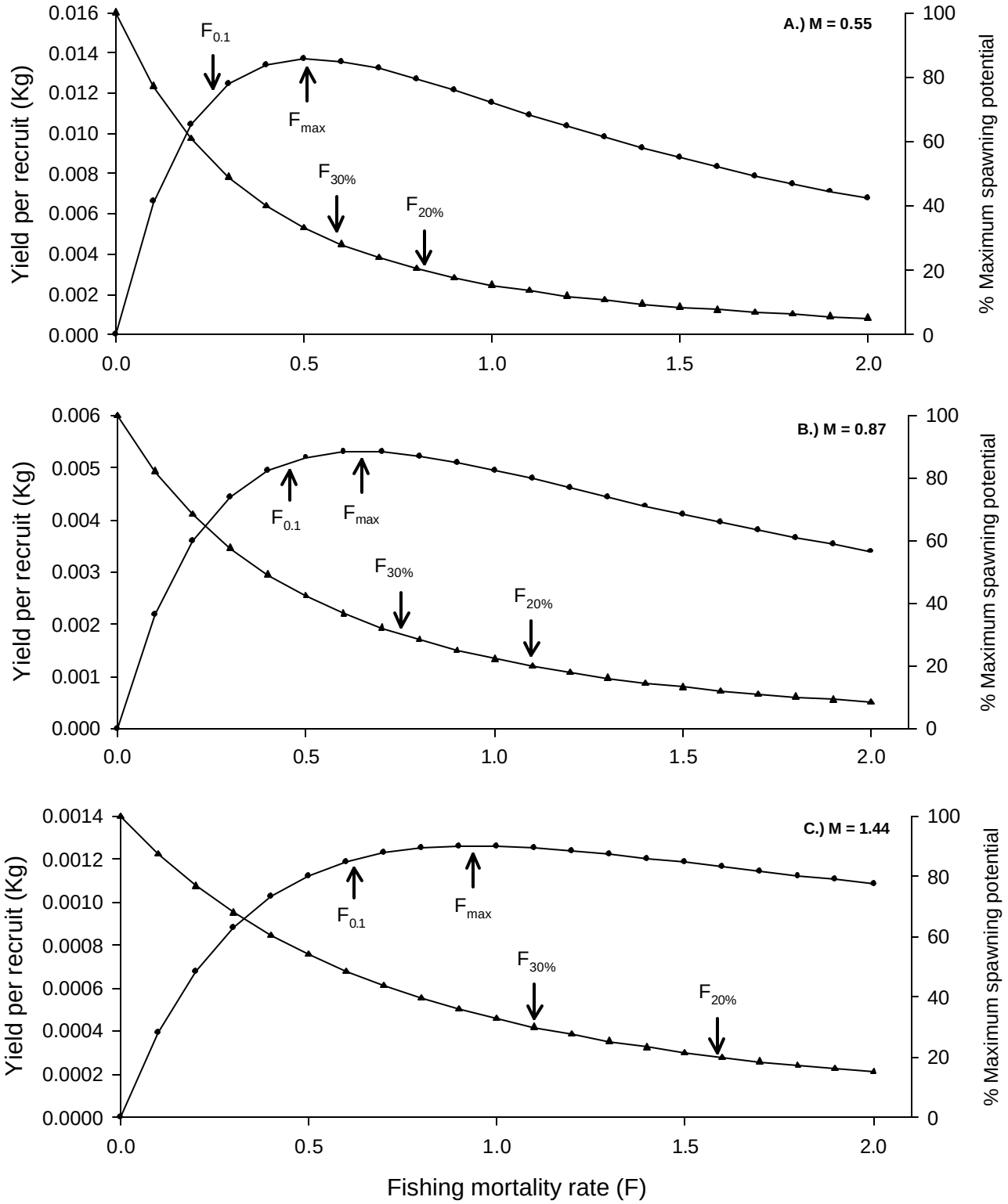


Figure 45. Results of Yield-per-recruit (YPR) and Spawning stock biomass-per recruit (SSBR) analysis for three different assumed natural mortality rates: A.) M = 0.55, B.) M = 0.87, and C.) M = 1.44. Growth was described by the von Bertalanffy growth equation generated from length-based modeling of Program 195 June and September trawl data (k = 0.47, L_{inf} = 216.9).