

PREDATION BY SUB-ADULT RED DRUM (*Sciaenops ocellatus*),
ON JUVENILE BLUE CRABS (*Callinectes sapidus*):
ESTIMATION OF DAILY RATION AND SEASONAL VARIATION IN THE
CONTRIBUTION OF BLUE CRAB TO THE DIET

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ABSTRACT

The blue crab (*Callinectes sapidus*) is a species of significant commercial importance across its range, and constitutes many highly valued fisheries. Downward trends in landings have prompted investigation into the factors which may limit the recruitment of blue crabs, specifically the role predators may play in the demographics of this species. Red drum (*Sciaenops ocellatus*) have been identified as a consistent and important predator of blue crab, yet the extent of their predation had not been quantified. Using a field based approach, we determined variation in the contribution of blue crab to the diet of red drum, estimated red drum daily rations, and quantified predation on blue crabs for two age classes of fish in the New River estuary between 2007 and 2009. Red drum showed both seasonal and ontogenetic patterns in their consumption of blue crabs. Age 1 fish showed blue crabs to be an overall greater component of their diets by frequency, weight, and number than age 0 fish, however this age class also showed greater interannual variability in diet composition. Both age classes of fish demonstrated strong diel feeding patterns, with peak feeding occurring during the hours after dark. The mean daily ration estimate for age 0 fish was 4.3% of predator body weight, and was higher than the 1.5% estimated for age 1 fish. Using the estimated mean consumption rates and the seasonal proportion and sizes of blue crabs consumed the average age 0 and age 1 red drum in the new river estuary were conservatively determined to consume approximately 294, and 98 individual blue crabs respectively, between the months of May and October. Given the current increasing population of red drum, and importance of blue crabs in their diets, future work is warranted to assess the relative predation impact that red drum have on juvenile blue crabs within estuarine habitats.

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INTRODUCTION

Over the last ten+ years there has been a strong movement for the implementation of ecosystem-based fishery management in response to passage of the Sustainable Fisheries Act of 1996. Due to the magnitude and complexity of interactions between physical and biotic factors within an entire ecosystem, and the socioeconomic importance of current fisheries, integration of a comprehensive ecosystem-based approach into current management practices has proven to be problematic to fishery professionals (Larkin 1996). As the objectives of management have shifted away from harvest maximization toward, precautionary goals and approaches based on the theory of maximum sustainable yield have given way to ideas of entire ecosystem protection, multi-scale biological, political, and social questions must be addressed (Grumbine 1997). A fundamental step toward taking a more holistic approach to management is to simply consider how the harvest of one species may impact other species in the ecosystem. However, even this distilled approach is hindered by the current lack of knowledge about the basic interactions between some of the most common and commercially significant species.

Predation as the primary structuring force in aquatic systems has been continuously documented throughout the foundational literature in ecology (e.g., Paine 1966; Menge 1976; Carpenter et al. 1985; Connolly and Roughgarden 1999; Menge 2000). Both community membership and abundance of numerous fish species have the potential to be shaped by predator-prey interactions (Mittelbach and Persson 1998). Mortality during the early life history of fish can have significant management implications, as even relatively small variations in survival rates of juveniles are able to

have large effects on adult abundance (Houde 1989). Predation can be the largest source of mortality for some juveniles, resulting in the recruitment of entire year classes to be severely limited (Hartman and Margraf 1993; Connel 1998). In marine systems, shallow estuarine environments provide essential juvenile habitat, supporting some of the most economically valuable fisheries worldwide (Blaber et al. 2000). Despite their key function in fisheries production, the complete role of predation in these systems remains somewhat unknown (Sheaves 2001). The majority of past fisheries management strategies have ignored predation and other ecological processes, focusing solely on less intricate single-species stock assessment models (Latour et al. 2003). Complex multi-species models have been developed for incorporation into contemporary fisheries management, but their application has been limited by a lack of empirical data to quantify essential biotic interactions such as predation (Whipple et al. 2000).

In order to understand trophic interactions within fisheries, diets of managed species must first be characterized. Various methodologies have been employed extensively in the analysis of predator stomach contents, and the topic has been subject to numerous critical reviews (e.g., Hyslop 1980; Cortes 1997). Standard methods in dietary analysis involve quantifying individual items from total stomach contents through numeric frequency counts, and volumetric or gravimetric measurements (Hyslop 1980). Numeric counts are valuable in determining patterns of feeding behavior, while volume or weight measurements provide more information on the relative nutritional contribution of food items (Macdonald and Green 1983). A compound index of relative importance can be derived by combining multiple indices, and can be useful as a common currency in comparative studies among different species (Cortes 1997). Species identification and

size information of ingested items can initially be unavailable due to the condition of the recovered prey. Diagnostic bony structures, such as otoliths and vertebrae, combined with predictive equations for length based on various morphologies, can be utilized to identify and reconstruct measurements for prey species (Scharf et al. 1997; Scharf et al. 1998; Granadeiro and Silva 2000). In addition, the collection of stomach contents from fish generally necessitates sacrificing the animal, which may not be a feasible option when studying protected species or population at low abundance (Light et al. 1983; Hayley 1998). However, non-lethal gastric lavage techniques have been developed and employed to effectively retrieve the stomach contents from live fishes (Light et al. 1983; Hartleb and Moring 1995; Hakala and Johnson 2004).

The further quantification of food habits information to estimate predator consumption is broadly divided into two approaches: bioenergetics modeling, and *in situ* sampling and experimentation. Bioenergetics models solve for components of the energy budget of an organism using mass balance equations adapted for a particular species (Hansen et al. 1993). The basic form of these equations calculate energy consumed as food as the sum of growth, metabolic costs, and waste (Ney 1993). Typically, the models partition these parameters into several more size- and temperature-specific rates, which are computed in units of energy (Rice and Cochran 1984). Bioenergetics models have been frequently applied in fisheries to estimate predatory demand and impact (Ney 1993). Modeling population wide consumption rates allows for greater investigation into food web relationships and ecosystem dynamics, yet even this theoretical approach relies heavily on observed data for parameterization of the models (Hansen et al. 1993). When the necessary physiological rates for the species of interest have not been determined by

controlled experimentation, researchers often substitute them with parameters gleaned from the literature on other species, leading to biases in the model output (Hansen et al. 1993). Thus, to enable simulation models to be used as forecasting tools, validation using independently collected data sets is required to ensure model accuracy. However this step is infrequently completed (Rice and Cochran 1984). For bioenergetics modeling to yield accurate results useful for trophic predictions, considerable supplemental laboratory and field-based research is often required (Ney 1993).

Direct field-base (*in situ*) methods used to estimate consumption in fishes first require information on predator gastric evacuation rates (Cortes 1997). Estimates of gastric evacuation rates are combined with temporal patterns of gut fullness to estimate daily ration, or the amount of prey consumed per 24 hour period. Controlled laboratory experiments are frequently employed to determine gastric evacuation rates, as well as the effects of factors such as water temperature, salinity, prey type, and predator size on both consumption and digestion rates (e.g., Persson 1979; Parrish and Margraf 1990; Buckel and Conover 1996; Wuenchel and Werner 2004). Typically, experimental designs involve housing animals in a controlled environment, allowing voluntarily feeding on meals of a known weight, and then sacrificing individuals after a predetermined time interval to weigh remaining gut contents (Persson 1979). The weight of remaining stomach contents is usually standardized for variation in predator size, by dividing gut content weight by fish weight and expressing the quotient as percent gut fullness (Héroux and Magnan 1996). Mean gut fullness values of replicate observations are plotted against time elapsed and a function is fitted to determine the rate at which the gut is emptied, with the slope of the function serving as an estimate of the gastric evacuation rate

(Parrish and Margraf 1990). Linear, square root, and exponential functions have each been used to describe the relationship, but the exponential function is generally considered the best fit (Héroux and Magnan 1996). Water temperature has been repeatedly demonstrated to have a significant effect on gastric evacuation rate, with higher temperatures producing a faster rate of gut emptying in numerous species (Persson 1979; Parrish and Margraf 1990; He and Wurtsbaugh 1993; Buckel et al. 1995; Wuenschel and Werner 2004). Although laboratory estimation of gastric evacuation is usually comprehensive and precise, the experiments are labor intensive and may produce results that are not applicable to fish in wild conditions (Parrish and Margraf 1990). It has been argued that even with sufficient information on the growth rate and daily food intake for a range of temperatures, the number of assumptions made when applying laboratory results to animals in a natural setting may be considerable enough to warrant the direct estimation of gastric evacuation rates from fish captured in the field (Elliot and Persson 1978).

The use of field-based sampling to determine gastric evacuation rates *in situ* has involved a variety of active (Boisclair and Legget 1988; Hayward et al. 1991), and passive gear types (Héroux and Magnan 1996; Jensen et al. 2006) depending on the study species. Both gear types can lead to biased estimates of consumption through either intensified feeding during active capture, or because of continued digestion during passive capture (Bromley 1994). Loss of stomach contents is possible through regurgitation in both sampling modes, and would result in an overall lowered estimation of feeding rates (Bromley 1994). Stomach content retention is affected by factors such as fish size, capture method, and season, and can lead to a systematic loss of information

(Sutton et al. 2004). Field estimation of gastric evacuation rate requires sampling throughout a complete 24 hour period, often completed at regular intervals that range from 3 to 8 hours dependent on the daily ration model selected (Hayward et al. 1991).

Daily ration estimation models can be divided into two major functional groups. Models that rely on the assumption that total food ingested daily equals that evacuated (e.g., Eggers 1979), and models that rely on the assumption that consumption during each sample period remains constant (e.g., Elliot and Persson 1978). Both models assume that the gastric evacuation rate is best described using an exponential decay function, however the Elliot-Persson (1978) model has been the most frequently used (Bromley 1994). The Elliot-Persson (1978) model requires the estimation of individual gastric evacuation rates for each of the sample periods, and then calculates daily consumption as the sum of all sample period estimates. This segmented analysis can be beneficial, as it is applicable to any temporal patterns in feeding, however its implementation can be hindered by its logistic demands and algebraic complexity (Boisclair and Leggett 1988). The occurrence of high variability in stomach content measurements can also create difficulty in precisely detecting differences between the relatively short sampling intervals, making this model vulnerable to natural variation (Bromley 1994). These limitations have inspired research into evaluating and advocating the greater use of cost-effective and equally functional alternate models (e.g. Boisclair and Leggett 1988; Hayward et al. 1991; Héroux and Magnan 1996).

The Eggers (1979) model assumes that daily consumption will equal daily evacuation. Consumption is calculated by simply multiplying the mean gut fullness value for the entire 24 hr period by the gastric evacuation rate. This model assumes

periodic feeding behavior, where initial gut fullness values equal the final values, however it has been found to be robust even in violation of these assumptions (Bromley 1994). This model also requires fewer sampling periods and sample sizes to effectively estimate daily ration when compared to the Elliott- Persson (1978) model (Boisclair and Leggett 1988). In light of critical reviews and evaluation, the Eggers (1979) model has been found to be equally suitable for the estimation of consumption compared to the more frequently used Elliott-Persson (1978) model, while being less consumptive of resources and computationally less demanding (Bromley 1994; Héroux and Magnan 1996).

The blue crab (*Callinectes sapidus*) is an estuarine-dependent member of the family Portunidae, with a broad distribution in the western Atlantic Ocean. Populations can be found ranging from Nova Scotia, Canada, to the species southern most limit of Argentina (Williams 1974). This benthic species of swimming crab inhabits a range of polyhaline habitats and is found at depths up to 90m in the coastal ocean, to the nearly fresh shallow-water reaches of estuaries (Williams 1974; Orth and van Montfrans 1987; Thomas et al. 1990; Ruiz et al. 1993; Posey et al. 2005). However, shallow soft bottoms in estuaries with moderate salinity (<25 ppt) are believed to be the preferred habitat (Hsueh et al. 1992; Guerin and Stickle 1997; NCDMF 2004). The life cycle of this species is complex, with adult females undergoing a migration to high salinity reaches at the mouth of estuaries to release newly hatched larvae (Orth and van Montfrans 1987). The planktonic larvae are transported offshore where they pass through 6 to 8 zoeal stages until they return to the estuary and transform into benthic megalopae (Orth and van Montfrans 1987; Heck et al. 2001; Moksnes and Heck 2006). Post-settlement juvenile

blue crabs utilize a variety of habitats within the estuary including oyster reefs, submerged aquatic vegetation, mud, and bare sand bottoms (Orth and van Montfrans 1987; Thomas et al. 1990; Heck et al. 2001; Moksnes and Heck 2006).

The blue crab is commercially and recreationally harvested over its entire range, with major US fisheries occurring in the Chesapeake Bay, Louisiana, and North Carolina (Williams 1974; NCDMF 2004). Within the state of North Carolina, the blue crab is the most commercially important species with regards to total landings, value of catch, employment, and amount of harvest gear used (Henry and McKenna 1998). In 2005, the North Carolina Division of Marine Fisheries (NCDMF) valued the total catch of blue crab at over \$20 million (NCDMF commercial landings data). Despite accounting for 31% of the value for all commercial fisheries combined within the state, the 2005 blue crab landings represented a ten year low in both weight and value (Figure 1) (NCDMF commercial landings data). This decrease in landings, and current listing of the blue crab stock status as one of “concern” by the NCDMF, has prompted investigation into the factors limiting recruitment and production of blue crab within the state.

The current harvest regulations in North Carolina, which include a minimum size limit of 127mm carapace width and a maximum carapace width of 172mm for females, are designed to protect juveniles and maintain the spawning stock of adult females (NCDMF 2004). Despite the maintenance of an elevated biomass of spawning females through harvest regulations, juvenile blue crab production may not be ultimately dictated by spawning stock biomass. Initial year-class strength can be affected by several environmental variables (e.g., wind, tidal circulation) that have been identified as affecting the number of crab larvae settling into appropriate estuarine nursery habitats

(Ulanowicz et al. 1982; Tang 1985; Eggleston et al. 1998; Etherington and Eggleston 2000). However, it has also been suggested that predation on post-settlement juveniles may significantly modify the initial patterns of larval supply, further limiting the number of recruits and influencing overall population dynamics (Heck et al. 2001). Post-settlement blue crabs have been shown to actively select for complex habitats such as sea grass, salt marshes and oyster reefs, and may use these habitats to avoid predation (Orth and van Montfrans 1987; Thomas et al., 1990). When evaluating the relative importance of these complex habitats compared to bare mud, Moksnes and Heck (2006) found that there was no significant difference in predation rates between habitats, and their findings even indicated potentially higher predation rates on later stage juvenile blue crabs in the structured habitats due to the aggregation of predators. The general lack of oyster beds and sea grasses in the river- dominated estuaries of southeastern North Carolina has led to research indicating the importance of low salinity reaches in these systems as nursery habitat for juvenile blue crabs (Posey et al. 2005).

Management of blue crab has been further hindered by the difficulty associated with determining natural mortality rates for crustaceans (Hewitt et al. 2007). Quantifying predation on blue crabs would contribute toward a more refined approximation of their natural mortality, and would provide species-specific data for ecosystem-based management. In a review of blue crab predators, Guillory and Elliot (1999) identified ninety-three individual species as predators of at least one life stage of blue crab, with 67 species of fish having included post-settlement juvenile blue crabs in their diet. A number of food habits studies for several local estuarine fish species such as the bonnethead shark (*Sphyrna tiburo*), oyster toadfish (*Opsanus tau*), striped bass (*Morone*

saxatilis), Atlantic croaker (*Micropogonias undulatus*), silver perch (*Bairdiella chrysoura*), and red drum (*Sciaenops ocellatus*) provide direct evidence of predation on blue crab pre-recruit life stages (Adams 1976; Overstreet and Heard 1978; Bisker et al. 1989; Cortes et al. 1996; Orth et al. 1999; Walter et al. 2003). Although various species prey on blue crabs, Guillory and Elliot (1999) concluded red drum to be the dominant predator based on a quantitative ranking of estuarine fish predators in the Gulf of Mexico.

The red drum is a member of the family Sciaenidae, and currently has a distribution in the western Atlantic Ocean that extends from the eastern shore of Delaware to Florida and also throughout the Gulf of Mexico (Wenner 1992). Historically, red drum were common further northward, with several records as far north as Massachusetts (McDowall 1969). However, showing a reduction of their range, there have been few landings north of the Chesapeake Bay since the 1950's (NOAA commercial landings database). In North Carolina, red drum are one of the most recreationally sought after fishes in the state (NCDMF 2001). Overfishing had led to a statewide decline of the red drum population through the 1980's. The first stock assessment completed in the early 1990's confirmed that the stock was being overfished and began a period of active management for this species (NCDMF 2001). Current regulations enacted in 2001 prohibit the targeting of red drum by commercial fisheries, and allow a recreational harvest of one fish per day between 457 and 686 mm total length. The current population assessment of red drum in North Carolina indicates a recovering population, with increasing numbers of juvenile recruits as a result of current harvest restrictions (Figure 2) (Takade and Paramore 2007).

Adult red drum inhabit the coastal ocean and major sounds, however as an estuarine- dependent species, polyhaline nursery habitats are utilized for feeding and reproduction (NCDMF 2001). After spawning, eggs and planktonic larvae are carried from the coastal ocean into estuaries where they settle out during the late summer and early fall into various structured habitats and develop through juvenile stages (Ross et al. 1995; Levin and Stunz 2005). Sub-adult red drum show a preference for estuarine creeks and tidal marshes where they reside until reaching sexual maturity around three years of age (Ross et al. 1995; Adams and Tremain 2000; NCDMF 2001).

Being large and relatively long-lived fish, red drum have been observed to reach a maximum size of 1,346mm fork length and an age of 56 years in North Carolina waters (Ross et al. 1995). Growth is rapid for the first three to four years until sexual maturity is reached for fish between 762 and 914mm in length (NCDMF 2001). A juvenile drum can achieve a total length of 355mm after one year of growth, and many fish can reach sizes larger than the top end of the current legal possession limit of 686mm by the end of their second year (Ross et al. 1995). In a large riverine estuary in North Carolina, juvenile red drum were observed to exhibit variable growth rates through time and across salinity gradients, however the greatest growth rates were found to occur in the mesohaline (15— 25 ppt) reaches of the river in late summer and early fall (Lanier and Scharf 2007). Laboratory experiments indicated that juvenile red drum achieved their highest growth rates at a salinity of 10 ppt and temperature of 31.1° C (Tomasso and Kempton 2000). These low salinity and elevated temperature conditions are present for a 4-6 month period from approximately May— Sept in the large riverine estuaries of southeastern North Carolina (Posey et al. 2005), and may facilitate the rapid growth

experienced by juvenile stages of red drum. Current data on the daily growth and consumption rates of red drum is limited, and based primarily on data from aquaculture production facilities (Tucker et al. 1997). Consumption rates must necessarily be high during the warm summer and early fall seasons to achieve the levels of growth observed. Indeed, a daily ration of up to 3—5% of individual body weight has been observed in tank-raised juvenile red drum during manipulative growth experiments (McGoogin and Gatlin 1999; Tomasso and Kempton 2000).

As an economically important fish, red drum diets in the Gulf of Mexico have been extensively studied (Knapp 1950; Boothby and Avault 1971; Bass and Avault 1975; Peters and McMichael 1987; Llanso et al. 1998; Scharf and Schlicht 2000). Ontogenetic shifts in dominant prey items tend to occur as red drum increase in size and shift habitat use patterns. Juvenile red drum less than 75mm total length primarily prey on planktonic copepods and mysid shrimp during the early part of their life history (Bass and Avault 1975; Lanier and Scharf 2007). As the juveniles grow during their first year, crustaceans (e.g., penaeid shrimp, portunid crabs, xanthid crabs) become dominant components of the diet (Bass and Avault 1975), and the NCDMF (2001) has stated that 96% of the diet of juvenile fish between 200 and 300 mm consists of decapods. As drum mature and move into deeper habitats, the importance of fish increases, with percent contribution by weight ranging between 17 and 82% (NCDMF 2001). This variability may be attributed to temporal changes in feeding selectivity demonstrated by red drum. In Galveston Bay, the diet of red drum exhibited considerable seasonal variation that was related to changes in prey abundances, however positive and negative prey species selectivity was also demonstrated (Scharf and Schlicht 2000). Feeding selectivity on the finer temporal scale

of a diel period has also been shown to exist. When comparing day and night feeding in red drum, Bass and Avault (1975) found the majority of prey consumed after sunset to be fish, however during the day stomach contents were dominated by decapods.

Importantly, red drum have been identified as a consistent predator of blue crabs in a variety of estuarine systems throughout their range (Boothby and Avault 1971; Bass and Avault 1975; Overstreet and Heard 1978; Guillory and Elliot 1999; Orth et al. 1999; Speir 1999; Scharf and Schlicht 2000). In the Chesapeake Bay, Orth et al. (1999) found between 64 and 100% of red drum sampled feeding in sea grass beds had consumed blue crabs. In the Gulf of Mexico, selection for smaller juvenile blue crabs is suggested. Although the mean size of blue crabs consumed did increase with fish size, 78% of the ingested crabs were less than 50mm in carapace width (Guillory and Prejean 1999). Similarly, Scharf and Schlicht (2000) found blue crabs between 25-75mm in carapace width were consumed most commonly by the red drum that they sampled. In a review of red drum predation on blue crabs in the Gulf of Mexico, Guillory and Prejean (1999) advocate the increasing importance of blue crabs to the diet of red drum throughout their ontogeny, with the percent frequency occurrence in stomachs of red drum greater than 200mm standard length averaging 30% in Louisiana, and 24% in Texas. In an analysis of Louisiana Department of Wildlife and Fisheries data, seasonal and diel variation in the consumption of blue crabs by red drum was observed. The frequency of occurrence of blue crabs in red drum stomachs was highest during both the spring (30%) and fall (26%) seasons, and the amount of blue crabs consumed by both weight and numbers was highest in the morning (Guillory and Prejean 1999). In response to growing concerns over decreased landings of blue crabs and increasing red drum abundance in the Gulf of

Mexico, an assumed conservative daily red drum consumption rate of 2% was combined with historic diet information to calculate an average annual ration of 701 individual blue crabs per kg of red drum (Guillory and Prejean 1999). Although hesitant to extrapolate this number to generate a population-level estimate, Guillory and Prejean (1999) concluded that the number of blue crabs consumed by the Louisiana population of red drum was “very high”.

Investigation into the extent and population-level effects of fish predation on blue crabs in North Carolina remains relatively unexplored. Given the current downward trend in blue crab landings, and the signs of recovery of one of their primary fish predators, this study examines predation on juvenile blue crabs, by red drum over two years in a North Carolina estuary. The specific research objectives were to: (1) determine seasonal and ontogenetic variation in the contribution of juvenile blue crabs to the diet of juvenile (age -0) and sub-adult (age -1) red drum, (2) evaluate red drum diurnal feeding periods and estimate gut evacuation rates and daily ration from diel patterns in gut fullness during seasons when red drum growth rates and juvenile blue crab spatial overlap is greatest, (3) quantify predation on blue crabs by juvenile and sub-adult in terms of both biomass and individual crabs consumed.

METHODS

Study system

The New River estuary (Figure 3) is a moderately-sized (419 sq. mile drainage) river-dominated estuarine system in southeastern North Carolina, which empties directly

into the Atlantic Ocean (Posey et al. 2005). Large portions of this river remain relatively free of riparian development, as it is nearly completely encompassed by the U.S. Marine Corps base Camp Lejeune. The New River is known to both significantly contribute to the statewide production of juvenile red drum (NCDMF 2001) and to generate consistent blue crab landings (NCDMF 2004), making it an ideal location to quantify predator-prey relationships between these species.

Field sampling

Beginning in July 2007, red drum (ages 0-1) were collected for both the characterization of their diet (diet sampling), and for the estimation of gastric evacuation rates (diel sampling). Sampling continued until February 2009, allowing data to be collected during the period of rapid growth for two consecutive annual cohorts of juvenile red drum (2006 and 2007 year classes). Scheduling of field collections was divided into two levels of sampling effort, heavy sampling (April- November), and moderate sampling (December-March). During the heavy sampling period, diet sampling occurred biweekly, and diel sampling on a monthly basis. During the moderate sampling period, only monthly diet sampling occurred. Collection of red drum was focused primarily in the mesohaline (15-25ppt) and oligohaline (5-15ppt) reaches of the river, to maximize both catch per unit effort (CPUE) for drum, and their spatial overlap with blue crab. Preliminary sampling within these habitats was completed to evaluate gear efficiency and identify potential sample locations to obtain the largest possible sample size of predators within sampling periods. However, rigidly fixed stations were avoided to reduce the possibility of localized depletions during sampling events.

Diet information sampling was conducted by capturing red drum with passively set monofilament gillnets. Two sizes of variable mesh nets, 45.7m long \times 2.4m deep were constructed for this study. Small mesh nets to capture age 0 fish (200-400mm TL) consisted of three 15.2m panels each of 5.1, 6.3, and 7.6cm stretched mesh; and large mesh nets for age 1 fish ($>$ 400mm TL) consisted of three 15.2m panels each of 10.2, 11.4, and 12.6cm stretched mesh. For each diet sampling event, 6 to 8 nets were anchored on the bank, extended perpendicular to the shoreline with the smallest mesh closest to the beach, and then fished overnight for approximately 12 hours.

Diel sampling was executed using a monofilament trammel net fished actively, a fishing technique referred to as “strike-netting” or “side-setting”. The trammel employed was 183m long by 2.1m deep with 35.6cm stretched outer mesh and 6.4cm stretched inner mesh. This one piece of gear was used to catch both age-0 and age-1 red drum simultaneously, allowing for a more efficient use of time and manpower during diel sampling events. During each strike set, one end of the trammel net was anchored to the shore, and the net dispensed from the boat as fast as possible (generally at speeds of 10-15kts) in an arc pattern. Once the end of the net was reached, it was anchored to another point on the shoreline, resulting in a semi-circular area being completely enclosed by the net. The area within the net was disturbed using the boat, with the goal of herding any fish encircled by the net into the mesh. After the water encircled by the net was agitated for approximately a 5 minute period, the net was retrieved. Diel sampling was conducted by completing strike net collections at least every 4 hours throughout a continuous 24 hour period. Using an active gear rather than soaking nets unattended for long time periods enabled the capture of fish in good condition, which were typically

processed for stomach contents and released alive. Active sampling also helped to minimize confounding factors, such as regurgitation or advanced prey digestion, and ensured that the collection of diet information from individual fish can be linked to a relatively discrete point in time.

At each location sampled, time, depth (m), GPS coordinates, water temperature (°C), dissolved oxygen (mg/l), and salinity (ppt) were recorded. A unique ID number was assigned to all captured red drum and recorded along with sample date, location, mesh size, total length, and weight. Stomach contents were recovered using non-lethal gastric lavage techniques as described by Hartleb and Moring (1995). Each fish had its gut contents flushed into a 0.5mm screen, and the buccal cavity carefully examined for any residual prey residue before being released. During diel sampling events, fish that were released were tagged using NCDMF internal anchor tags before being returned to the water. Marking of previously sampled fish prevented the collection of gut contents from the same individual more than once during a single diel sampling event. Retrieved stomach contents were placed in plastic bags, labeled with the corresponding fish ID number, and stored on ice until returned to the laboratory for processing.

Diet analysis

Prey items were identified to lowest possible taxon, enumerated, blotted dry, weighed to the nearest 0.01 g, and measured to the nearest mm. A two-part condition factor was assigned to each prey item delineating both wholeness of the organism and state of digestion. Carapace widths of intact blue crabs were measured; however, widths of broken or incomplete carapaces will be reconstructed using predictive equations

relating carapace width to distances between orbital teeth (Scharf and Schlicht 2000). Otoliths of highly digested fish prey were as both diagnostic and reconstructive structures. To assist with prey identification and reconstruction of original prey size, both a reference collection of otoliths and a series of predictive equations relating otolith size to body size were developed for several commonly eaten local prey species. Multiple dietary indices were calculated to express the relative importance of blue crabs and other prey to the diets of red drum. These include percent frequency of occurrence (%FO = the fraction of stomachs with food that contain a particular prey item), percent by weight (%W = the weight of each prey type eaten relative to the total weight of all prey eaten), and percent by number (%N = the number of each prey type eaten relative to the total number of all prey eaten). The three dietary indices will also be combined into a single index of relative importance (IRI), calculated as $(\%N + \%W) \times \%FO$, and expressed as a percentage. All diet data from both field seasons was pooled to characterize the overall diet for each age class. To assess inter-annual and seasonal variation in the contribution of prey types, separate dietary indices were calculated for the each year, as well partitioning the pooled data into three month blocks.

Estimating daily ration

To assess diel feeding patterns, the mean gut fullness value for all fish captured within each four hour sampling interval was plotted as a single point, resulting in a possible time series of six points over the entire 24 hour sampling event. Gut fullness values (F) were calculated by dividing total stomach content weight (G) by total weight of the fish (W) less the stomach content weight, or $F = G/(W-G)$. Points of elevated

mean gut fullness were interpreted as periods of heavy feeding, while periods of lower gut fullness were interpreted as periods of reduced or ceased feeding. When strong patterns of declining gut fullness were present, they were used to obtain field estimates of gastric evacuation rates (G_e). Mean gut fullness values for fish captured in each gear haul (strike net set) were plotted as a time series, treating each individual net set as a replicate. Each point was weighted according to the sample size it represented, preventing values from single fish to have excessive influence. Gastric evacuation rates were then calculated for the weighted data by fitting the following non-linear exponential decay model:

$$S_t = S_0 * e^{-G_e * t}$$

where

S_t = gut fullness at time t, expressed as g prey per g predator

S_0 = gut fullness at starting point of decline, expressed as g prey per g predator

t = time in hours

The Eggers (Eggers 1977) equation was used to estimate consumption (C) in grams of prey eaten per gram of predator per day:

$$C = 24 * \bar{S} * G_e$$

where

\bar{S} = mean stomach fullness (grams prey per gram predator) throughout the diel period

G_e = instantaneous rate of gastric evacuation

Quantifying predation on blue crab

Once the diet of juvenile red drum had been collected and field estimates of consumption rates were calculated, red drum daily rations were estimated separately for blue crabs. The mean value from all estimates of daily ration for each age class was used to represent the daily feeding rate (g prey per g predator per day) for the entire period of rapid growth (May – October). The appropriate seasonal dietary index %W for blue crab prey was used to partition the diet on a monthly basis. The mean consumption rate, was multiplied by the corresponding %W, resulting in an estimate of grams of blue crab per gram of red drum consumed daily during each study month. This ration was applied to the average weight of red drum observed in the field during each month and expanded to reflect a 30 or 31 day period, resulting in a monthly total estimate of grams of blue crab consumed by an individual red drum in the New River estuary. Carapace widths of blue crabs recovered whole, or reconstructed from partial remains recovered in the gut contents, were plotted through time, allowing for the determination of monthly average sizes of blue crab consumed. Using predictive equations relating blue crab carapace width to weight (Pullen and Trent 1970), the weights for the average monthly size of crabs consumed were established. The monthly total blue crab weight was divided by the average weight of blue crab consumed each month to generate an estimate of the mean number of individual blue crabs consumed per month by the average red drum in the New River estuary. A high level of blue crab consumption was calculated by substituting the maximum observed gut fullness value for the mean daily consumption rate, and a low level was also calculated by using the lowest estimated consumption rate for all diel trips.

RESULTS

Field sampling

A total of 55 field sampling days, occurring between May 2007 and February 2009, resulted in the capture of 880 juvenile red drum ranging in size from 113mm to 731mm total length (TL). Over the course of the study individuals from the 2005, 2006, and 2007 cohorts were collected, and included 591 age-0, and 289 age-1 fish. Both age classes of fish displayed prominent periods of rapid growth during May through October, followed by periods of reduced or ceased growth between November and April (Figure 4). The average age-0 fish measured 135mm TL in May, and reached 389mm TL by October. The average age-1 fish measured 448mm TL in May, and reached 600mm TL by October. Growth rates for this period in the ontogeny of age-0 and age-1 fish were calculated to be 4.50 and 9.02 g/d, respectively (Figure 5). Average daily water temperatures reached and remained at the seasonal high between May and October, ranging between 25 - 32 °C, and then dropped to the seasonal low range of 7 - 12 °C between December and February (Figure 6). All red drum were captured in salinities between 1.7 - 35 ppt, however the majority of fish were collected in moderate salinities between 10 - 25 ppt (Figure 7).

Diet analysis of age-0 red drum

Age-0 red drum preyed on at least 29 different species, consuming 14 types of fish and 15 types of invertebrates (Table 1). Penaeid shrimp (30.6 %) dominated the diet by percent weight, followed by Atlantic menhaden (27.5%), then blue crab (9.6%) (Table 1). Other frequently consumed fish species included Atlantic croaker, spot, mullet, pinfish, spotfin mojarra, and snake eels (Table 1). The other invertebrate taxa represented in the diet of age-0 red drum included polychaete worms, snails, clams, insects, isopods, grass shrimp, marsh crabs, fiddler crabs, and mud crabs (Table 1). Plant material (20.4% FO) as well as inert objects such as rope, gravel and fishing lures were also encountered in the stomach contents of this age class (Table 1).

Age-0 red drum demonstrated both seasonal and inter-annual variability in the utilization of major prey groups in their diets. The major prey groups were partitioned as blue crab, penaeid shrimp, Atlantic menhaden, other bony fish (all other fish not including menhaden), other decapods (all other decapods not including blue crabs and penaeid shrimp), and other (remainder of invertebrate or inert prey). In 2007 the majority of the diet by weight consisted of penaeid shrimp (45%), though in 2008 penaeids only represented 13.1% (Figure 8). The proportion of Atlantic menhaden in the diet was 3.27% by weight in 2007, but increased to 56.7% in 2008 (Figure 8). The contribution of blue crabs to the diet by weight remained relatively consistent between the two years, decreasing from 11.1% (19.5 % FO) in 2007 to 7.7% (6.5% FO) in 2008 (Figure 8).

Examination of seasonal patterns in age-0 diets illustrated a shift from crustaceans comprising roughly 50% by weight during May to October, but decreasing to only about

25% during November to January when bony fish became dominant (72.8%) (Figure 9). Atlantic menhaden constituted the majority of all fish species preyed upon from May until October, however from November until January they declined to less than 5% of all fish prey (Figure 9). Predation on blue crab by this age class also displayed some seasonality, with blue crabs composing 8.8% (9.0% FO) of the diet by weight from May to July, increasing to 15.0% (18.6% FO) from August to October, and then nearly disappearing from the diet from November to January (0.5% W) (5.9% FO) (Figure 9).

Diet analysis of age-1 red drum

Age-1 red drum preyed on at least 20 different species, consuming 11 types of fish and 9 types of invertebrates (Table 2). Blue crab (35.1 %), dominated the diet by percent weight, followed by Atlantic menhaden (15.4%), then pinfish (10.1%) (Table 2). Other frequently consumed fish species included Atlantic croaker, spot, mullet, snake eels, and flounder (Table 2). The other invertebrate taxa represented in the diet of age-1 red drum included penaeid shrimp, clams, insects, isopods, grass shrimp, fiddler crabs, and mud crabs (Table 2). Plant material (18.2% FO) as well as inert objects such as metal, gravel and fishing lures was also encountered in the stomach contents of this age class (Table 2).

Seasonal and inter-annual variability also existed in the inclusion of major prey groups in age-1 red drum diets. The major prey groups were partitioned as blue crab, penaeid shrimp, Atlantic menhaden, other bony fish (all other fish not including menhaden), other decapods (all other decapods not including blue crabs and penaeid shrimp), and other

(remainder of invertebrate or inert prey). In 2007 84.1% of the diet by weight consisted of fish (32% menhaden, 52% other), however, in 2008 fish only represented 47.1%, primarily due to a decrease in the proportion of menhaden down to 4.6% (Figure 10). The amount of penaeid shrimp in the diet of age-1 fish was low, but increased from 0.4% by weight in 2007 to 1.7% in 2008 (Figure 10). The contribution of blue crabs to the diet by weight varied between the two years, jumping from 12.0% (28.9% FO) in 2007 to 45.5% (36.4% FO) in 2008 (Figure 10). Seasonal patterns in age-1 red drum diets showed a shift from crustaceans comprising over 50% by weight during February to July, but decreasing to around 19% during August to October and to near 8% in November through January (Figure 11). Atlantic menhaden were absent from the diet from February to April, then increased to 5.0% by weight in May through July, increased again to 21.9% in August through October. However, from November until January they declined to 1.8% by weight of the diet when other species of bony fish made up the majority of prey (83.8%) (Figure 11). Predation on blue crab by this age class also demonstrated a high degree of seasonality, with blue crabs composing 31.1% (22.8% FO) of the diet by weight from February to April, increasing to 60.5% (42.5% FO) from May to July, decreasing to 18.2% (19.5% FO) from August to October, and then dropping to 4.9% (11.1% FO) from November to January (Figure 11).

Estimating daily ration of age-0 red drum

Age-0 fish were captured during each of the 12 diel sampling trips, and generally showed similar mean gut fullness patterns through time (Figure 12). Peak mean gut

fullness values, representing periods of heavy feeding, typically occurred during the hours after dark, followed by declining gut fullness values during the overnight and into the daylight hours. This pattern of declining gut fullness values was strongly demonstrated during the July 2008 sampling period (Figure 12). Strong patterns of declining gut fullness during six of the twelve sampling periods [July 2007 (Figure 13), August 2007 (Figure 14), October 2007 (Figure 15), November 2007 (Figure 16), July 2008 (Figure 17), and August 2008 (Figure 18)] allowed multiple separate field estimates of gastric evacuation and daily consumption rate to be generated for age-0 fish. Estimates of gastric evacuation rates were relatively similar across these time periods, ranging from 0.112 to 0.228, with a mean of 0.142 (Table 3). Mean daily gut fullness values calculated for all 12 sampling periods were more variable, ranging from 0.9 - 3.2% predator mass·day⁻¹, with a mean value of 1.6% predator mass·day⁻¹, with a maximum gut fullness value observed for an age-0 fish of 9.3% predator mass·day⁻¹ (Table 3). The resulting estimates of daily ration ranged from 3.0 - 5.7% predator mass·day⁻¹, with a mean value of 4.3% predator mass·day⁻¹ (Table 3).

Estimating daily ration of age-1 red drum

Age-1 fish were captured at relatively low abundance during only 9 of the diel sampling trips, and generally showed variable gut fullness patterns (Figure 19). Only in May 2008 was there a declining pattern in gut fullness, and a sufficient sample size to allow for the estimation of gastric evacuation and daily ration (Figure 20). The estimate of gastric evacuation rate for May 2008 was 0.134 (Table 4). Mean daily gut fullness

values for all 9 months were low, ranging from 0.1% to 1.8% predator mass·day⁻¹, with a mean value of 0.5% predator mass·day⁻¹. The maximum gut fullness value observed for an age-1 fish was 4.8% predator mass·day⁻¹ (Table 4). The resulting estimate of daily ration for age-1 fish in May was 1.6% predator mass·day⁻¹ (Table 4).

Quantifying red drum predation on blue crabs

Age-0 red drum were found to prey on blue crabs ranging between 10 and 41mm carapace width, with the average size crab consumed by this age class measuring 23.5mm carapace width (Figure 21). Age-1 red drum were found to prey on a larger size range of blue crabs, from 8 to 124mm in carapace width (CW), with the average size individual consumed measuring 40.3mm CW (Figure 21). The mean carapace width of blue crabs consumed by both age classes of drum increased through time, from 18.5mm in June to 33.1mm by October for age-0 fish, and from 23.5mm in May to 62.8mm in October for age-1 fish (Table 5).

Using a mean daily ration of 4.3% for age-0 fish, the number of individual blue crabs consumed by the average age-0 drum during the period of rapid growth between May and October was 294 (Figure 22; Table 5). Monthly ration of blue crab by weight (g) for age-0 fish increased each month to a high in October, however peak monthly consumption of individual blue crabs occurred in August (124) (Table 5). A high estimate of blue crab consumption for this age class was calculated using the maximum observed gut fullness value of 9.3% as the daily ration (yielding a total estimate of 637

individual crabs consumed) as well as a low estimate using the lowest calculated daily ration estimate of 3.0% (yielding a total estimate of 207 individual blue crabs consumed) (Figure 22; Table 5).

Using the single daily ration estimate of 1.6% calculated for age-1 fish, the number of individual blue crabs consumed by the average age-1 drum during the period of rapid growth from May to October was 98 (Figure 22; Table 6). Monthly ration of blue crab by weight (g) for age-1 fish increased each month from May to a peak in July, then dropped to a low in August (Table 6). Peak monthly consumption of individual blue crabs occurred in July (27), and the minimum occurred in September (7) (Figure 22; Table 6). A high estimate of blue crab consumption for this age class was calculated using the maximum observed gut fullness value of 4.8% as the daily ration (yielding a total estimate of 314 individual crabs consumed), however since only one estimate of daily ration was calculated for this age class no low estimate was calculated (Figure 22; Table 6).

DISCUSSION

Blue crab occurrence in red drum diets

Examination of both age-0 and age-1 red drum diets revealed that blue crabs were indeed an important prey resource in the moderate salinity reaches of the New River estuary. Blue crab ranked third in percent index of relative importance for total age-0 diet, after Atlantic menhaden and penaeid shrimp, and ranked highest for the total diet of

age-1 fish. This pattern of higher blue crab use by age-1 fish was also reflected in their frequency of occurrence in the examined stomach contents (12% age-0, 29% age-1). The consistent importance of blue crabs, similar patterns in frequency of occurrence, and ontogenetic increases in the contribution to red drum diets have also been documented across numerous studies from the Gulf of Mexico reviewed by Guillory and Prejean (2001). Specifically, blue crabs were found to increase from occurring in 12% of the stomachs of red drum measuring 70 – 149mm SL (standard length) to 32% for fish measuring 150 – 179mm SL, with a mean %FO of approximately 15% for all fish between 40 – 179mm (representing age-0) (Bass and Avault 1975). The frequency of occurrence of blue crabs (63%) found in the stomachs of larger red drum (age-1 fish measuring 359 – 499mm SL) in the Gulf of Mexico was also found to be higher than that of smaller, younger fish (Overstreet and Heard 1978). This trend has also been previously observed along the US South Atlantic coast, with adult red drum showing a 3-fold increase in the proportion of portunid crabs in their diet relative to sub-adult fish (Wenner 1992).

Age-0 and age-1 red drum each demonstrated seasonal patterns in the proportion by weight and frequency of occurrence of blue crab in their diets. Blue crabs were prevalent in the diets of both age classes throughout much of the year, until becoming uncommon between November and January. The sharp decline during winter corresponds to a seasonal period of low abundance of juvenile blue crabs found within the New River estuary (Posey et al. 2005). Seasonal patterns in the percent weight of blue crab included in red drum diets have also been observed in the Gulf of Mexico, however in these studies the percent frequency of occurrence remained fairly consistent

seasonally (Scharf and Schlight 2000; Guillory and Prejean 2001). The pooled seasonal percent frequency of occurrence of blue crab in red drum diets showed relatively high variability (5.9% to 18.6%, age-0; 11.1% to 42.5%, age-1). This variability was also observed in the percent by weight of blue crabs in the diet. The magnitude of difference between peak and minimum seasonal percent weight of blue crabs consumed in the New River (30x age-0, 12.3x age-1), was much higher than the differences in maximum and minimum percent by weight as observed between seasons by Scharf and Schlight (2000) (2x), or Guillory and Prejean (2001) (2.3x) in the Gulf of Mexico. The greater seasonal variability in the proportion of blue crabs consumed by red drum observed in the New River during this study may be driven by differences in seasonal temperatures or latitudinal changes in the estuarine community structure along the western Atlantic (Engle and Summers 1999). Inter-annual variation in the percent contribution of blue crab to red drum diets was relatively low for both age classes across dietary indices. One notable exception was the nearly 4-fold increase in percent weight of blue crabs eaten by age-1 fish between 2007 and 2008. With little difference in percent number between the two years, this suggests a probable difference in the sizes of blue crabs consumed. In fact, the mean carapace width of blue crabs preyed on by age-1 fish in 2007 was 65.8 mm compared with 30.7 mm in 2008. This difference may be attributable to actual inter-annual variability in size distributions and abundance of juvenile blue crabs that existed within the New River (Posey et al. 2005). However, the number of age-1 red drum ($n = 52$) sampled in 2007 was much lower than the number sampled in 2008 ($n = 220$), possibly resulting in sample size related bias.

For all red drum sampled, the size range of blue crabs consumed was 8 – 124mm CW, which is consistent with the sizes of blue crabs eaten by red drum in Texas and Louisiana (Scharf and Schlight 2000; Gullory and Prejean 2001). The majority of recovered blue crabs were able to be measured directly. Additional blue crab carapace widths were reconstructed from recovered partial prey using a set of predictive equations. The vast majority of blue crabs eaten were between 15 and 80mm CW, with any larger individuals typically being recently molted or soft shell crabs. On several occasions, only the chelipeds of very large soft shell crabs were recovered, though the reconstructed lengths of these individuals were not included in the data analysis. The two age classes of red drum displayed overlap in the sizes of smaller crabs consumed, however age-0 red drum consumed smaller maximum sizes of blue crabs and did not prey on blue crabs >50mm CW. The trend of increasing maximum prey size consumed as predator body size increases, while continuing to include relatively small prey in the diet corresponded with previous predator-prey size relationships observed for these two species (Scharf and Schlight 2000). Despite the broad size range of crabs consumed by a red drum of any given length, the mean CW of crab preyed upon in the New River by red drum increased with predator size and through time each year. Given the strong effects both temperature and salinity can have on growth rates and the length of the intermolt period for blue crabs, the size at maturity for blue crabs can be highly variable (Guerin and Stickle 1997). At 25°C and 20 ppt (conditions prevalent in the middle reaches of the New River estuary from May – October), 50% maturity for female blue crabs should be attained at approximately 121 mm CW, with even greater sizes at maturity in less saline conditions (Fisher 1999). Considering the range of blue crab carapace widths preyed upon by red

drum in this study, age-0 and age-1 red drum primarily feed on immature blue crabs, with the occasional consumption of recently molted adult crabs. Current regulations place the recreational or commercial minimum carapace width at 127 mm for males, and 172 mm for females, for the harvest of blue crab in the state of North Carolina. This suggests there is no direct overlap in crab sizes experiencing predation from age-0 and age-1 red drum with those harvested by the fishery. However, through direct interaction with pre-recruit juveniles, red drum predation may still have the potential to impact blue crab recruitment and ultimately affect population dynamics and potential fishery yields.

Diel feeding patterns and in situ estimation of gastric evacuation

Red drum in this study displayed diel patterns in gut fullness indicating that the majority of feeding occurred in the hours after sunset. These patterns suggest that red drum foraging behavior is most likely initiated during the crepuscular period around sunset, resulting in peak gut fullness several hours after dark. Gut fullness typically declined throughout the day, suggesting that red drum had stopped, or at least reduced feeding during the daylight hours. Dresser and Kneib (2007) found that sub adult red drum in a Georgia salt marsh only showed movement associated with changes in habitat use and feeding only occurred during the daylight hours on flood tides. They suggested that red drum may have remained stationary during the night to avoid predation. The study site was located in a channelized tidal salt marsh subject to 2.1m tidal ranges, which significantly altered the habitat type available to the fish during each tidal cycle. In the New River, tidal variation is often erratic due to prevailing winds, and habitat type

is relatively homogenous regardless of tidal stage. The patterns of almost exclusive crepuscular or nocturnal activity observed in the New River as opposed to the nearly exclusive diurnal activity of red drum observed by Dresser and Kneib (2007) perhaps implies differential predation pressure in these two systems. Both crepuscular and nocturnal feeding patterns have been documented previously in red drum (Bass and Avault 1975; Minello and Zimmerman 1983; Guillory and Prejean 2001). During a caging study to examine predation on brown shrimp, Minello and Zimmerman (1983) observed red drum to display peak feeding during the crepuscular periods, with intermittent feeding throughout the rest of the diel period. In our study, the nearly exclusive nocturnal activity of red drum made their capture during the daylight hours a challenge. Virtually no red drum were captured during the daylight hours using passive techniques, reflecting their lack of movement and feeding during this time (Hayward et al. 1989). Even with the use of active gear, the inability to collect large sample sizes of fish evenly spread through the entire 24 hr period made it difficult to assess diel patterns thoroughly.

In situ methods for determining fish daily ration were employed as an alternative to labor and cost intensive laboratory experiments, and also to better reflect natural conditions (Boisclair and Leggett 1988; Hayward et al. 1991). Initial efforts involved regular collections of reliably abundant smaller red drum at fixed time intervals, resulting in a single linear plot of mean gut fullness values over time (Boisclair and Leggett 1988; Hayward et al. 1991). However, obtaining adequate sample sizes (especially for age-1 fish) from a single collection event was often not possible. To compensate, continuous collections of red drum were made over the entire 24-hour period. Using this approach,

gut fullness information could be analyzed on a finer temporal scale, or pooled to homogenize individual fish variation and more clearly illustrate diel patterns. In contrast to previously published field estimates of gastric evacuation, we fit the gastric evacuation rate function to the mean of multiple gut fullness values per gear haul over time (e.g., Boisclair and Leggett 1988; Hayward et al. 1991; Héroux and Magnan 1996; Tuomikoski et al. 2008). Due to variability in catch rates among time intervals, sample sizes (number of individual fish) varied among each mean. To reduce the potential for a single fish with an extreme gut fullness value (low or high) to have excessive influence on estimates of gastric evacuation, each mean was weighted based on the number of fish used to calculate it prior to fitting the exponential decay function. This approach generated consistent estimates of gastric evacuation rate and allowed individual net sets to be appropriately treated as replicates.

Consistent instantaneous rates of gastric evacuation ranging from 0.11 to 0.15 were estimated when water temperatures were between 22°C and 30°C, while the fastest instantaneous rate of 0.23 was observed at a water temperature of 13°C. For several fish species, gastric evacuation rates obtained during laboratory experiments show a strong positive relationship with temperature (Parrish and Margraf 1990; Buckel and Conover 1996; Wuenschel and Werner 2004). In contrast, our observations predicted the highest gastric evacuation rate at the coldest temperature. However, this should be interpreted cautiously since it represents only a single point estimate and not a trend. Typically, gastric evacuation experiments are undertaken in a controlled laboratory setting to assess the effects of a single variable, and avoid confounding factors such as differences in predator size and meal composition (Bromley 1994). Although rates of gastric

evacuation were mostly similar through time, differences in mean gut fullness across the entire diel period affected daily ration estimates.

The field collection techniques employed to both capture red drum and retrieve their gut contents can produce additional variation in gut fullness values and resulting estimates of gastric evacuation rates. Strike setting using a monofilament trammel net offered a minimal amount of bias for estimates of catch per unit effort. Actively fishing the net reduced the duration of time during which the fish were entangled and potentially stressed. Although total gear deployment time was typically short (< 40 minutes), large catches of target and non target species sometimes extended the total set and retrieval time to several hours. Fish in the net or being held in the live well on the boat were no longer able to feed, and continued to digest the food in their stomachs for an extended period of time. Estimates of gut fullness for some fish may therefore be biased low. Conversely, when fish are experiencing stress, such as during capture and holding, the digestive process can be stopped or slowed (Bromley 1994). To account for the unavoidable variation in net set duration, each fish was assigned a time value corresponding to the midpoint of the total gear deployment time. Regurgitation of stomach contents by fish captured in gillnets has also been observed, with regurgitation rates being shown to depend on the entanglement method (Sutton et al. 2004). For striped bass, Sutton et al. (2004) found the lowest rates of regurgitation when fish were gilled (2%) or simply entangled (5%), and the highest rates for fish with the midsection of their bodies wedged into the mesh (17%). Due to the design and mesh sizes of the trammel net employed for this study, the majority of age-0 fish captured were gilled, while the majority of age-1 fish were entangled. Thus, potential rates of regurgitation

during active sampling were likely minimized. Gastric lavage techniques have been employed to retrieve gut contents for numerous species of fish, and generally have proven effective (Light et al. 1983). We initially sacrificed a small subset of fish to confirm the complete removal of gut contents and found that gastric lavage worked well for sub-adult red drum. The potential does exist for gastric lavage to be ineffective in the removal of large prey items from predator stomachs (Hartleb and Moring 1995). We found it possible to palpate the ventral surface of captured red drum and detect the presence of prey, particularly large items, and thus felt confident in our ability to completely empty red drum stomachs. If the initial attempt to flush the contents of the stomach resulted in no prey items recovered, yet prey items were able to be felt through the body wall of the fish, a repeated attempt at lavage usually yielded stomach contents. Gastric lavage could have led to a systematic bias in the estimation of evacuation rates and daily ration. As soft bodied prey items reached states of higher digestion, the flushing action of gastric lavage would often result in prey items such as menhaden being rinsed from the gut in mostly liquid form and thus, underestimated. This could generate lower estimates of gut fullness and potentially faster estimates of the decline in gut fullness than if the fish had been sacrificed and the well digested prey retained and weighed. Higher estimates of gastric evacuation rate would lead to an overall higher consumption rate, however, the loss of highly digested liquified prey would also lead to a lower estimate of mean gut fullness over the diel period, which would tend to lower consumption rate estimates. The two different biases may in fact counteract each other resulting in no net change in the estimate of consumption rate.

Red drum consumption and growth rates

The results of this study are the first field estimates of daily ration made for juvenile red drum, and reflect the natural environmental conditions present in the New River estuary. Since red drum are frequently produced in aquaculture operations, there has been some investigation into feeding rates for commercial applications allowing for comparison. The mean rates of daily ration that we calculated for both age-0 and age-1 red drum during the period of rapid growth between May and October fall within the range of daily rations (2 – 6%) routinely offered to aquaculture red drum to maximize growth (Davis 1990; McGoogin and Gatlin 1999). The field estimates of daily ration generated here overlapped the range of daily rations observed for juvenile red drum reared in the laboratory and fed daily to satiation on commercial feeds (Tomasso and Kempton 2000), however our field estimates displayed a greater maximum and mean value. Daily rations would be expected to be higher under natural conditions, as prepared feed for aquaculture operations is generally designed to have the highest energy content possible to minimize the necessary ration amounts (Talbot 1993). Both the average estimate of daily ration, and the maximum gut fullness values we observed were higher for age-0 red drum compared with age-1 fish. Body size has been shown to be correlated with consumption rates in manipulative experiments, with larger fish generally demonstrating lower weight-specific daily rations (e.g., Buckel et al. 1995). Higher daily ration rates are required by smaller juvenile fishes to fuel higher weight-specific metabolic rates and higher relative growth rates (Davis 1990; Talbot 1993).

Our use of maximum gut fullness values observed as a proxy for maximum possible daily consumption rates, as well as the minimum daily rations that we estimated, allowed for a range of consumption rates to be estimated for each age class. The assumption was made that the most extreme value of gut fullness observed represented the physical upper limit of the stomach for meal size. Given the environmental conditions (e.g., temperature and prey availability) conducive to growth during summer months, it would not be unrealistic to assume that red drum in the New River may be capable of feeding at close to their maximum potential to achieve the rapid growth observed during this season. Fish are some of the most efficient organisms in their ability to convert prey to somatic growth, however the relationship between consumption and growth rate is typically asymptotic, reaching a point where increased consumption will no longer yield higher growth rates (Talbot 1993). Examining the gross growth efficiencies that would be required to achieve the somatic growth experienced by both age-0 and age-1 drum in the New River allows us to evaluate our range of daily ration estimates. For age 0-fish the required growth efficiencies to achieve the growth rates observed in the field would be 40% for our low daily ration estimate, 28% for the average daily ration, and 13% for the maximum daily ration. For age-1 fish the required growth efficiencies would be 34% for the average daily ration, and 11% for the maximum daily ration. In teleost fishes, the highest gross growth efficiencies typically occur when fish are in their larval stage, with mean values across taxa at 30% (Houde and Zastrow 1993). Juvenile bluefish, another rapidly growing estuarine fish species, were found to have gross growth efficiencies near 28%, with decreases to 20% as body size increased over 3 months during a series of mesocosm experiments (Buckel et al. 1995). Red drum raised

commercially have also shown declining growth efficiency with increasing fish size, to the point of becoming less profitable commercially at body sizes above 4.7 kg (Tucker et al. 1997). Given the required growth efficiencies, it is likely that estuarine red drum (especially age-1 fish) are feeding at daily rations that lie between the average and maximum rates that we calculated.

Our average rates of daily ration used to quantify red drum predation on blue crabs could be viewed as conservative. The type of field estimation completed in this study is prone to underestimate daily consumption rates due to the assumptions of the model. When estimates of gastric evacuation are made during periods of declining gut fullness, no feeding is assumed. Although red drum in the New river did demonstrate strong diel feeding patterns, feeding probably still occurs sporadically after the early evening peak that would cause us to underestimate the total daily ration. When Guillory and Prejean (2001) quantified predation on blue crabs in Louisiana to be between 679 and 710 blue crabs/red drum/year, they used an assumed feeding daily feeding rate of 2% body weight for all sizes of red drum captured over the entire year. They also used a fixed percent contribution of blue crab to the diet, and a single estimate of average blue crab size consumed. Given our observations, taking into account the variation in daily ration, prey sizes consumed, and seasonal contributions to the diet would be advisable to more fully quantify red drum predation.

Juvenile blue crab mortality and future work

Current blue management generally attributes variation in year class strength to adequate larval supply reaching nursery areas. Along the northern Gulf of Mexico coast, strong associations between the abundance of juvenile blue crabs and patterns of larval supply typically dissipate less than 2 weeks after the initial settlement event (Heck et al. 2001). The decline in juvenile blue crab abundances appear to be related to crab density, suggesting predation as a structuring force (Heck et al. 2001). Recently settled blue crabs are still quite small; even after 16 days post-settlement they are typically only 2.2 to 4.2 mm carapace width (Etherington and Eggleston 2000). This size range is below the size of the smallest individual we observed in the diets of both age classes of red drum, meaning it is unlikely that red drum represent a significant predator during the very early post-settlement period of blue crab. Smaller age-0 red drum (30 – 55 mm), maintained in artificial enclosures within the New River, have been shown to feed on the megalops of portunid crabs (16% FO) (Lanier and Scharf 2007), however this may have been an artifact of disproportionate crab settlement to the artificial enclosures. Cannibalism by larger blue crabs as a source of predation on recently settled blue crabs has been implicated to be the major factor in determining the loss rates for crabs between 4.1 and 6mm CW (Moksnes and Heck 2006). During spring and summer months in the New River estuary juvenile blue crabs between 13 – 24 mm CW are mostly found in salinities <15 ppt, with this lower salinity habitat proposed to serve as a refuge from predation from larger conspecifics (Posey et al. 2005). Age-0 drum in the New River during the spring and summer months were found to prey on blue crabs with a mean carapace width of 18.5 mm, however during this time period blue crabs were only found in 9% of all

stomachs containing prey, the lowest percentage of any non-winter period. Additionally, roughly 35% of all red drum sampled in the New River during our study were captured in salinities less than 15 ppt. Perhaps if our diet sampling efforts were focused on the lowest salinity reaches, the observed predation rates by red drum on recently settled juvenile blue crabs may have been greater. The relatively low observed predation rate and the lower importance of blue crab to the diet of age-0 red drum during the spring/early summer period would be consistent with the assertion that cannibalism is the major source of predation on this size range of juvenile crabs. In fact, cannibalism as a major source of blue crab mortality is a topic that has received much attention in the literature (e.g., Dittel et al. 1995; Hines and Ruiz 1995; Moksnes et al. 1997; Heck et al. 2001). Hines and Ruiz (1995) estimated that between 75 – 97% of the mortality of juvenile blue crabs between 30 and 70 mm CW in the shallow portions of the Chesapeake Bay could be attributed to cannibalism. Yet, we found this same size range of juvenile blue crabs to be the dominant prey item for age-1 red drum, with each individual fish consuming on average over one crab per day within a five month period in the New River estuary. Clearly our findings, along with numerous previous studies (reviewed in detail by Guillory and Elliot 2001), demonstrate the potential red drum have to create predation pressure on juvenile blue crabs, although without further investigation we are currently unable to determine the magnitude of this pressure.

We have demonstrated blue crabs to be an important component of red drum diets and quantified seasonal predation rates, however these are just the first steps required in assessing the proportion of blue crab mortality caused by red drum predation. Future research will require estimates of both predator and prey densities over time, allowing for

predation impact to be determined by comparing predation rates to total prey loss rates (Tuomikoski et al. 2008). Determination of this predator impact will allow our quantification of predation on blue crab to be viewed as biologically significant or not in the larger picture of the total natural mortality of blue crabs. Controlled laboratory based validation of our field estimates of daily ration, and the examination of the effects of variables such as temperature and prey type on gastric evacuation rates, will be necessary to use these rates as parameters in large ecosystem based multispecies simulation models. One fascinating aspect of this predator-prey interaction that could also be explored is the possibility for synergistic effects of red drum predation and cannibalism on juvenile blue crab mortality. Juvenile blue crabs were shown to have proportional mortality rates due to cannibalism that were inversely density dependent, with this type of predation response having the potential to lead to localized extinctions (Dittel et al. 1995). Could red drum predation, have an interactive effect with the inversely density dependent mortality juvenile blue crabs experience from cannibalism? Do red drum show density dependent predation rates on juvenile blue crabs, and do thresholds exist where predation outweighs or even reduces cannibalism? Answers to questions such as this will require a synthesis of our work with future research, with the goal of realizing a deeper knowledge of the natural mortality of blue crabs. Understanding the role which red drum play in altering blue crab populations will allow for the improved co-management of these species.

LITERATURE CITED

- Adams, D. H., and D. M. Tremain. 2000. Association of large juvenile red drum, *Sciaenops ocellatus*, with an estuarine creek on the Atlantic coast of Florida. *Environmental Biology of Fishes* 58(2):183-194.
- Adams, S. M. 1976. Feeding Ecology of Eelgrass Fish Communities. *Transactions of the American Fisheries Society* 105(4):514-519.
- Bass, R. J., and J. W. Avault. 1975. Food-habits, length-weight relationship, condition factor, and growth of juvenile red drum, *Sciaenops-ocellata*, in Louisiana. *Transactions of the American Fisheries Society* 104(1):35-45.
- Bisker, R., M. Gibbons, and M. Castagna. 1989. Predation by the oyster toadfish, *Opsanus tau* (Linnaeus), on blue crabs and *Mercenaria mercenaria* (Linnaeus, 1758). *Journal of Shellfish Research* 8:25-31.
- Blaber, S. J. M., D.P. Cyrus, J.-J. Albert, Chong Ving Ching, J.W. Day, M.E. Elliott, M.S. Fonseca, D.E. Hoss, J. Orensanz, I.C. Potter, and W. Silvert. 2000. Effects of fishing on the structure and functioning of estuarine and nearshore ecosystems. *ICES J. Mar. Sci.* 57(3):590-602.
- Boisclair, D., and W. C. Leggett. 1988. An insitu experimental evaluation of the Elliott and Persson and the Eggert models for estimating fish daily ration. *Canadian Journal of Fisheries and Aquatic Sciences* 45(1):138-145.
- Boothby, R. N., and J. W. Avault. 1971. Food habits, length-weight relationship, and condition factor of the red drum (*Sciaenops ocellata*) in Southeastern Louisiana. *Transactions of the American Fisheries Society* 100(2):290-295.
- Bromley, P. J. 1994. The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. *Reviews in Fish Biology and Fisheries* 4(1):36-66.
- Buckel, J. A., and D. O. Conover. 1996. Gastric evacuation rates of piscivorous young-of-the-year bluefish. *Transactions of the American Fisheries Society* 125(4):591-599.
- Buckel, J. A., N. D. Steinberg, and D. O. Conover. 1995. Effects of temperature, salinity, and fish size on growth and consumption of juvenile bluefish. *Journal of Fish Biology* 47(4):696-706.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading Trophic Interactions and Lake Productivity. *BioScience* 35(10):634-639.
- Connell, S. D. 1998. Effects of predators on growth, mortality and abundance of a juvenile reef-fish: evidence from manipulations of predator and prey abundance. *Marine Ecology Progress Series* 169:251-261.

- Connolly, S. R., and J. Roughgarden. 1999. Theory of marine communities: competition, predation, and recruitment-dependent interaction strength. *Ecological Monographs* 69(3):277-296.
- Cortes, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: Application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 54(3):726-738.
- Cortes, E., C. A. Manire, and R. E. Hueter. 1996. Diet, feeding habits, and diel feeding chronology of the bonnethead shark, *Sphyrna tiburo*, in southwest Florida. *Bulletin of Marine Science* 58(2):353-367.
- Davis, J.T. 1990. Red drum production of food fish. Sothern Regional Aquaculture Center publication number 32.
- Dittel, A.I, A.H. Hines, G.M. Ruiz, and K.K. Ruffin. 1995. Effects of shallow water refuge on behavior and density-dependent mortality of juvenile blue crabs in Chesapeake Bay. *Bull Mar. Sci.* 57:902-916.
- Dresser, B.K, and R.T. Kneib. 2007. Site fidelity and movement patterns of wild subadult red drum, *Sciaenops ocellatus* (Linnaeus), within a salt marsh-dominated estuarine landscape. *Fisheries Management and Ecology* 14:183-190
- Eggers, D. M. 1977. Factors in interpreting data obtained by diel sampling of fish stomachs. *Journal of the Fisheries Research Board of Canada* 34(2):290-294.
- Eggers, D. M. 1979. Some recent methods for estimating food-consumption by fish - reply. *Journal of the Fisheries Research Board of Canada* 36(8):1018-1019.
- Eggleston, D. B., L. L. Etherington, and W. E. Ellis. 1998. Organism response to habitat patchiness: species and habitat-dependent recruitment of decapod crustaceans. *Journal of Experimental Marine Biology and Ecology* 223(1):111-132.
- Elliott, J. M., and L. Persson. 1978. Estimation of daily rates of food-consumption for fish. *Journal of Animal Ecology* 47(3):977-991.
- Engle, V. D., and J. K. Summers. 1999. Latitudinal Gradients in Benthic Community Composition in Western Atlantic Estuaries. *Journal of Biogeography* 26(5):1007-1023.
- Etherington, L. L., and D. B. Eggleston. 2000. Large-scale blue crab recruitment: linking postlarval transport, post-settlement planktonic dispersal, and multiple nursery habitats. *Marine Ecology-Progress Series* 204:179-198.
- Fisher. M. R. 1999. Effect of temperature and salinity on size at maturity of female blue crabs. *Trans. Am. Fish. Soc.* 128(3):499-506.
- Granadeiro, J. P., and M. A. Silva. 2000. The use of otoliths and vertebrae in the identification and size-estimation of fish in predator-prey studies. Pages 383-393

- Grumbine, R. E. 1997. Reflections on "what is ecosystem management?". *Conservation Biology* 11(1):41-47.
- Guerin, J. L., and W. B. Stickle. 1997. A comparative study of two sympatric species within the genus *Callinectes*: osmoregulation, long-term acclimation to salinity and the effects of salinity on growth and moulting. *Journal of Experimental Marine Biology and Ecology* 218(2):165-186.
- Guillory, V., and M. Elliot. 1999. A review of blue crab predators. Pages 68-83 *in* Blue Crab Mortality Symposium. Gulf States Marine Fisheries Commission.
- Guillory, V., and P. Prejean. 1999. Red drum predation on blue crabs. Pages 93-104 *in* Blue Crab Mortality Symposium. Gulf States Marine Fisheries Commission.
- Hakala, J. P., and F. D. Johnson. 2004. Evaluation of a gastric lavage method for use on largemouth bass. *North American Journal of Fisheries Management* 24(4):1398-1403.
- Haley, N. 1998. A gastric lavage technique for characterizing diets of sturgeons. *North American Journal of Fisheries Management* 18(4):978-981.
- Hansen, M. J., D. Boisclair, S.B. Brandt, S.W. Hewett, J.F. Kitchell, M.C. Lucas, and J.J. Ney. 1993. Applications of bioenergetics models to fish ecology and management - where do we go from here. *Transactions of the American Fisheries Society* 122(5):1019-1030.
- Hartleb, C. F., and J. R. Moring. 1995. An improved gastric lavage device for removing stomach contents from live fish. *Fisheries Research* 24(3):261-265.
- Hartman, K. J., and F. J. Margraf. 1993. Evidence of predatory control of yellow perch, *Perca flavescens*, recruitment in Lake Erie, U.S.A. *Journal of Fish Biology* 43(1):109-119.
- Hayward, R.S., F.J. Margraf, C.T. Knight, and D.J. Glomski. 1989. Gear bias in field estimation of the amount of food consumed by fish. *Canadian Journal of Fisheries and Aquatic Sciences*. 46:874-876
- Hayward, R. S., F. J. Margraf, D. L. Parrish, and B. Vondracek. 1991. Low-cost field estimation of yellow perch daily ration. *Transactions of the American Fisheries Society* 120(5):589-604.
- He, E. Q., and W. A. Wurtsbaugh. 1993. An empirical-model of gastric evacuation rates for fish and an analysis of digestion in piscivorous brown trout. *Transactions of the American Fisheries Society* 122(5):717-730.
- Heck, K. L., L. D. Coen, and S. G. Morgan. 2001. Pre- and post-settlement factors as determinants of juvenile blue crab *Callinectes sapidus* abundance: results from the north-central Gulf of Mexico. *Marine Ecology-Progress Series* 222:163-176.

- Henry, L. T., and S. McKenna. 1998. Status and management of the blue crab fishery in North Carolina. *Journal of Shellfish Research* 17(2):465-468.
- Heroux, D., and P. Magnan. 1996. In situ determination of food daily ration in fish: Review and field evaluation. *Environmental Biology of Fishes* 46(1):61-74.
- Hewitt, D. A., D.M. Lambert, J.M. Hoenig, R.N. Lipcius, D.B. Bunnell, and T.S. Miller. 2007. Direct and indirect estimates of natural mortality for Chesapeake Bay blue crab. *Transactions of the American Fisheries Society* 136(4):1030-1040.
- 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.* 57:884-901.
- Houde, E.D. 1989. Subtleties and episodes in the early life of fishes. *Journal of Fish Biology* 35(sA):29-38.
- Houde, E.D., and C.E. Zastrow. 1993. Ecosystem – and taxon- specific dynamic and energetic properties of larval fish assemblages. *Bull. Mar. Sci.* 53(2):290-335.
- Hsueh, P.-W., J. B. McClintock, and T. S. Hopkins. 1992. Comparative study of the diets of the blue crabs *Callinectes similis* and *C. sapidus* from a mud-bottom habitat in Mobile Bay, Alabama. *Journal of Crustacean Biology* 12(4):615-619.
- Hyslop, E. J. 1980. Stomach contents analysis - a review of methods and their application. *Journal of Fish Biology* 17(4):411-429.
- Jensen, H., P. A. Amundsen, J. M. Elliott, T. Bohn, and P. E. Aspholm. 2006. Prey consumption rates and growth of piscivorous brown trout in a subarctic watercourse. *Journal of Fish Biology* 68(3):838-848.
- Knapp, F. T. 1950. Menhaden utilization in relation to the conservation of food and game fishes of the Texas gulf coast. *Transactions of the American Fisheries Society* 79(1):137-144.
- Lanier, J. M., and F. S. Scharf. 2007. Experimental investigation of spatial and temporal variation in estuarine growth of age-0 juvenile red drum (*Sciaenops ocellatus*). *Journal of Experimental Marine Biology and Ecology* 349:131-141.
- Larkin, P. A. 1996. Concepts and issues in marine ecosystem management. *Reviews in Fish Biology and Fisheries* 6(2):139-164.
- Latour, R. J., M. J. Brush, and C. F. Bonzek. 2003. Toward ecosystem-based fisheries management. *Fisheries* 28(9):10-22.
- Levin, P. S., and G. W. Stunz. 2005. Habitat triage for exploited fishes: Can we identify essential "essential fish habitat?". *Estuarine Coastal and Shelf Science* 64(1):70-78.

- Light, R. W., P. H. Adler, and D. E. Arnold. 1983. Evaluation of gastric lavage for stomach analyses. *North American Journal of Fisheries Management* 3(1):81-85.
- Llansó, R. J., S. S. Bell, and F. E. Vose. 1998. Food habits of red drum and spotted seatrout in a restored mangrove impoundment. *Estuaries* 21(2):294-306.
- Macdonald, J. S., and R. H. Green. 1983. Redundancy of variables used to describe importance of prey species in fish diets. *Canadian Journal of Fisheries and Aquatic Sciences* 40(5):635-637.
- McGoogan, B. B., and D. M. Gatlin. 1999. Dietary manipulations affecting growth and nitrogenous waste production of red drum, *Sciaenops ocellatus* I. Effects of dietary protein and energy levels. *Aquaculture* 178(3-4):333-348.
- Menge, B. A. 1976. Organization of the New England rocky intertidal community: Role of predation, competition, and environmental heterogeneity. *Ecological Monographs* 46(4):355-393.
- Menge, B. A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. *Journal of Experimental Marine Biology and Ecology* 250:257-289.
- Minello, T.J., and R.J. Zimmerman. 1983. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: The effect of simulated *Spartina* structure on predation rates. *J. Exp. Mar. Biol. Ecol.* 72:211-231
- Mittelbach, G. G., and L. Persson. 1998. The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences* 55(6):1454-1465.
- Moksnes, P.O., R.N. Lipcius, L. Phil, and J. van Montfrans. 1997. Cannibal-prey dynamics in young juveniles and postlarvae of the blue crab. *Journal of Experimental Marine Biology and Ecology* 215:157-187.
- Moksnes, P. O., and K. L. Heck. 2006. Relative importance of habitat selection and predation for the distribution of blue crab megalopae and young juveniles. *Marine Ecology-Progress Series* 308:165-181.
- NCDMF. 2001. Red drum fishery management plan. North Carolina Division of Marine Fisheries, Morehead City, NC.
- NCDMF. 2004. Blue crab fishery management plan. North Carolina Division of Marine Fisheries, Morehead City, NC.
- Ney, J. J. 1993. Bioenergetics modeling today - growing pains on the cutting edge. *Transactions of the American Fisheries Society* 122(5):736-748.

- Orth, R. J., J. van Montfrans, and J. Fishman. 1999. Report to the Virginia Marine Resources Commission: A preliminary study of predation on blue crabs by three fish predators in a seagrass bed. Virginia Institute of Marine Science.
- Orth, R. J., and J. van Montfrans. 1987. Utilization of a seagrass meadow and tidal marsh creek by blue crabs *Callinectes-sapidus*: Seasonal and annual variations in abundance with emphasis on postsettlement juveniles. *Marine Ecology-Progress Series* 41(3):283-294.
- Overstreet, R. M., and R. W. Heard. 1978. Food of the Atlantic croaker *Micropogonias undulatus*, from Mississippi Sound and the Gulf of Mexico. *Gulf Res. Rep.* 6:145-152.
- Overstreet, R. M., and R. W. Heard. 1978. Food of the red drum, *Scianops ocellata*, from Mississippi Sound. *Gulf Res. Rep.* 6(2):131-135.
- Paine, R. T. 1969. A note on trophic complexity and community stability. *The American Naturalist* 103(929):91.
- Parrish, D. L., and J. Margraf. 1990. Gastric evacuation rates of white perch, *morone-americanana*, determined from laboratory and field data. *Environmental Biology of Fishes* 29(2):155-158.
- Persson, L. 1979. Effects of temperature and different food organisms on the rate of gastric evacuation in perch (*Perca-fluviatilis*). *Freshwater Biology* 9(2):99-104.
- Peters, K., and R. McMichael. 1987. Early life history of the red drum, *Sciaenops ocellatus* (Pisces: Sciaenidae), in Tampa Bay, Florida. *Estuaries and Coasts* 10(2):92-107.
- Posey, M. H., T. D. Alphin, H. Harwell, and B. Allen. 2005. Importance of low salinity areas for juvenile blue crabs, *Callinectes sapidus* Rathbun, in river-dominated estuaries of southeastern United States. *Journal of Experimental Marine Biology and Ecology* 319(1-2):81-100.
- Pullen, E. J., and W. L. Trent. 1970. Carapace width-total weight relation of blue crabs from Galveston Bay, Texas. *Transactions of the American Fisheries Society* 99(4):795-798.
- Rice, J. A., and P. A. Cochran. 1984. Independent evaluation of a bioenergetics model for largemouth bass. *Ecology* 65(3):732-739.
- Ross, J. L., T. M. Stevens, and D. S. Vaughan. 1995. Age, growth, mortality, and reproductive-biology of red drums in North-Carolina waters. *Transactions of the American Fisheries Society* 124(1):37-54.
- Ruiz, G. M., A. H. Hines, and M. H. Posey. 1993. Shallow-water as a refuge habitat for fish and crustaceans in nonvegetated estuaries - an example from Chesapeake Bay. *Marine Ecology-Progress Series* 99(1-2):1-16.

- Scharf, F. S., and K. K. Schlicht. 2000. Feeding habits of red drum (*Sciaenops ocellatus*) in Galveston Bay, Texas: Seasonal diet variation and predator-prey size relationships. *Estuaries* 23(1):128-139.
- Scharf, F. S., R. M. Yetter, A. P. Summers, and F. Juanes. 1998. Enhancing diet analyses of piscivorous fishes in the Northwest Atlantic through identification and reconstruction of original prey sizes from ingested remains. *Fishery Bulletin* 96(3):575-588.
- Scharf, F. S., J. A. Buckel, F. Juanes, and D. O. Conover. 1997. Estimating piscine prey size from partial remains: Testing for shifts in foraging mode by juvenile bluefish. *Environmental Biology of Fishes* 49(3):377-388.
- Sheaves, M. 2001. Are there really few piscivorous fishes in shallow estuarine habitats? *Marine Ecology-Progress Series* 222:279-290.
- Spier, H. 1999. A review of predation on blue crabs in Chesapeake Bay. Department of Natural Resources.
- Sutton, T. M., M. J. Cyterski, J. J. Ney, and M. C. Duval. 2004. Determination of factors influencing stomach content retention by striped bass captured using gillnets. *Journal of Fish Biology* 64(4):903-910.
- Takade, H. M., and L. M. Paramore. 2007. Stock status of the northern red drum stock. North Carolina Division of Marine Fisheries, Morehead City.
- Talbot, C. 1993. Some aspects of the biology of feeding and growth in fish. *Proceedings of the nutrition society*. 52:413-416
- Tang, Q. S. 1985. Modification 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. *Fisheries Research* 3(1):13-21.
- Thomas, J. L., R. J. Zimmerman, and T. J. Minello. 1990. Abundance patterns of juvenile blue crabs (*Callinectes-sapidus*) in nursery habitats of 2 Texas bays. *Bulletin of Marine Science* 46(1):115-125.
- Tomasso, J. R., and C. J. Kempton. 2001. Effects of temperature on production characteristics of red drum, *Scianops ocellatus*. *Journal of Applied Aquaculture* 10(2):73-79.
- Tuomikoski, J.E., P.J. Rudershausen, J.A. Buckel, and J.E. Hightower. 2008. Effects of age-1 striped bass predation on juvenile fish in western Albemarle Sound. *Trans. Am. Fish. Soc.* 137:324-339.
- Tucker, J. W., W. A. Lellis, G. K. Vermeer, D. E. Roberts, and P. N. Woodward. 1997. Growth of red drum, *Sciaenops ocellatus*, to maturity on experimental diets. *Journal of Applied Aquaculture* 7(4):93-108.

- Ulanowicz, R., J. Lindsay, W. Caplins, and T. Polgar. 1982. Simulating the lateral transport of ichthyoplankton in the Potomac estuary. *Estuaries and Coasts* 5(1):57-67.
- Walter, J. F., A. S. Overton, K. H. Ferry, and M. E. Mather. 2003. Atlantic coast feeding habits of striped bass: a synthesis supporting a coast-wide understanding of trophic biology. *Fisheries Management and Ecology* 10:349–360.
- Wenner, C. 1992. Red drum: Natural history and fishing techniques in South Carolina. South Carolina Department of Natural Resources, Charleston.
- Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84(5):1083-1100.
- Whipple, S. J. 2000. Models of predation and fishing mortality in aquatic ecosystems. *Fish and Fisheries* 1(1):22-40.
- Williams, A. B. 1974. Swimming Crabs of Genus *Callinectes* (Decapoda-Portunidae). *Fishery Bulletin* 72(3):685-798.
- Wuenschel, M. J., and R. G. Werner. 2004. Consumption and gut evacuation rate of laboratory-reared spotted seatrout (*Sciaenidae*) larvae and juveniles. *Journal of Fish Biology* 65(3):723-743.

Table 1. Dietary indices calculated for all stomach contents recovered from age 0 drum sampled between 2007 and 2009.

Prey type	% FO	% W	% N	% IRI
Total Invertebrates	60.714	42.826	36.161	30.215
Worm (Polychaeta)	0.42	0.08	0.17	< 0.01
Clam (Bivalvia)	1.05	0.02	0.51	0.02
Snail (Gastropoda)	0.21	< 0.01	0.09	< 0.01
Isopods (Isopoda)	1.47	0.06	0.60	0.02
Insects (Hexapoda)	0.84	< 0.01	0.34	0.01
Grass shrimp (<i>Palaemonetes</i> spp.)	2.52	0.40	3.51	0.37
Total Penaeid shrimp	29.20	30.65	19.28	21.77
Brown shrimp (<i>Farfantepenaeus aztecus</i>)	1.68	2.81	1.37	0.26
Pink shrimp (<i>Farfantepenaeus duorarum</i>)	0.84	0.13	0.34	0.02
White shrimp (<i>Litopenaeus setiferus</i>)	8.19	17.70	8.23	8.01
Unidentified Penaeidae	18.49	10.01	9.34	13.49
Marsh crab (<i>Sesarma</i> spp.)	0.42	0.01	0.17	0.00
Fiddler crab (<i>Uca</i> spp.)	1.26	0.08	0.51	0.03
White fingered mud crab (<i>Rhithropanopeus harrisi</i>)	0.63	0.10	0.60	0.02
Unidentified mud crab (Xanthidae)	0.84	0.07	0.34	0.01
Unidentified Decapoda	7.35	0.80	3.00	0.77
Total Portunid crab	14.50	10.55	7.03	7.18
Blue crab (<i>Callinectes sapidus</i>)	11.97	9.60	6.00	7.04
Lesser blue crab (<i>Callinectes similis</i>)	0.42	0.04	0.17	0.00
Unidentified Callinectes	2.10	0.91	0.86	0.14
Total Bony Fish	71.64	55.81	54.76	62.75
Atlantic silverside (<i>Menidia menida</i>)	0.63	0.02	0.34	0.01
Bay anchovy (<i>Anchoa mitchilli</i>)	1.26	0.56	2.14	0.13
Bighead searobin (<i>Prionotus tribulus</i>)	0.21	< 0.01	0.09	< 0.01
Blackcheek tongue fish (<i>Symphurus plagiosa</i>)	0.21	0.22	0.09	< 0.01
Croaker (<i>Micropogonias undulatus</i>)	0.42	2.00	0.17	0.03
Goby (<i>Gobiosoma</i> spp.)	0.42	0.01	0.17	< 0.01
Menhaden (<i>Brevortia tyrannus</i>)	24.58	27.35	27.51	50.83
Mullet, striped (<i>Mugil cephalus</i>)	1.47	2.40	0.77	0.18
Mullet, white (<i>Mugil curema</i>)	1.05	4.48	0.69	0.20
Mullet, unidentified (<i>Mugil</i> spp.)	3.99	3.38	2.23	0.84
Mummichog (<i>Fundulus heteroclitus</i>)	0.63	0.83	0.34	0.03
Pinfish (<i>Lagodon rhomboides</i>)	4.62	2.39	2.14	0.79
Shrimp eel (<i>Ophichthus gomesi</i>)	0.21	0.01	0.09	< 0.01
Snake eel, unidentified (Ophichthidae)	3.36	0.91	2.83	0.47
Speckled worm eel (<i>Myrophis punctatus</i>)	2.10	0.44	1.54	0.16
Spot (<i>Leiostomus xanthurus</i>)	4.41	2.33	1.89	0.70
Spotfin mojarra (<i>Eucinostomus argenteus</i>)	6.09	5.90	4.28	2.34
Unidentified Bony Fish	15.97	2.59	7.46	6.04
Total "Other"	22.27	1.35	9.08	7.01
Bone (non fish)	0.42	0.01	0.17	< 0.01
Fishing lure	0.84	0.52	0.34	0.03
Gravel	0.42	0.05	0.17	< 0.01
Nylon rope	0.21	< 0.01	0.09	< 0.01
Plant material	20.38	0.78	8.31	6.98

Table 2. Dietary indices calculated for all stomach contents recovered from age 1 drum sampled between 2007 and 2009.

Prey type	% FO	% W	% N	% IRI
Total Invertebrates	50.25	38.18	37.84	64.37
Clam (<i>Bivalvia</i>)	4.43	0.24	4.76	0.81
Isopods (<i>Isopoda</i>)	1.97	0.15	1.00	0.05
Insects (<i>Hexapoda</i>)	0.99	0.02	0.50	0.02
Grass shrimp (<i>Palaemonetes spp.</i>)	0.49	0.01	0.25	< 0.01
Total Penaeid shrimp	6.40	1.11	3.51	0.79
Brown shrimp (<i>Farfantepenaeus aztecus</i>)	0.99	0.31	0.50	0.03
Unidentified Penaeidae	5.42	0.79	3.01	0.76
Fiddler crab (<i>Uca spp.</i>)	0.99	0.07	0.50	0.02
Unidentified mud crab (<i>Xanthidae</i>)	0.99	0.03	0.50	0.02
Unidentified Decapoda	0.99	0.03	0.50	0.02
Total Portunid crab	33.00	36.53	26.32	62.64
Blue crab (<i>Callinectes sapidus</i>)	28.57	35.08	24.06	62.04
Unidentified Callinectes	4.43	1.46	2.26	0.60
Total Bony Fish	68.47	60.10	51.38	28.69
Bay anchovy (<i>Anchoa mitchilli</i>)	0.49	0.09	0.50	0.01
Blackcheek tongue fish (<i>Symphurus plagiosa</i>)	1.48	0.83	1.00	0.10
Croaker (<i>Micropogonias undulatus</i>)	5.42	7.76	3.01	2.14
Flounder, southern (<i>Paralichthys lethostigma</i>)	3.45	2.04	2.01	0.51
Flounder, summer (<i>Paralichthys dentatus</i>)	0.49	0.32	0.25	0.01
Flounder, unidentified (<i>Paralichthys spp.</i>)	0.99	1.87	0.50	0.09
Hogchoker (<i>Trinectes maculatus</i>)	0.49	0.17	0.25	0.01
Menhaden (<i>Brevoortia tyrannus</i>)	8.87	15.39	7.52	7.46
Mullet, white (<i>Mugil curema</i>)	2.46	6.95	2.51	0.85
Mullet, unidentified (<i>Mugil spp.</i>)	1.48	1.55	2.01	0.19
Pinfish (<i>Lagodon rhomboides</i>)	10.34	10.07	7.77	6.78
Shrimp eel (<i>Ophichthus gomesi</i>)	0.49	1.86	0.25	0.04
Snake eel, unidentified (<i>Ophichthidae</i>)	4.93	2.95	3.51	1.17
Speckled worm eel (<i>Myrophis punctatus</i>)	4.43	4.68	7.27	1.94
Spot (<i>Leiostomus xanthurus</i>)	7.39	1.89	4.76	1.80
Unidentified Bony Fish	15.27	1.70	8.27	5.59
Total "Other"	21.18	1.72	10.78	6.94
Fishing lure	1.48	0.55	0.75	0.07
Gravel	0.99	0.22	0.50	0.03
Metal	0.49	< 0.01	0.25	< 0.01
Plant material	18.23	0.96	9.27	6.85

Table 3. Results from diel sampling trips for age 0 fish. Highlighted numbers show where field estimates of gastric evacuation (G_e), and daily ration were made. Mean gut fullness is the grand mean of each plotted time point over the 24-hour period in grams of prey per gram of predator. Max gut fullness is the maximum gut fullness value observed in an individual fish that date. Daily ration is expressed in g prey per predator per day.

Date	Mean temp (°C)	Sample size	G_e	Mean gut fullness	Max gut fullness	Daily ration estimate
23- 24 Jul 2007	27.5	14	0.126	0.0118	0.0420	0.0356
25- 27 Aug 2007	30.6	23	0.121	0.0127	0.0331	0.0369
14- 16 Sep 2007	25.1	12	-	0.0172	0.0268	-
12- 14 Oct 2007	22.3	23	0.112	0.0211	0.0702	0.0567
16- 18 Nov 2007	12.6	63	0.228	0.0076	0.0466	0.0417
19- 21 May 2008	25.2	10	-	0.0272	0.0589	-
12- 14 Jun 2008	27.3	14	-	0.0318	0.0934	-
24- 26 Jul 2008	28.8	63	0.154	0.0159	0.0768	0.0586
28- 30 Aug 2008	27.4	61	0.115	0.0109	0.0572	0.0303
22- 23 Sep 2008	23.9	46	-	0.0127	0.0497	-
23- 24 Oct 2008	16.2	8	-	0.0095	0.0221	-
26- 27 Nov 2008	10.0	22	-	0.0109	0.0357	-

Table 4. Results from diel sampling trips for age 1 fish. Highlighted numbers show where field estimates of gastric evacuation (G_e), and daily ration were made. Mean gut fullness is the grand mean of each plotted time point over the 24-hour period in grams of prey per gram of predator. Max gut fullness is the maximum gut fullness value observed in an individual fish that date. Daily ration is expressed in g prey per predator per day.

Date	Mean temp (°C)	Sample size	G_e	Mean gut fullness	Max gut fullness	Daily ration estimate
23- 24 Jul 2007	27.5	2	-	0.0012	0.0024	-
25- 27 Aug 2007	30.6	8	-	0.0045	0.0151	-
14- 16 Sep 2007	25.1	7	-	0.0025	0.0095	-
12- 14 Oct 2007	22.3	2	-	0.0131	0.0259	-
16- 18 Nov 2007	12.6	0	-	-	-	-
19- 21 May 2008	25.2	19	-	0.0048	0.0130	-
12- 14 Jun 2008	27.3	18	0.136	0.0183	0.0481	0.0157
24- 26 Jul 2008	28.8	8	-	0.0025	0.0090	-
28- 30 Aug 2008	27.4	3	-	0.0005	0.0017	-
22- 23 Sep 2008	23.9	6	-	0.0024	0.0029	-
23- 24 Oct 2008	16.2	0	-	-	-	-
26- 27 Nov 2008	10.0	0	-	-	-	-

Table 5. Results from quantifying monthly individual age 0 red drum predation on blue crabs. Highlighted rows show mean, low, and high estimates of individual blue crabs consumed monthly by an average age 0 red drum within the new river.

	May	Jun	Jul	Aug	Sep	Oct
Mean red drum weight (g)	26.0	67.4	172.2	204.1	495.2	651.0
Mean blue crab CW (mm)	0	19	19	19	33	33
Mean blue crab weight (g)	0.0	0.3	0.3	0.3	2.7	2.7
Blue crab in diet (% W)	0	8.8	8.8	15	15	15
Mean consumption rate (%)	4.3	4.3	4.3	4.3	4.3	4.3
Mean daily ration (g)	1.1	2.9	7.4	8.8	21.3	28.0
Mean monthly ration of blue crab (g)	0.0	7.7	20.2	40.8	95.8	130.2
Mean estimate # blue crabs consumed	0	23	61	124	36	49
Low consumption rate (g/g)	3.0	3.0	3.0	3.0	3.0	3.0
Low daily ration (g)	0.8	2.0	5.2	6.2	15.0	19.7
Low monthly ration of blue crab (g)	2.1	5.4	14.2	28.8	67.5	91.7
Low estimate # blue crabs consumed	0	16	43	87	25	34
High consumption rate (g/g)	9.3	9.3	9.3	9.3	9.3	9.3
High daily ration (g)	2.4	6.3	16.1	19.1	46.3	60.8
High monthly ration of blue crab (g)	6.6	16.6	43.9	88.6	208.1	282.7
High estimate # blue crabs consumed	0	51	133	270	78	106

Table 6. Results from quantifying monthly individual age 1 red drum predation on blue crabs. Highlighted rows show mean and high estimates of individual blue crabs consumed monthly by an average age 1 red drum within the new river.

	May	Jun	Jul	Aug	Sep	Oct
Mean red drum weight (g)	918.2	1074.2	1230.6	2043.4	2304.6	2583.7
Mean blue crab CW (mm)	23	51	51	51	63	63
Mean blue crab weight (g)	12.9	12.9	12.9	12.9	26.7	26.7
Blue crab in diet (% W)	60.5	60.5	60.5	18.2	18.2	18.2
Mean consumption rate (%)	1.5	1.5	1.5	1.5	1.5	1.5
Mean daily ration (g)	13.8	16.1	18.5	30.7	34.6	38.8
Mean monthly ration of blue crab (g)	258.3	292.5	346.2	172.9	188.8	218.7
Mean estimate # blue crabs consumed	20	23	27	13	7	8
High consumption rate (g/g)	4.8	4.8	4.8	4.8	4.8	4.8
High daily ration (g)	44.1	51.6	59.1	98.1	110.6	124.0
High monthly ration of blue crab (g)	826.6	935.9	1107.8	553.4	604.0	699.7
High estimate # blue crabs consumed	64.1	72.6	85.9	42.9	22.6	26.2

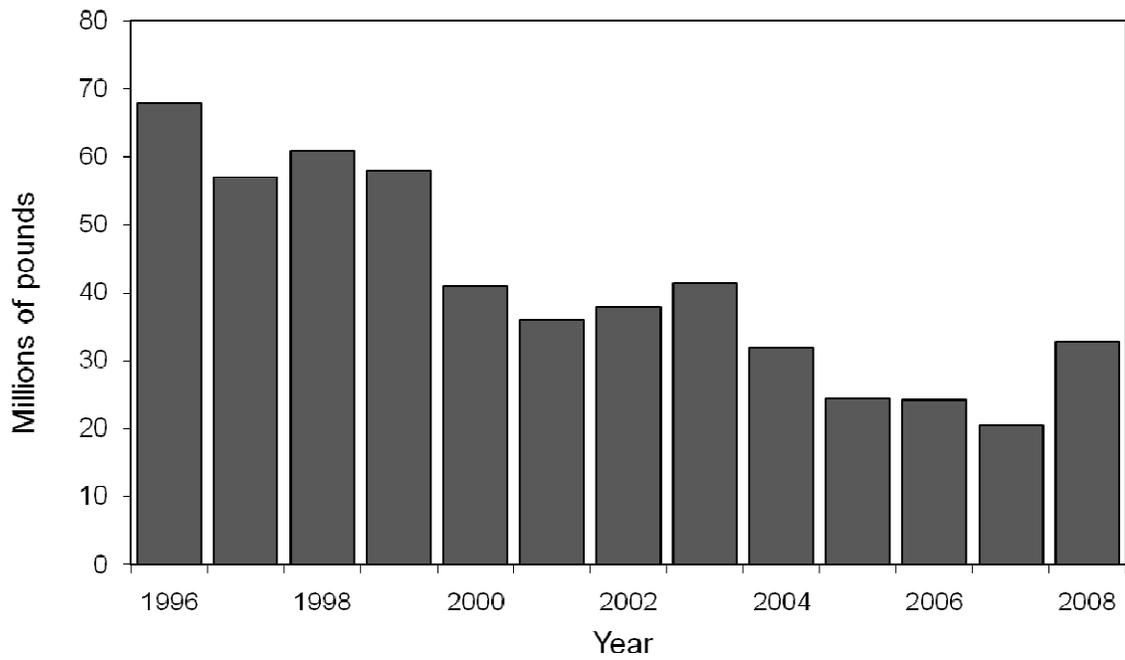


Figure 1. North Carolina Division of Marine Fisheries (NCDMF) blue crab commercial landings data, showing a downward trend until reaching a ten-year low in 2007.

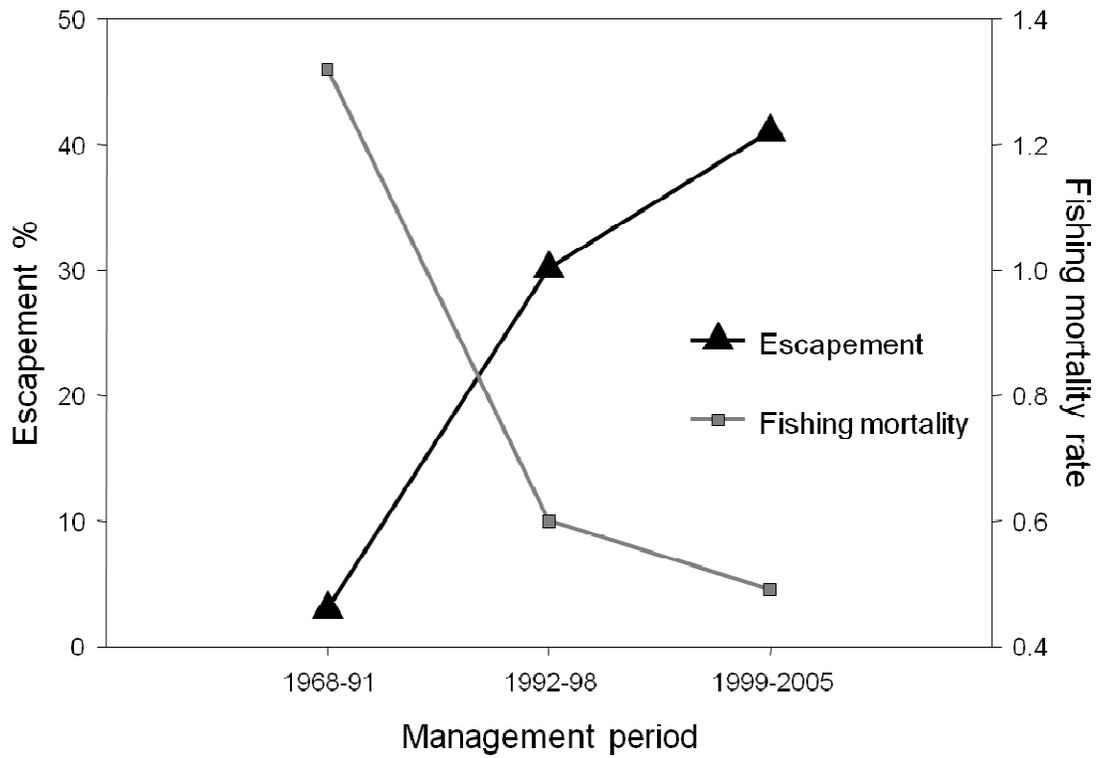


Figure 2. Escapement and fishing mortality as a function of management period for red drum in North Carolina (data reproduced from NCDMF red drum fishery management plan), showing an increase in the amount of fish able to recruit to the adult population and a decline in fishing mortality as a result of conservation measures.

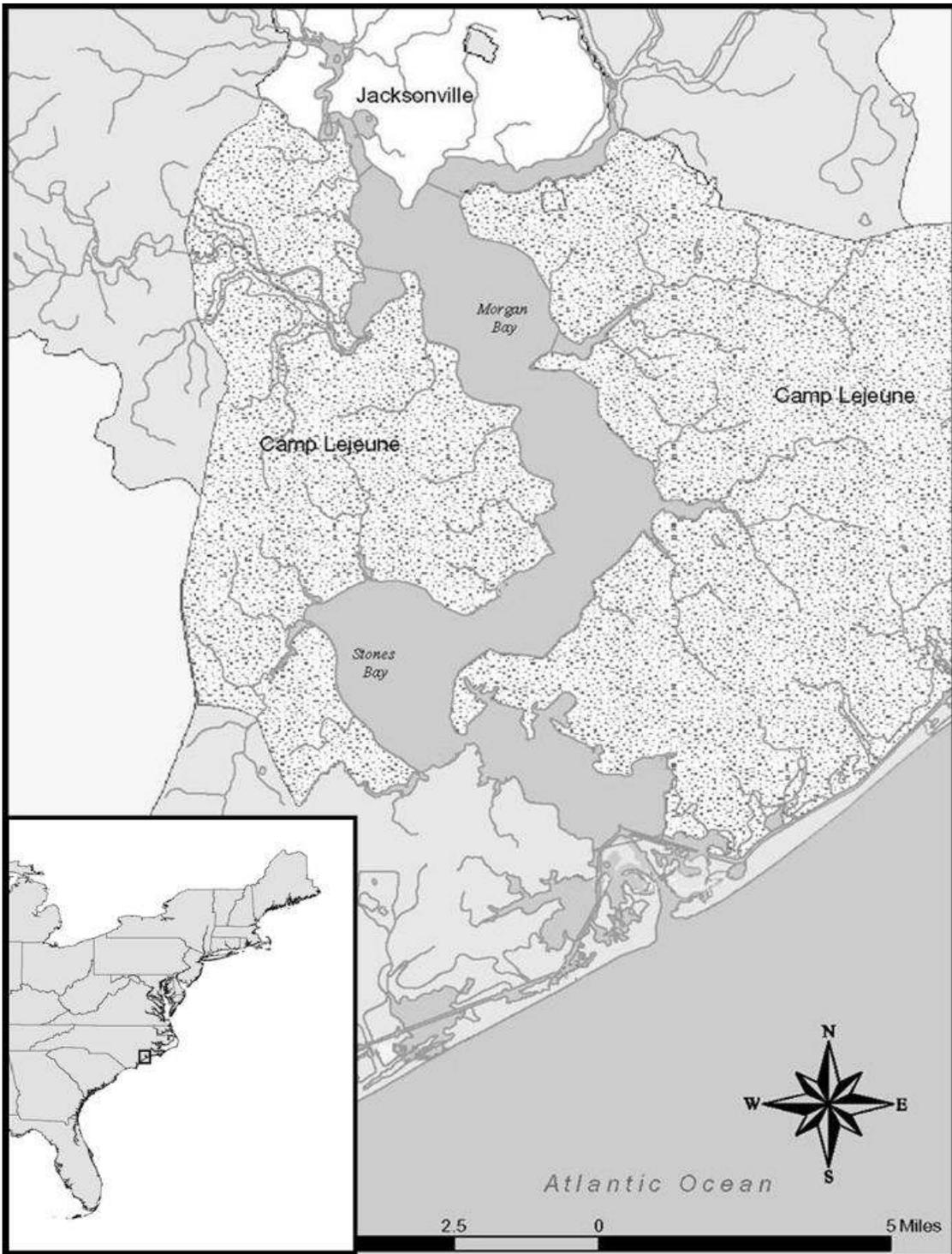


Figure 3. A map of the New River estuary located in Onslow county, NC. Field sampling was mainly conducted between the City of Jacksonville and Stones Bay.

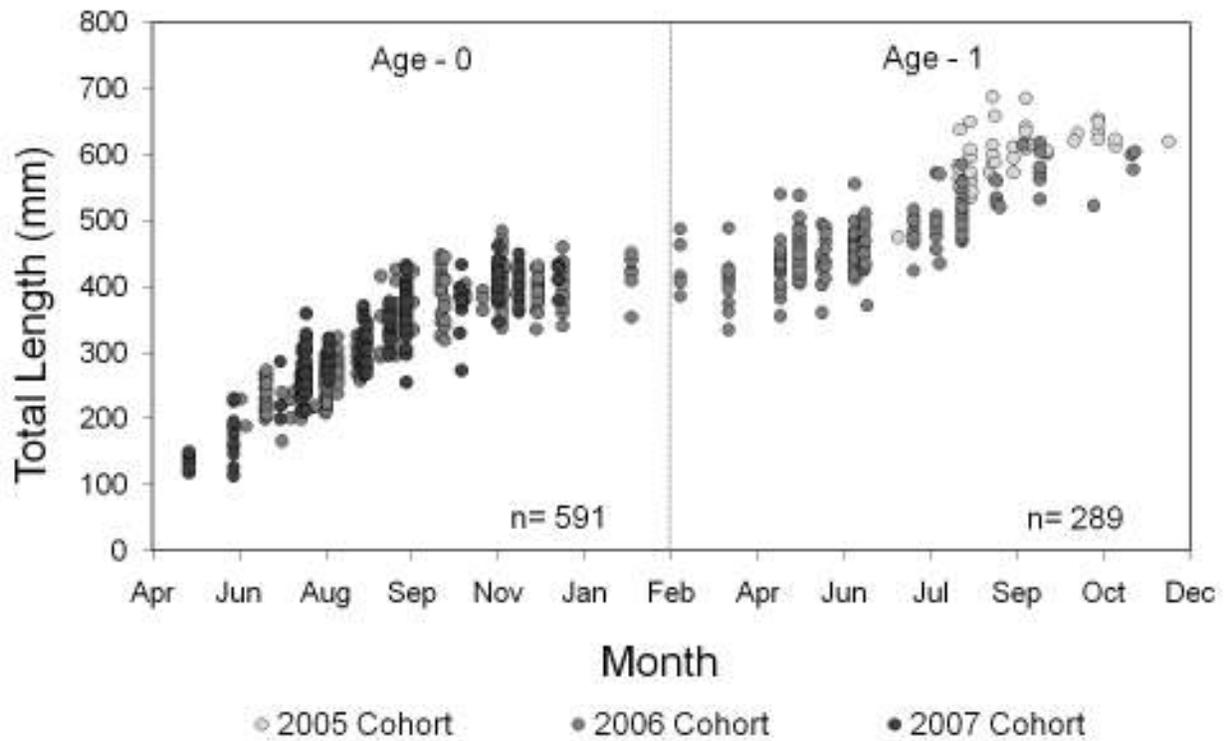


Figure 4. Total length vs. date of capture for 3 cohorts of juvenile red drum representing age-0 and age-1 fish. A period of rapid growth can be seen for both age classes (May – October), separated by a period of reduced or no growth (November – April).

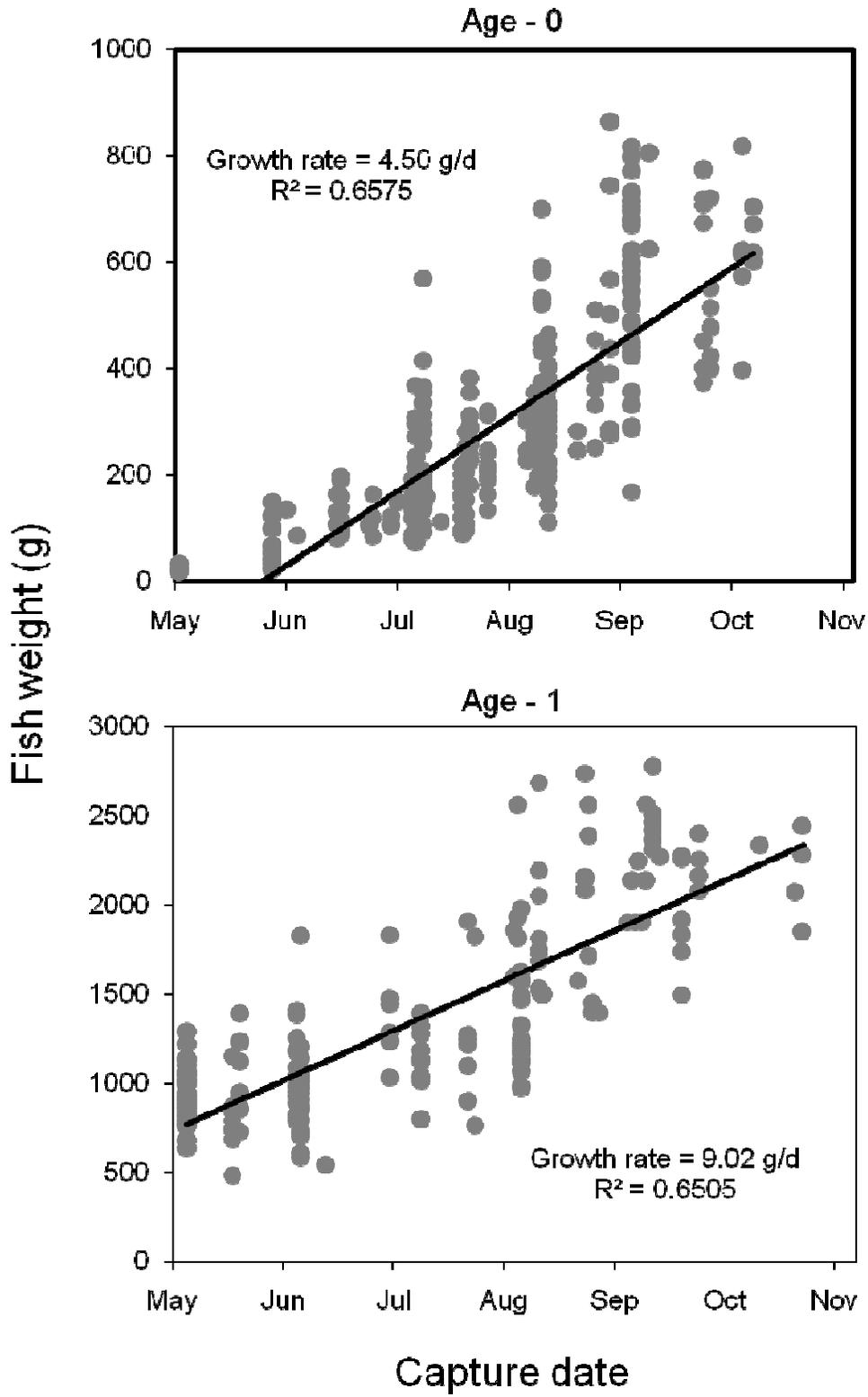


Figure 5. Growth rates for both age-0 and age-1 red drum during the period of rapid growth between May and October.

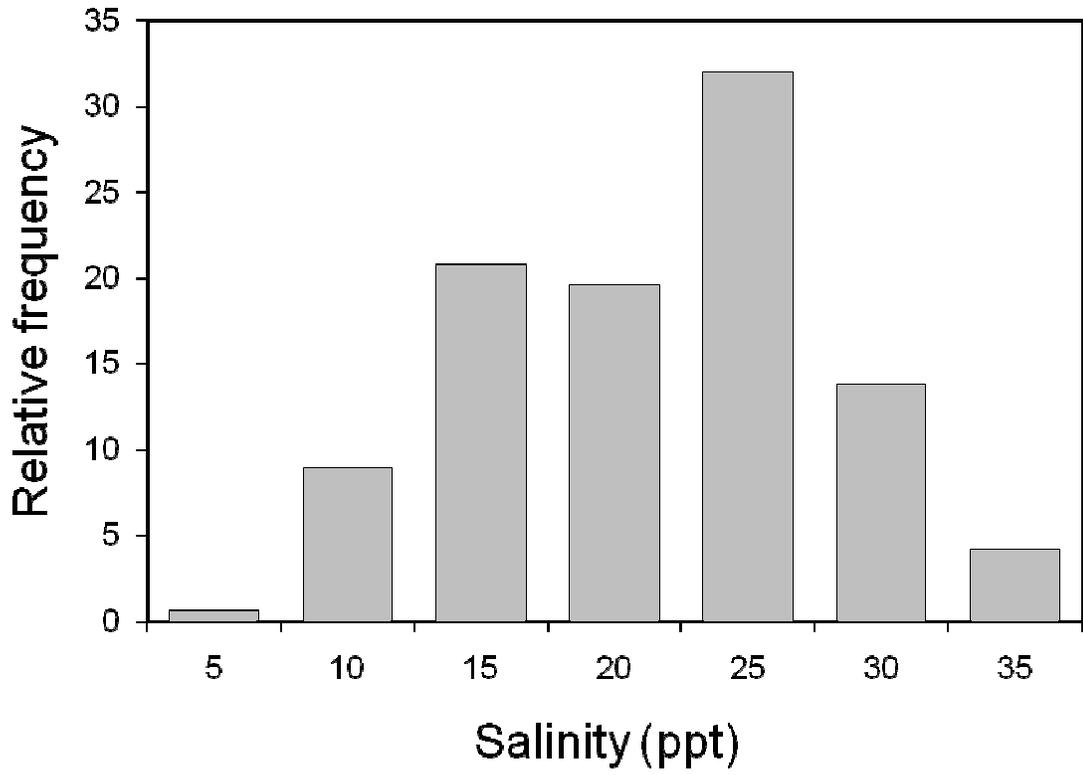


Figure 7. Distribution of the total catch of red drum between 2007 and 2009 across the salinity (ppt) gradient in the New River estuary.

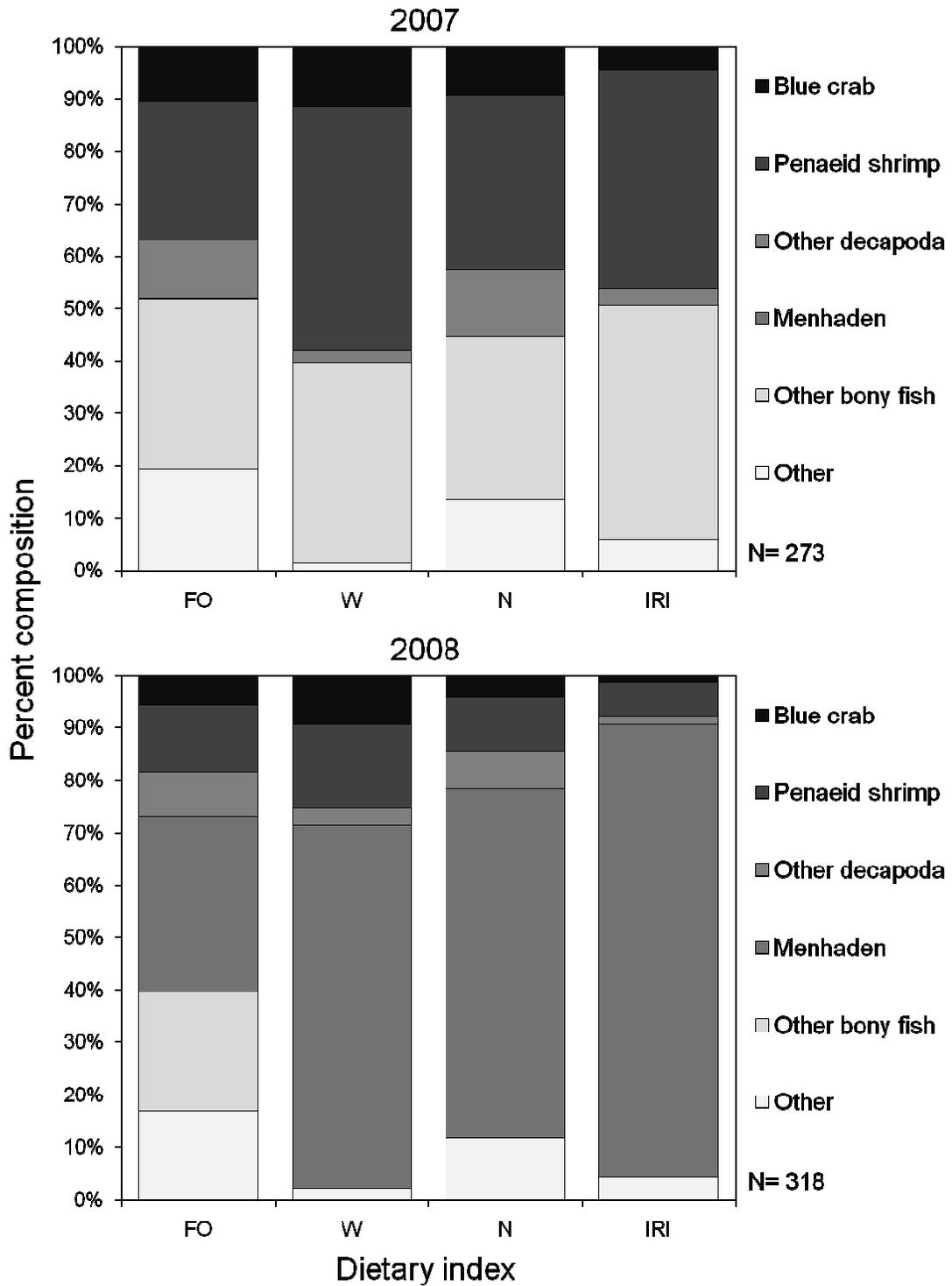


Figure 8. Percent frequency of occurrence (normalized to 100%) (FO), percent weight (W), percent number (N), and the index of relative importance (IRI) for age-0 red drum captured in 2007 (top panel) and 2008 (bottom panel).

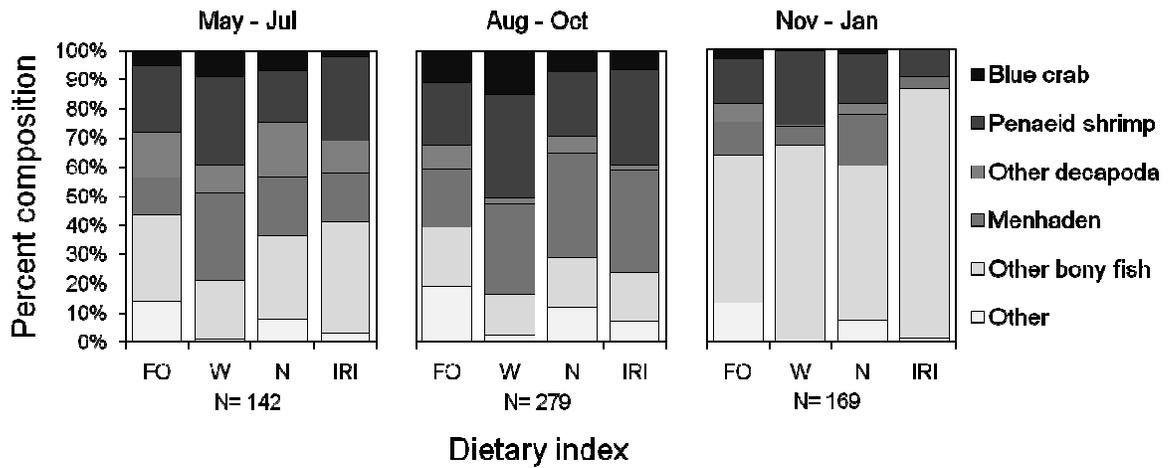


Figure 9. Percent frequency of occurrence (normalized to 100%) (FO), percent weight (W), percent number (N), and the index of relative importance (IRI) for age-0 red drum captured during both field seasons, and analyzed in three month seasons.

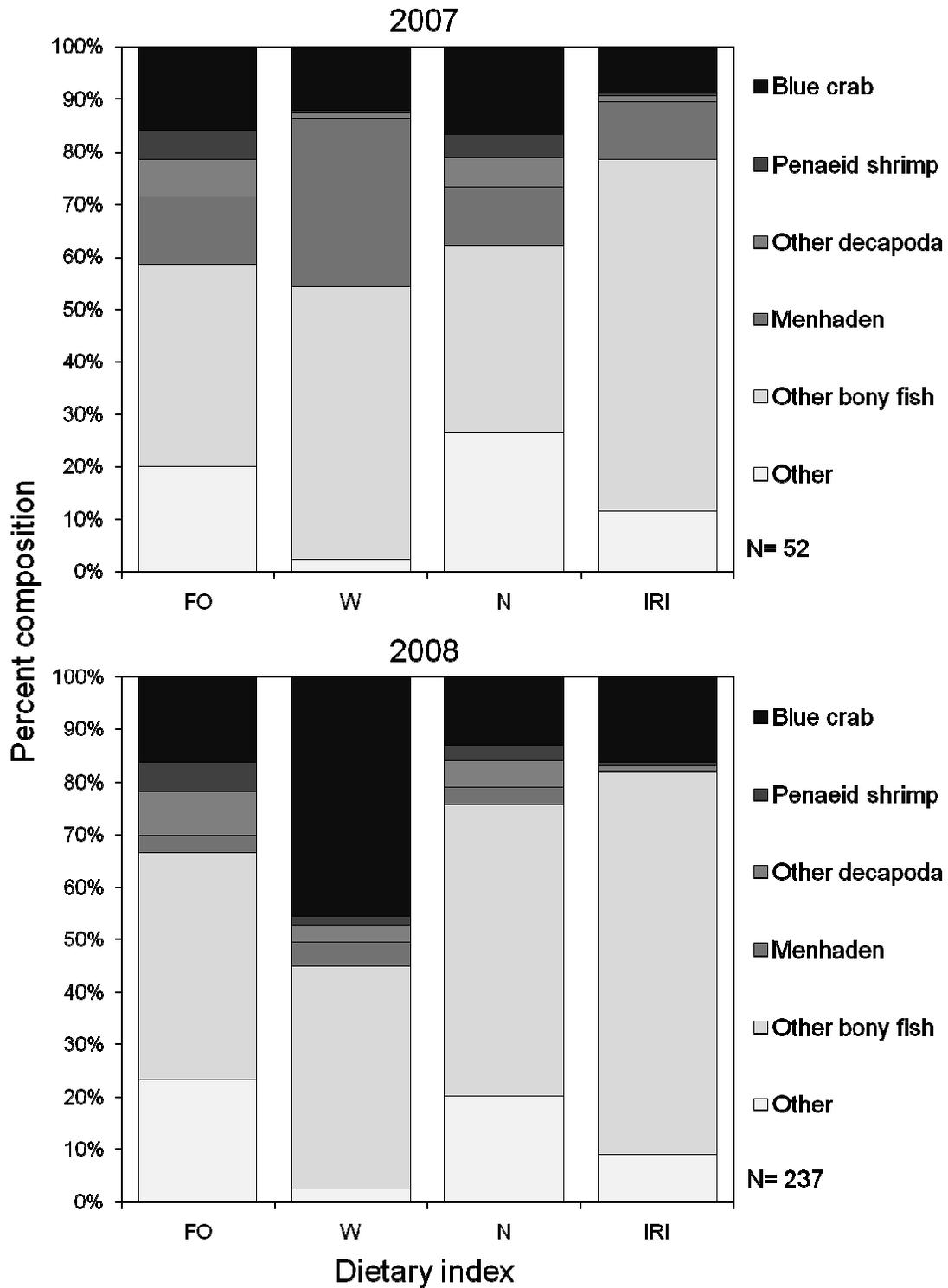


Figure 10. Percent frequency of occurrence (normalized to 100%) (FO), percent weight (W), percent number (N), and the index of relative importance (IRI) for age-1 red drum captured in 2007 and 2008.

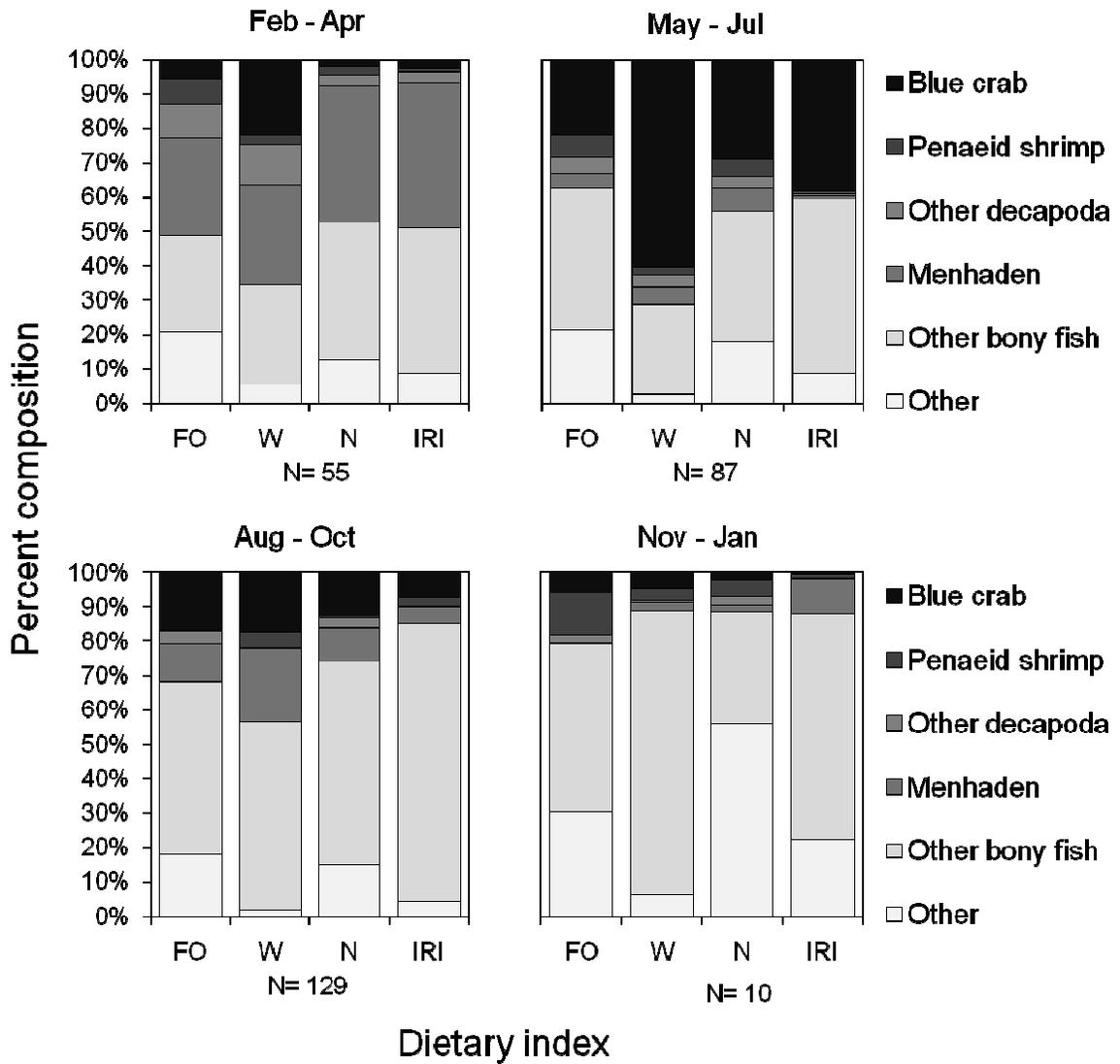


Figure 11. Percent frequency of occurrence (normalized to 100%) (FO), percent weight (W), percent number (N), and the index of relative importance (IRI) for age-1 red drum captured during both field seasons, and analyzed by three month seasons.

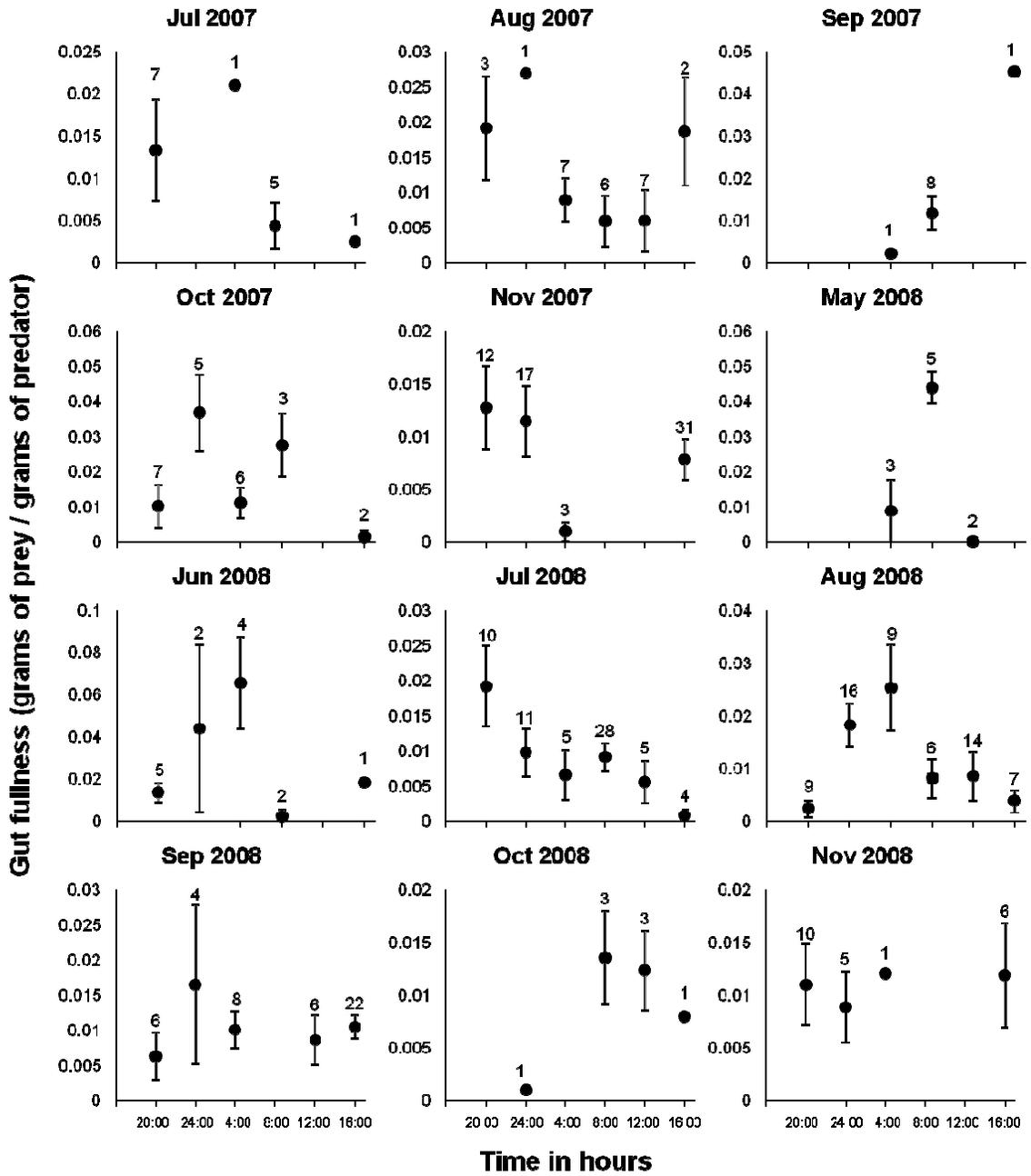


Figure 12. Mean gut fullness within 4 hour time blocks vs. time of capture for age-0 fish from all twelve diel sampling trips. Error bars represent standard error, and sample sizes for each time block are shown above the bars.

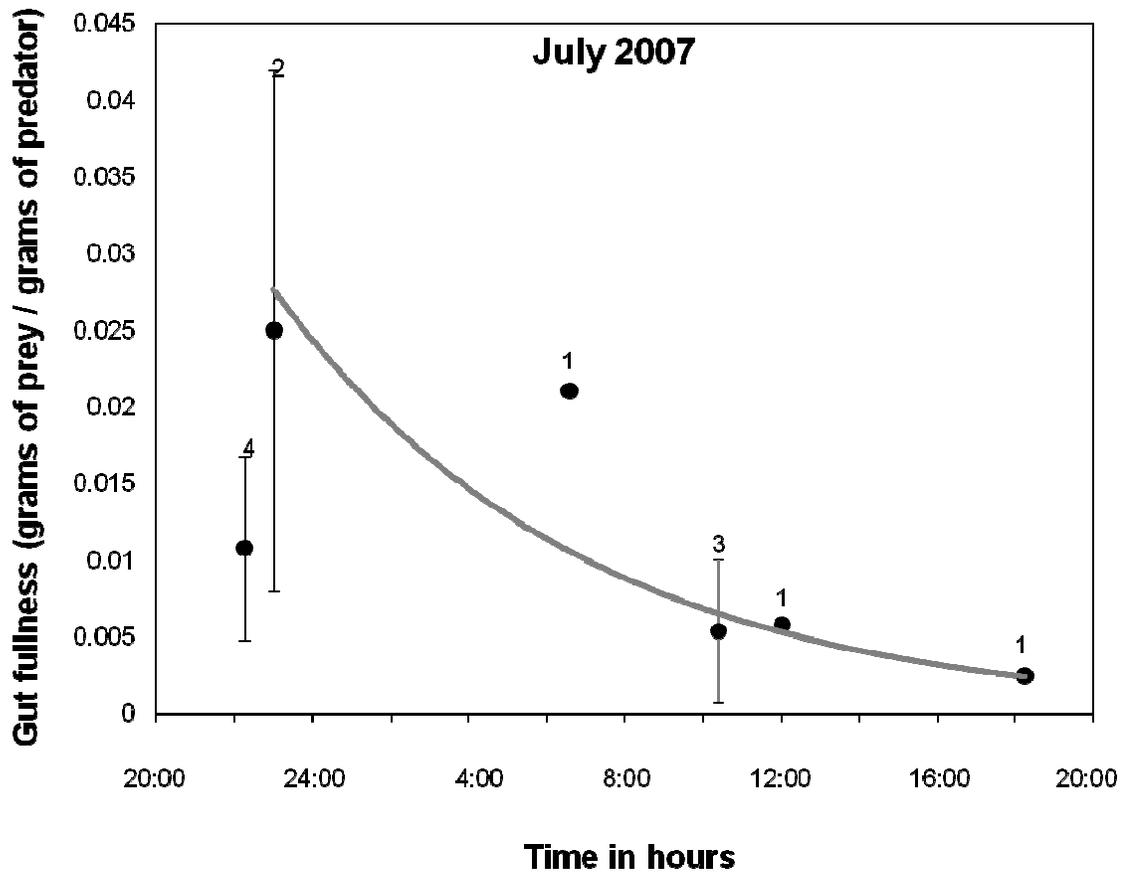


Figure 13. Mean gut fullness values from each net set vs. time of capture for age-0 fish on 23-24, July 2007. Error bars represent standard error, and sample sizes for each time block are shown above the bars. The gray line represents the fit of the gastric evacuation function.

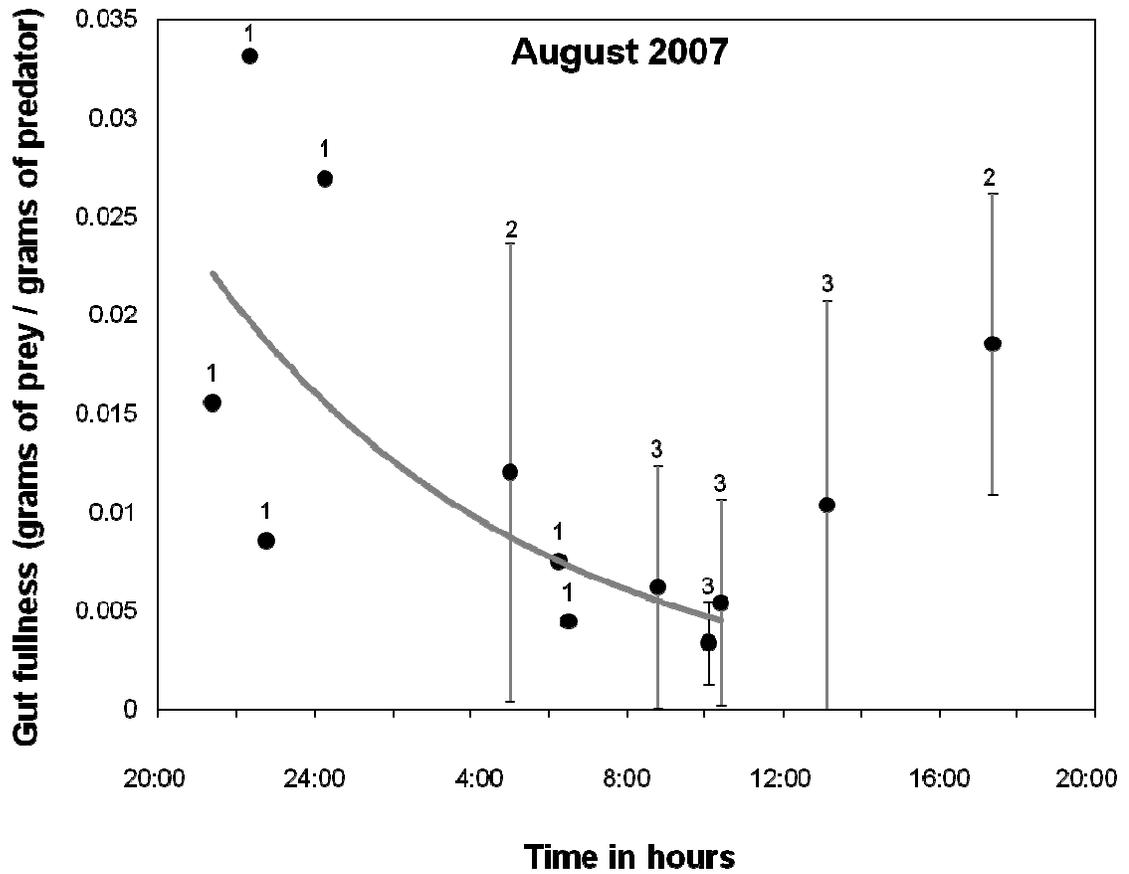


Figure 14. Mean gut fullness values from each net set vs. time of capture for age-0 fish on 25-27, August 2007. Error bars represent standard error, and sample sizes for each time block are shown above the bars. The gray line represents the fit of the gastric evacuation function.

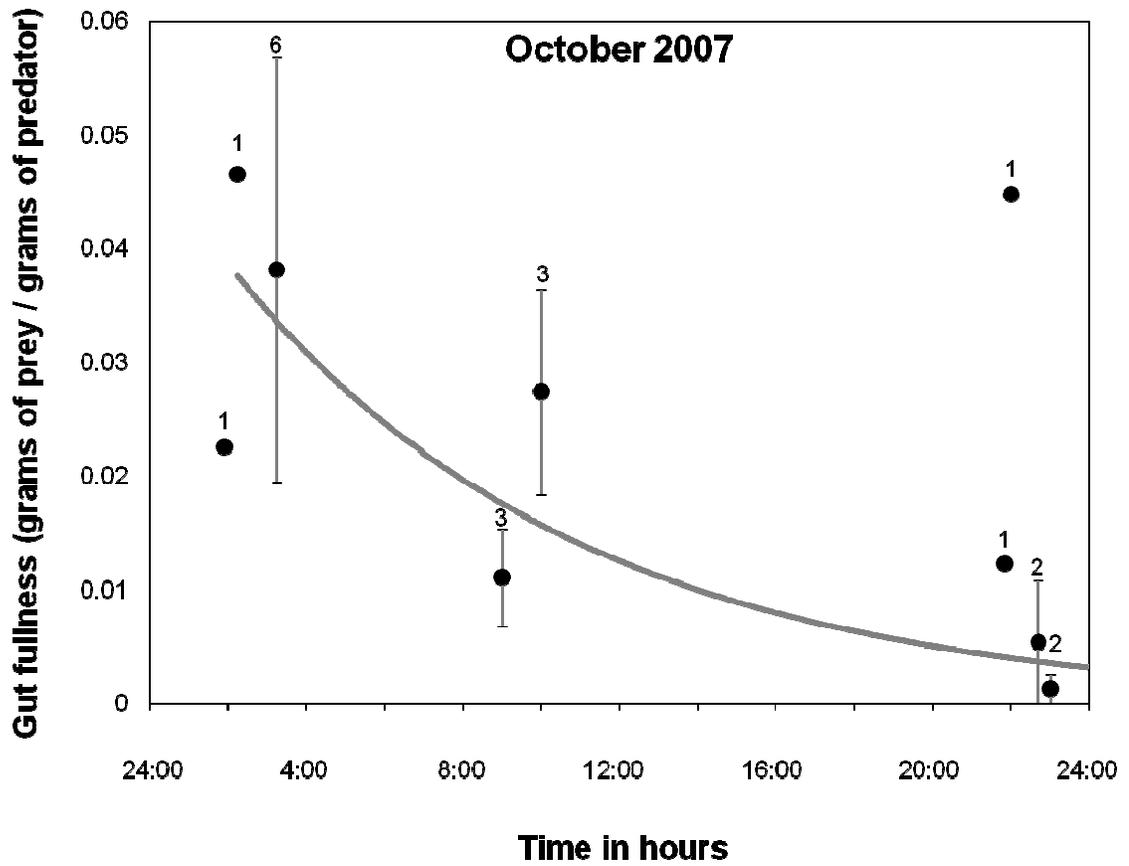


Figure 15. Mean gut fullness values from each net set vs. time of capture for age-0 fish on 12-14, October 2007. Error bars represent standard error, and sample sizes for each time block are shown above the bars. The gray line represents the fit of the gastric evacuation function.

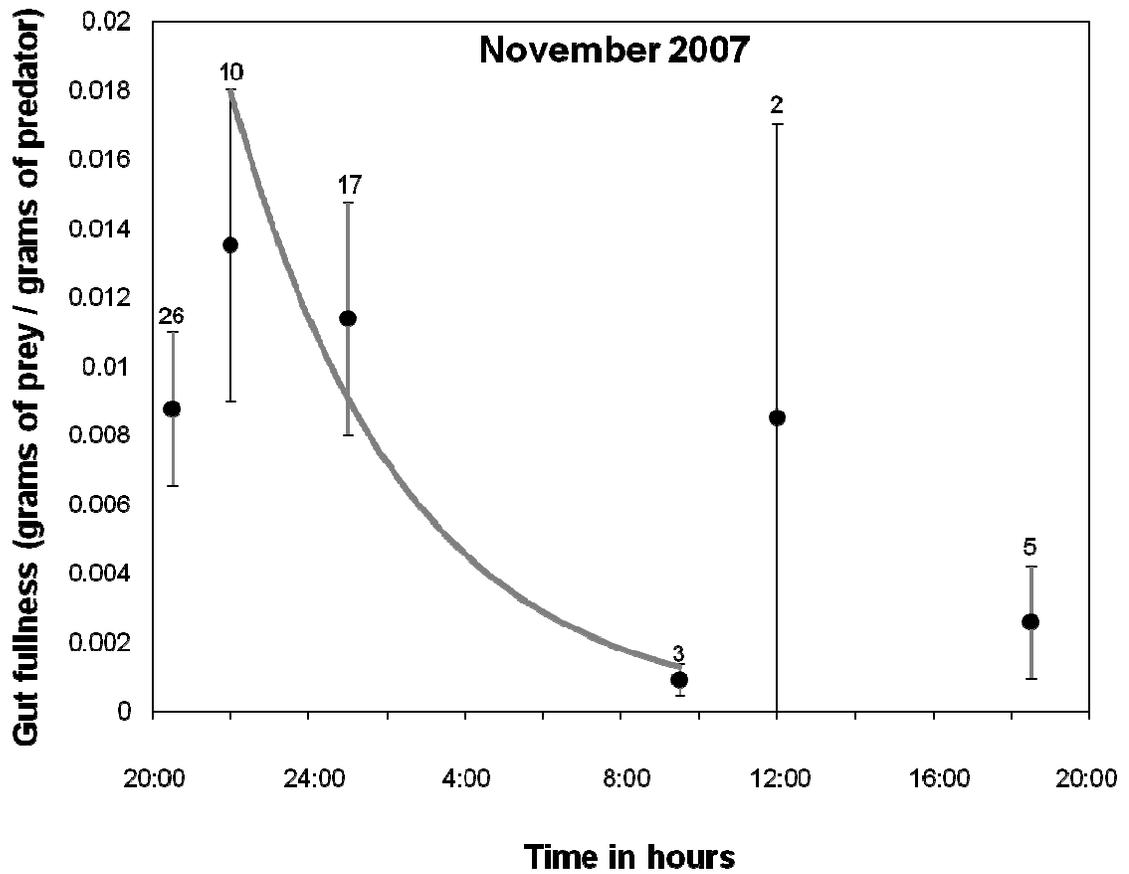


Figure 16. Mean gut fullness values from each net set vs. time of capture for age-0 fish on 16-18, November 2007. Error bars represent standard error, and sample sizes for each time block are shown above the bars. The gray line represents the fit of the gastric evacuation function.

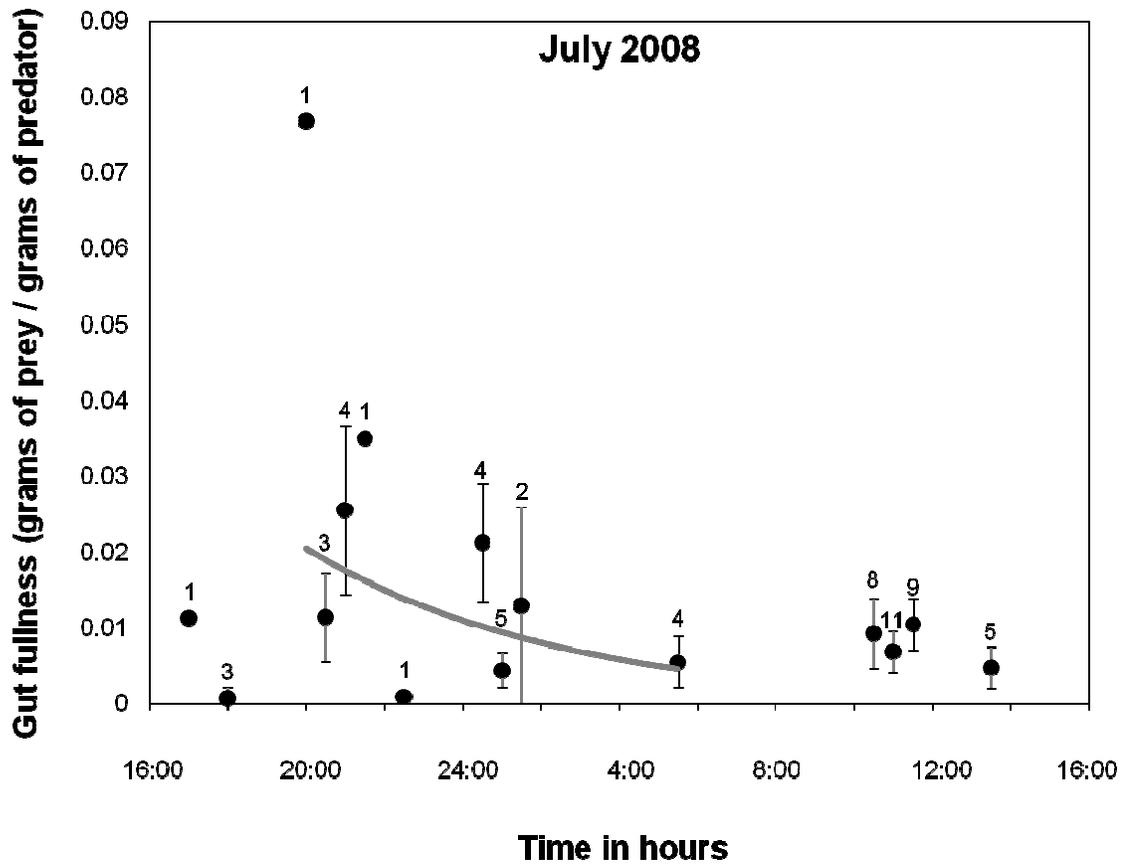


Figure 17. Mean gut fullness values from each net set vs. time of capture for age-0 fish on 24-26, July 2008. Error bars represent standard error, and sample sizes for each time block are shown above the bars. The gray line represents the fit of the gastric evacuation function.

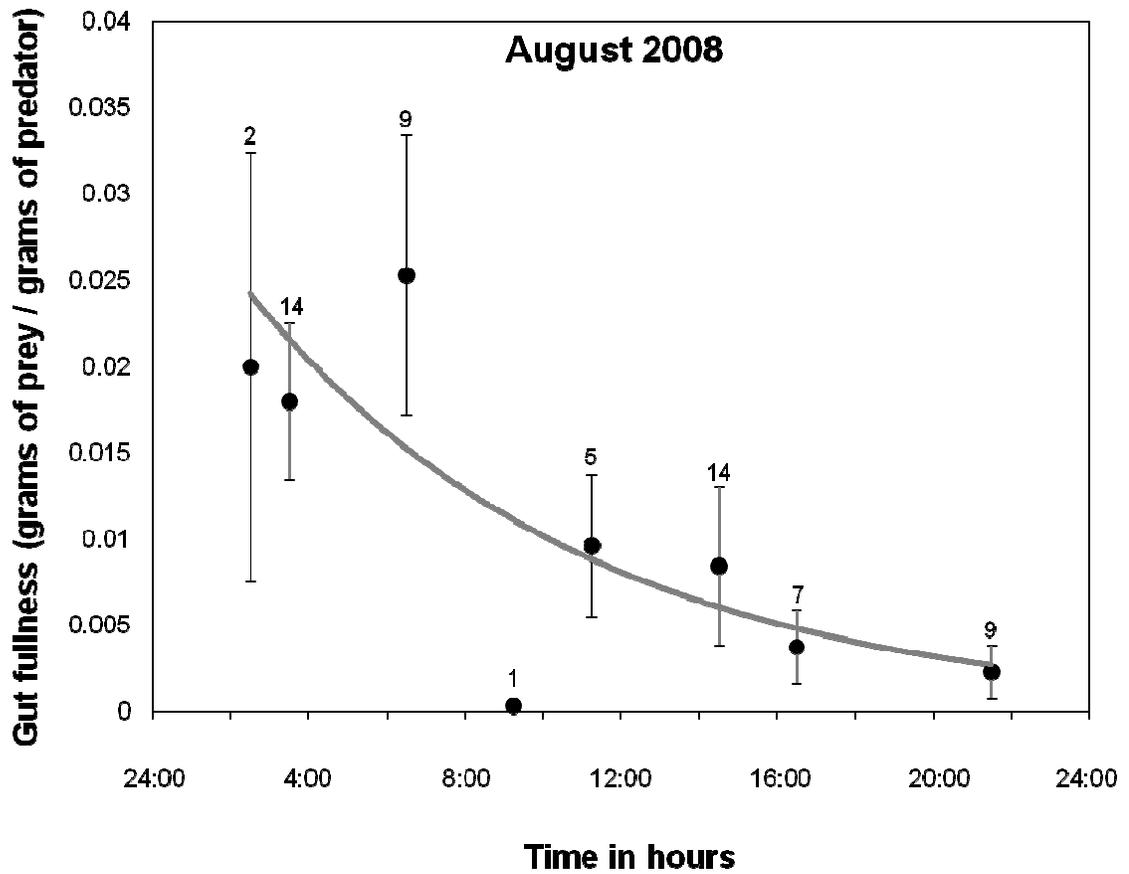


Figure 18. Mean gut fullness values from each net set vs. time of capture for age-0 fish on 28-30, Aug 2008. Error bars represent standard error, and sample sizes for each time block are shown above the bars. The gray line represents the fit of the gastric evacuation function.

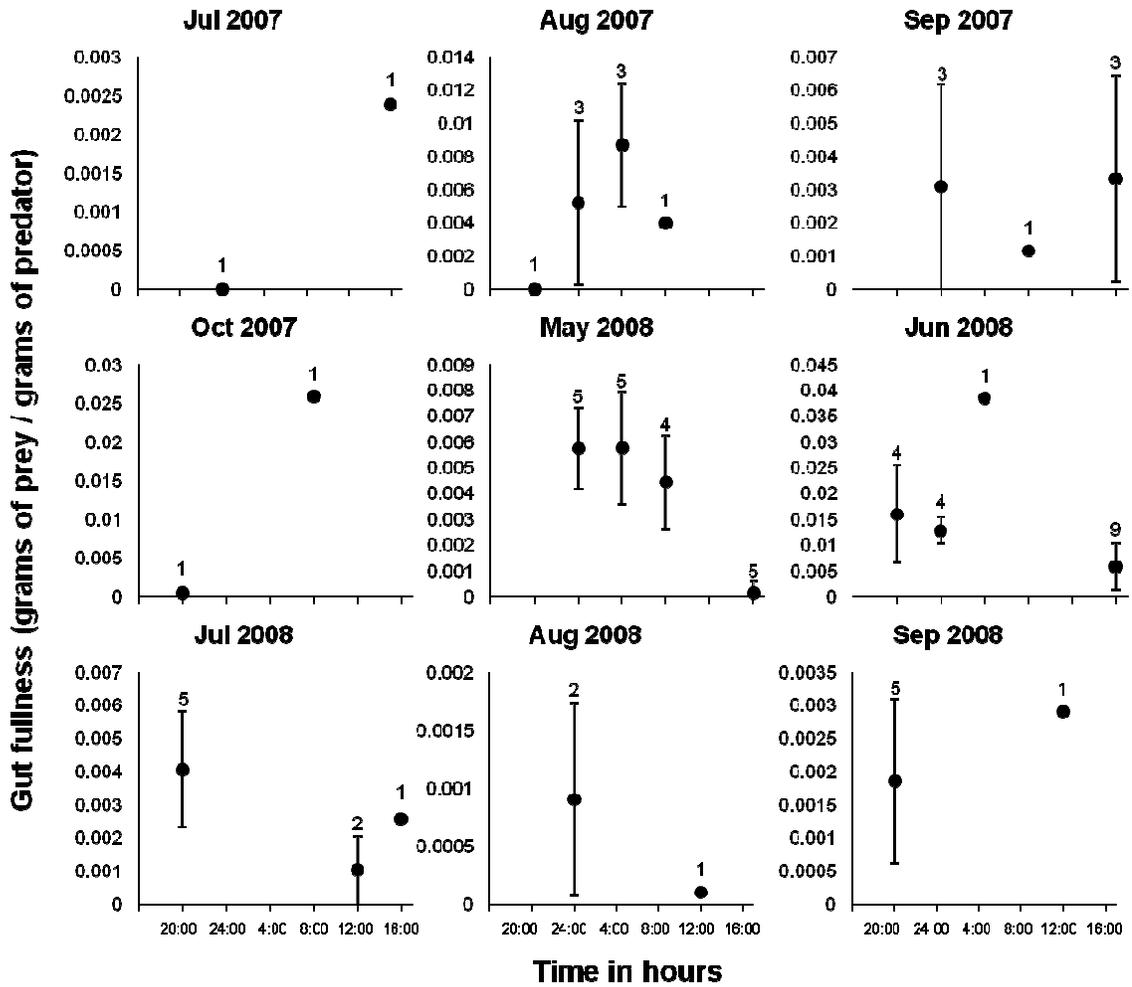


Figure 19. Mean gut fullness within 4 hour time blocks vs. time of capture for age-1 fish from all nine diel sampling trips that resulted in the capture of this age class. Error bars represent standard error, and sample sizes for each time block are shown above the bars.

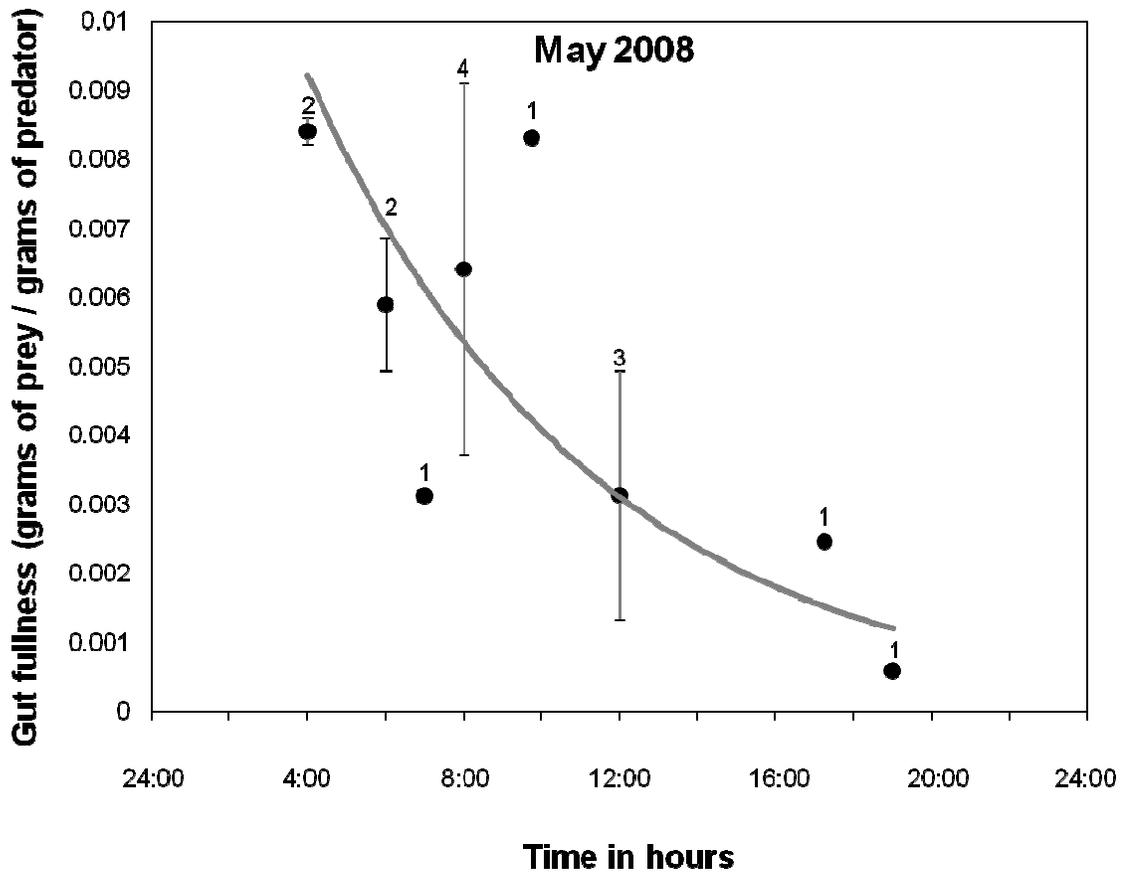


Figure 20. Mean gut fullness values from each net set vs. time of capture for age-1 fish on 19-21, May 2008. Error bars represent standard error, and sample sizes for each time block are shown above the bars. The gray line represents the fit of the gastric evacuation function.

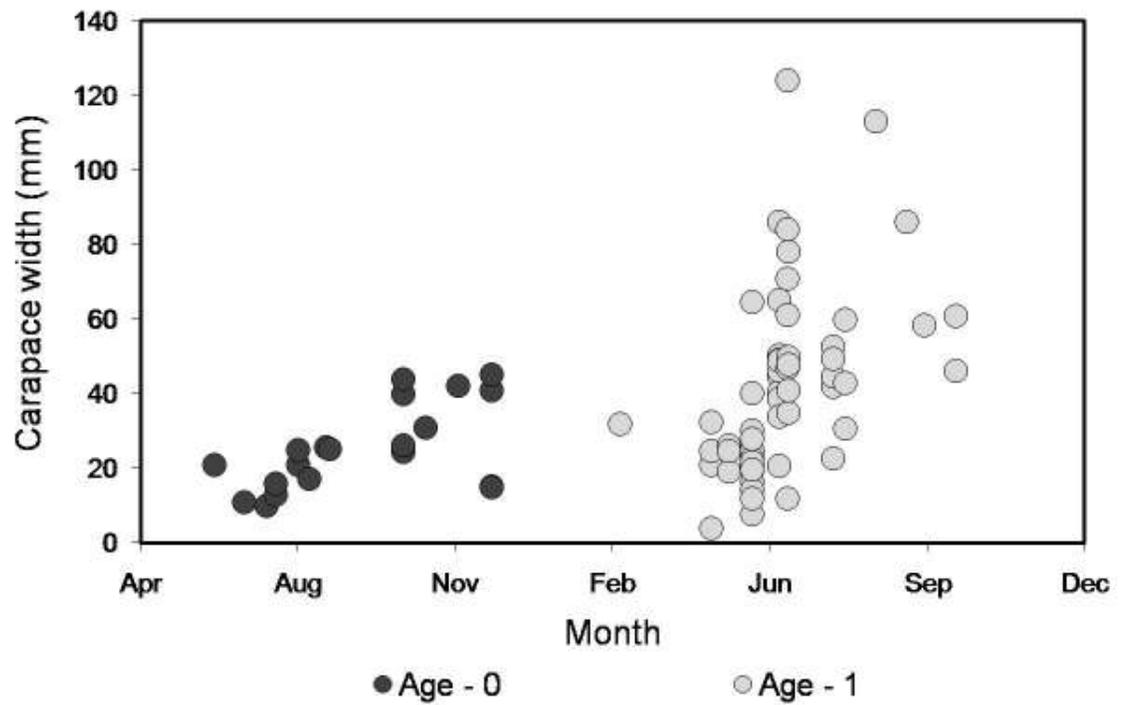


Figure 21. Blue crab carapace widths (mm) recovered from red drum stomachs vs. capture month. These data were used to estimate average seasonal sizes of blue crab consumed.

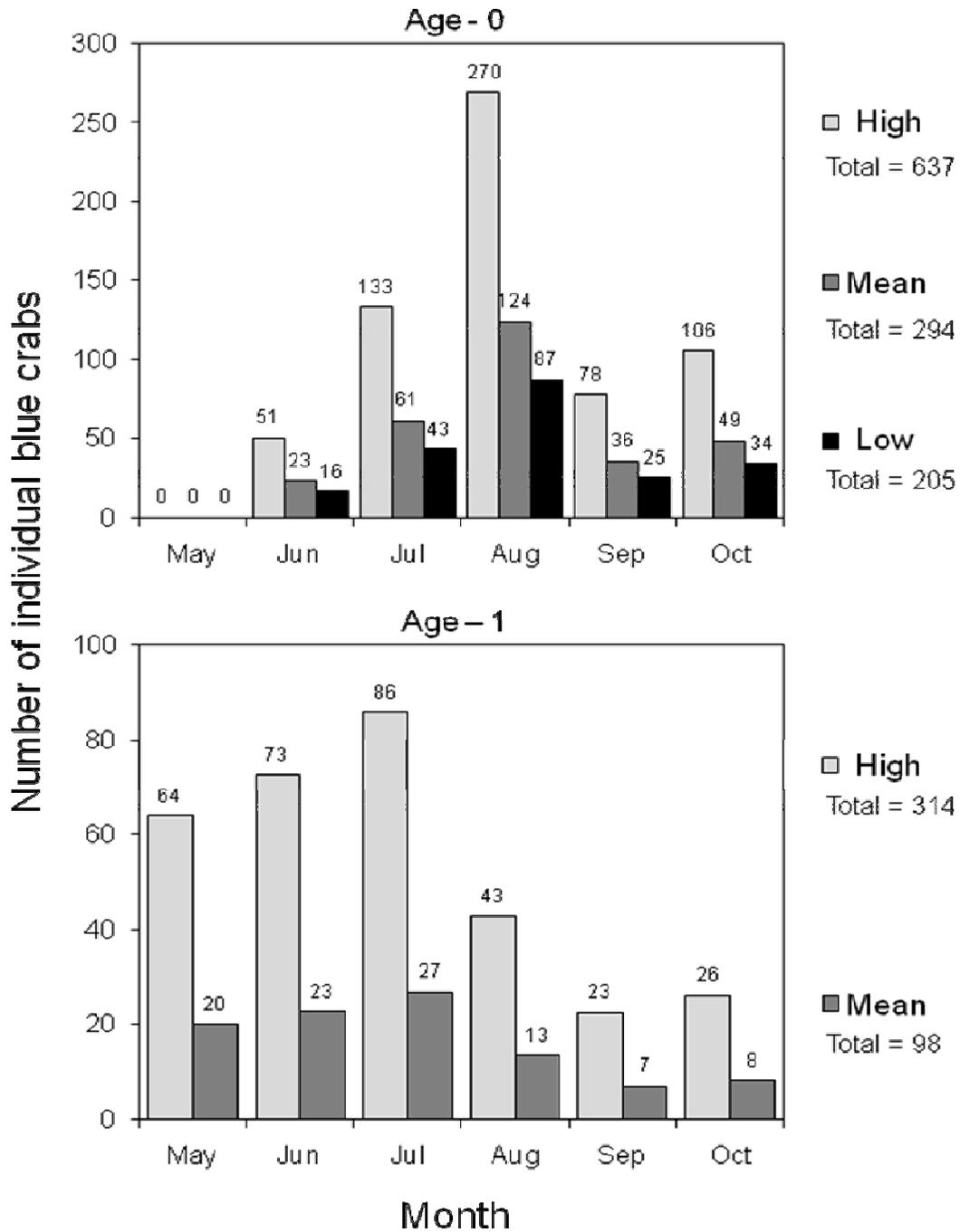


Figure 22. Monthly consumption estimates of individual blue crabs by average age-0 and age-1 red drum from the New River estuary. The mean estimate was calculated using the mean field estimated daily ration, the high consumption estimate was calculated using the maximum observed gut fullness value as a daily ration, and the low estimate was calculated using the minimum observed field estimate of daily ration. Only one field estimate of daily ration was made for age-1 fish, not allowing for a low blue crab consumption estimate to be made.