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ARTICLE

Seasonal and Ontogenetic Variation in the Diet and Daily Ration of Estuarine Red Drum as Derived from Field-Based Estimates of Gastric Evacuation and Consumption

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Abstract

The application of ecosystem-based approaches in fisheries management has been limited by a lack of empirical data for quantifying the ecological interactions among many common and valuable fishery species. The red drum *Sciaenops ocellatus*, a large, carnivorous member of estuarine communities, is experiencing population recovery throughout its range in the U.S. South Atlantic and Gulf of Mexico. Using a field-based approach, we determined seasonal and ontogenetic variation in the contribution of valuable fishery resource species to red drum diets, estimated red drum daily ration, and quantified per capita and population-level predation by juvenile and subadult red drum in a North Carolina estuarine system. Despite seasonal, interannual, and ontogenetic variation in diet composition, red drum fed mainly on macrocrustaceans and juvenile fishes, including several economically important resource species (e.g., blue crab *Callinectes sapidus*, penaeid shrimp, and Atlantic menhaden *Brevoortia tyrannus*). Both juvenile and subadult red drum demonstrated strong diel feeding patterns, with peak feeding occurring during the hours just after dark. Gastric evacuation rates during periods of declining gut fullness were estimated on seven sampling dates and produced mean daily ration estimates between 1.2% and 3.4% of predator mass depending on age-group. Combining field-observed red drum growth rates with published laboratory estimates of gross growth efficiency suggested that our estimates of daily ration were likely biased low. During the seasonal period of rapid growth, the aggregate consumption of blue crabs, penaeid shrimp, and Atlantic menhaden by juvenile and subadult red drum in North Carolina waters was estimated at 3.4×10^6 to 5.1×10^6 kg/year.

One fundamental step toward taking a more holistic approach to fishery management is to simply consider how the abundance of one species may directly impact other species within the ecosystem. Although the majority of fishery management strategies have historically focused on single-species assessments and have generally ignored predation and other species interactions (Latour et al. 2003), multispecies models have been developed and applied in a fishery management context (Hollowed et al. 2000; Whipple et al. 2000; Jurado-Molina et al. 2005). However, the application of these models has been limited by a lack of empirical data for quantifying essential biotic interactions; even the incorporation of potentially strong species interactions is hindered by poor knowledge of the basic ecological relationships among many common and valuable fishery species (Link et al. 2002). Predation as a primary structuring force in aquatic systems has been well established (e.g., Brooks and Dodson 1965; Paine 1969; Carpenter et al. 1985), with upper-trophic-level predators causing direct and indirect effects on prey populations. In marine and estuarine systems, several recent cases have confirmed the potential for

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fish predators to impact prey population dynamics (Buckel et al. 1999; Harvey et al. 2008; Tuomikoski et al. 2008).

The use of shallow estuarine environments as nursery areas by many valuable fishery species (Costanza et al. 1997; Blaber et al. 2000) calls for the collection of empirical information on key species interactions to fully define the role of predation as a potential regulatory process in these systems. The red drum *Sciaenops ocellatus* is a principal member of estuarine fish communities throughout the U.S. South Atlantic and the Gulf of Mexico (Mercer 1984; Wenner et al. 1990). Immature fish (up to ages 3 and 4) reside primarily in estuaries and coastal waters, where they achieve rapid growth on a mostly carnivorous diet of fishes and macrocrustaceans. The foraging ecology of red drum has been examined in several Gulf of Mexico studies (Knapp 1950; Boothby and Avault 1971; Bass and Avault 1975; Peters and McMichael 1987; Llansó et al. 1998; Guillory and Prejean 1999; Scharf and Schlicht 2000), which collectively indicate the existence of ontogenetic shifts in dominant prey items that are related to changes in red drum body size and habitat use patterns. Similar patterns in food habits have been documented for red drum in U.S. South Atlantic estuaries (Wenner et al. 1990; Orth et al. 1999; Speir 1999; Lanier and Scharf 2007; Bacheler et al. 2009). After settlement to benthic habitats in summer and early fall, small (<75 mm total length [TL]) juvenile red drum feed primarily on planktonic copepods and mysid shrimp (Bass and Avault 1975; Lanier and Scharf 2007). As fall progresses and the red drum increase in size (~100–300 mm TL), macrocrustaceans (e.g., penaeid shrimp, portunid crabs, and xanthid crabs) begin to dominate the diet (Bass and Avault 1975; Wenner et al. 1990; Guillory and Prejean 1999; Speir 1999). This is followed by an increased importance of fish in the diet as the red drum grow larger and exhibit greater use of deeper habitats (Boothby and Avault 1971; Wenner et al. 1990; Scharf and Schlicht 2000). Red drum have also shown considerable seasonal variability in diet composition, which is believed to be due to fluctuations in prey availability (Scharf and Schlicht 2000).

Importantly, the large number of studies describing red drum food habits reveal that red drum are consistent predators of several valuable fishery resource species, including the blue crab *Callinectes sapidus*, penaeid shrimp, Atlantic menhaden *Brevoortia tyrannus*, Gulf menhaden *Brevoortia patronus*, and spot *Leiostomus xanthurus*. For example, Orth et al. (1999) found that 64–100% of red drum that were collected while feeding in Chesapeake Bay seagrass beds had consumed blue crabs. Scharf and Schlicht (2000) found that blue crabs and penaeid shrimp occurred in 25% and 60% of red drum stomachs, respectively, during fall in Galveston Bay, whereas spring diets were dominated by Gulf menhaden and other fish prey. To assess potential predation impact by estuarine red drum in Louisiana, Guillory and Prejean (1999) combined historic diet data with an assumed daily consumption rate of 2% of body mass to estimate an average ration of 701 blue crabs·kg of red drum^{-1}·year^{-1}, which they concluded was likely conservative. Furthermore, the dominant prey of red drum represent some of the most economically valuable species harvested in southern U.S. estuaries. In North Carolina, the combined dockside value of blue crab and penaeid shrimp landings has equaled or exceeded the value of all finfish landings several times during the past decade (North Carolina Division of Marine Fisheries 2012).

Red drum experience very rapid growth until sexual maturity is reached at age 3 or 4 (Ross et al. 1995; Porch et al. 2002). By the end of their first year, red drum can reach 300–400 mm TL, and many red drum grow to sizes (600–700 mm TL) above the legal slot limits by the time they reach age 3. To achieve the high levels of growth observed during the warmer seasons (May–October), rates of consumption by red drum are likely to be considerable. Indeed, daily rations of up to 3–5% of individual body weight have been observed in tank-raised juvenile red drum during manipulative growth experiments (McGoogan and Gatlin 1999; Tomasso and Kempton 2000). However, estimates of red drum consumption rates, which are necessary to initiate an assessment of potential predatory impact, only exist for fish that have been held in commercial aquaculture operations (e.g., Tucker et al. 1997); there are no field-based or bioenergetic estimates of red drum daily ration.

In the U.S. South Atlantic, red drum stocks have recently experienced strong recoveries after high exploitation rates were associated with depressed stocks during the 1980s (SEDAR 2009). In light of the improving status of red drum stocks, this study was designed to assess the extent and potential population-level impact of predation by red drum during the estuarine phase of their life history. The specific objectives were to (1) determine seasonal and ontogenetic variation in the contribution of valuable fishery resource species to the diets of juvenile and subadult (ages 0–2) red drum, (2) evaluate red drum diurnal feeding periods and estimate gastric evacuation rates and daily ration from diel patterns in gut fullness during the warmer months that coincide with rapid red drum growth, and (3) quantify potential annual predation by red drum in terms of the prey biomass eaten relative to the biomass of commercial landings of major prey.

METHODS

Study site.—The New River (34°37′N, 77°22′W) in southeastern North Carolina is a moderately sized (670-km^2 drainage), river-dominated estuarine system that empties directly into the Atlantic Ocean (Ensign et al. 2004). The river consists of a series of shallow (1–2 m), broad lagoons with a mean tidal range of less than 1 m (Dame et al. 2000). Large portions of the river remain relatively free from riparian development since it is nearly completely encompassed by Camp Lejeune, a U.S. Marine Corps base. Stations within the New River contribute to a fishery-independent beach seine survey that is used to index age-0 red drum year-class strength (Bacheler et al. 2008), and past research has identified the estuary as an important juvenile nursery (Stewart and Scharf 2008).

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Field sampling.—Sampling was conducted during May 2007 through February 2009 and targeted two age (size) groups of red drum: juvenile fish transitioning from age 0 to age 1 (~100–400 mm TL; hereafter, "age 0–1") and subadult fish transitioning from age 1 to age 2 (~400–700 mm TL; hereafter, "age 1–2"). The field sampling design combined monthly collections of red drum stomach contents during all seasons with diel sampling during the period of rapid growth (May–November). We did not conduct diel sampling during winter and early spring because of reduced feeding activity and growth at colder water temperatures. Collection of red drum was concentrated in the mesohaline (15–25‰) and oligohaline (5–15‰) reaches of the river to maximize catch per unit effort. Preliminary sampling within these habitats was completed to evaluate gear efficiency and to identify potential sites that would consistently produce large numbers of predators. During each sampling trip, locations were selected based on environmental conditions (e.g., tide, wind, and prior rainfall amounts) and previous catch experience.

Diet sampling was completed by capturing red drum with passively fished monofilament gill nets. Two sizes (small and large mesh) of variable-mesh-panel nets (each 45.7 m long × 2.4 m deep) were used. Small-mesh nets were used to capture age-0–1 fish and consisted of three 15.2-m panels constructed of 5.1-, 6.4-, and 7.6-cm stretched mesh. Large-mesh nets were used to capture age-1–2 fish and consisted of three 15.2-m panels constructed of 10.2-, 11.4-, and 12.7-cm stretched mesh. For each diet sampling event, six to eight 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 h.

Diel sampling was executed using a monofilament trammel net that was fished actively—a fishing technique referred to as "strike-netting" or "side-setting"—by using a 6.7-m skiff with an outboard engine. The trammel net was 183 m long × 2.1 m deep, with 35.6-cm stretched outer mesh and 6.4-cm stretched inner mesh. The trammel net effectively captured a broad size range (~100–700 mm TL) of red drum, allowing for more efficient use of man-hours during diel sampling events. During each set, one end of the trammel net was anchored to the shore, and the net was deployed from the boat in a semicircular pattern at speeds of up to 18.52–27.78 km/h (10–15 knots). The trailing end of the net was anchored to another point on the shoreline, resulting in a semicircular area being completely enclosed by the net. The area within the net was then disturbed by use of the boat; the goal of this step was to herd any fish that were encircled by the net into the mesh walls. After the water encircled by the net was agitated for approximately 5 min, the net was retrieved by hand. Diel sampling included a minimum of one trammel-net set every 4 h throughout a continuous 24-h period. For logistical reasons, some diel sampling events were partitioned into two 12-h sampling blocks that were separated by approximately 24 h; environmental conditions affecting red drum foraging and prey availability were assumed to have remained similar between the two 12-h time blocks. The use of an active gear for diel sampling (i.e., rather than soaking unattended nets for long time periods) enabled the capture of fish that were in good condition. Active sampling also helped to minimize the influence of potentially confounding factors, including prey regurgitation or advanced prey digestion that can be common when using passive gill-net soaks (Sutton et al. 2004). Thus, the use of active sampling ensured that the diet information from each individual fish could be linked to a relatively discrete point in time.

At each sampling location, the time of day, depth (m), latitude, longitude, water temperature (°C), dissolved oxygen (mg/L), and salinity (‰) were recorded. A unique identification number was assigned to each captured red drum and was recorded along with the sample date, mesh size, fish TL, and fish weight (g). Stomach contents were recovered using nonlethal gastric lavage techniques as described by Hartleb and Moring (1995). Stomach contents were flushed into a 0.5-mm screen, and the buccal cavity was carefully examined for any residual prey material before each fish was released. Other recent studies have noted the efficiency of prey retrieval from red drum when gastric lavage techniques are used (Bacheler et al. 2009), and the postlavage sacrifice of a small subset of fish during the present study revealed that all prey had been retrieved. During diel sampling, red drum that were released alive were first tagged with a unique internal anchor tag from the North Carolina Division of Marine Fisheries. Marking of previously sampled fish prevented the collection of foraging information from the same individual multiple times during a single diel sampling event. Retrieved stomach contents were placed in plastic bags, labeled with the corresponding fish identification number, and stored on ice until they could be taken to the laboratory for processing.

Diet analysis.—Prey items were identified to the lowest possible taxon, enumerated, blotted dry, weighed to the nearest 0.01 g, and measured to the nearest millimeter. A condition factor was assigned to each prey item based on the relative wholeness of the organism and the state of digestion. Blue crabs recovered whole were measured for carapace width (CW); widths of broken or incomplete carapaces were reconstructed by using predictive equations relating CW to distances between the orbital teeth (Scharf and Schlicht 2000). To assist with identification and the reconstruction of original size for highly digested fish prey, a reference collection of otoliths and a series of predictive equations relating otolith size to body size were developed for several local estuarine prey fishes that are commonly eaten by red drum. In this study, however, otoliths were rarely the only evidence of fish prey in red drum stomachs; typically, the digested fish carcass was recovered and the otoliths were used as a diagnostic key. The percent frequency of occurrence (%FO = the fraction of nonempty stomachs that contained a particular prey type) and the percent by weight (%W = the weight of each prey type eaten relative to the combined weight of all prey types eaten) of different prey taxa were calculated to express the relative importance of taxa to the diets of red drum. All stomach content data were initially pooled to characterize the

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overall diet of juvenile and subadult red drum. To assess interannual and seasonal variation in the contribution of common prey types, data were first normalized into four major prey categories: blue crabs, penaeid shrimp, Atlantic menhaden, and other bony fishes (i.e., all fishes except Atlantic menhaden). Separate dietary indices were then calculated for each year and for 3-month seasonal periods that were pooled across years.

Estimation of daily ration.—Gut fullness values were calculated for each red drum as (total weight of recovered prey)/(total weight of the predator − total weight of recovered prey). The gut fullness values for each fish captured in a single trammel-net set were averaged. Each separate gear set was thus treated as an independent replicate and individual fish were treated as pseudoreplicates since the gut fullness values of fish captured in the same net set were unlikely to be independent. Mean gut fullness values were weighted based on the number of red drum captured in each separate net set; this was done to prevent exceedingly high or low gut fullness values for single fish from having a large influence on gastric evacuation rate estimates. To identify the overall diel feeding pattern, gut fullness values were pooled across sampling dates into 2-h blocks and were analyzed using a piecewise regression model. The model fits two linear segments and estimates the breakpoint where a change in slope occurs. Periods of declining gut fullness on individual sampling dates were used to generate multiple independent field estimates of red drum gastric evacuation rate. The instantaneous rate of gastric evacuation (G) during periods of declining gut fullness was calculated by fitting the nonlinear exponential decay model,

$$S_t = S_0 e^{-Gt},$$

where S_t = gut fullness (expressed as g of prey/g of predator) at time t; S_0 = initial gut fullness; e = the base of natural logarithms; and t = time (h). The model of Eggers (1977) was used to estimate consumption (C; g of prey eaten·g of predator^{-1}·d^{-1}):

$$C = 24 \times \bar{S} \times G,$$

where $\bar{S}$ = mean gut fullness (g of prey/g of predator) throughout the diel period, and G = instantaneous rate of gastric evacuation as estimated above.

Quantifying predation by red drum.—The seasonal contribution of prey to red drum diets and field estimates of consumption rate were combined to estimate the daily consumption of major prey taxa (blue crabs, penaeid shrimp, and Atlantic menhaden). For each red drum age-group, the mean of all independent estimates of daily ration was used to represent the daily consumption rate (g of prey·g of predator^{-1}·d^{-1}) during the period of rapid growth (May–October). The seasonal %W for each prey type was used to partition the diet on a monthly basis. For each prey type, the mean consumption rate was multiplied by the monthly %W, resulting in a daily estimate of the grams of prey eaten per gram of red drum during each study month. This ration was applied to the average weight of red drum observed in the field during each month and was expanded to reflect a 30- or 31-d period, resulting in a monthly total estimate of the grams of prey consumed by an individual red drum in the New River estuary. Error in the monthly prey consumption estimates was estimated by using the SD calculated for red drum daily ration.

Estimates of red drum daily ration during May–October in the New River estuary were extrapolated to project potential population-level consumption by red drum for the entire North Carolina coast. Abundance estimates of age-1–3 red drum for the northern Atlantic region (North Carolina and Virginia) were obtained from the most recent stock assessment (SEDAR 2009). The abundance estimates for the northern region were assumed to be a rough approximation of the stock size in North Carolina because more than 75% of the recreational catch and nearly all of the commercial harvest of red drum in the northern region during 2005–2007 occurred in North Carolina (NMFS 2012). Age-1–3 fish were evaluated because red drum occupy primarily estuarine habitats up to age 3 (Mercer 1984; Wenner et al. 1990), and the assumption was made that diets and feeding rates of age-3 fish would be similar to those of the oldest fish (late age-1 and early age-2 individuals) included in the present study. First, numbers at each age were converted to biomass by using von Bertanlanffy and weight–length equations from the most recent assessment. The biomass estimates were then summed across age-groups for the three most recent years (2005–2007) included in the assessment to generate consumption estimates for a representative range of red drum population biomass estimates. Individual red drum consumption was set at the average daily ration (2.92 g·g^{-1}·d^{-1}) for the two age-groups observed in the field. The percent contribution (i.e.,%W) of blue crab, penaeid shrimp, and Atlantic menhaden was averaged for each month by using the observed diet data for age-0–1 and age-1–2 red drum.

RESULTS

Field Sampling

A total of 55 field sampling days resulted in the capture of 880 juvenile and subadult red drum with a size range of 113–731 mm TL. Throughout the study, fish from three separate year-classes (the 2005, 2006, and 2007 cohorts) were collected, including 591 age-0–1 individuals and 289 age-1–2 individuals. Both age-groups showed clear periods of rapid growth between May and October, followed by periods of reduced or no growth during November–April (Figure 1). Fish transitioning from late age 0 to early age 1 achieved a mean specific growth rate of 1.73% per day and increased from approximately 100 to 400 mm in TL during the rapid growth period. Late age-1 and early age-2 red drum realized a mean specific growth rate of 0.56% per day and increased from approximately 450 to 700 mm TL during the same time period. Average daily water temperatures reached seasonal highs between 25°C and 32°C during May–October before declining to a seasonal low range of 7–12°C during December–February, which coincided with

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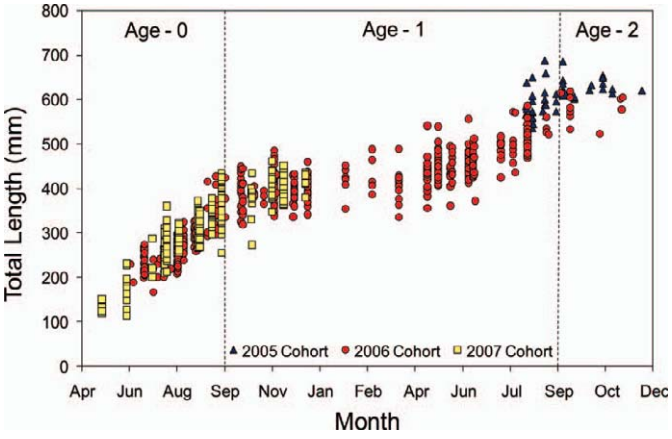


FIGURE 1. Total length versus date of capture for the three red drum cohorts that were encountered during 2007–2009 sampling in the New River estuary, North Carolina. Dashed vertical lines denote the biological birthdate of 1 September. Daily ration estimation was completed during the May–October period of rapid growth.

the slow growth period. The majority of red drum (>70% in both years) were collected at moderate salinities between 10‰ and 25‰.

Diet Analysis

Age-0–1 juvenile red drum preyed on at least 29 different species that included 14 fish taxa and 15 invertebrate taxa (Table 1). Penaeid shrimp dominated the diet by weight (%W = 30.7%), followed by Atlantic menhaden (27.4%) and blue crabs (9.6%). Other commonly recovered fish prey included Atlantic croakers, spot, mullets, pinfish, spotfin mojarras, and snake eels. Other invertebrate taxa represented in the diet included polychaete worms, snails, clams, insects, isopods, grass shrimp, marsh crabs, fiddler crabs, and mud crabs. Plant material (%FO = 20.4%) and inert objects such as rope, gravel, and fishing lures were also encountered routinely in red drum stomachs.

Age-1–2 red drum also exhibited a diverse diet, which included 20 different prey taxa (Table 1). Blue crabs dominated the diet by weight (%W = 35.1%), followed by Atlantic menhaden (15.4%) and pinfish (10.1%). In contrast to age-0–1 red drum, penaeid shrimp were not a major component (%W = 1.1%; %FO = 6.4%) of the diet for larger, older red drum. Other fish species were the predominant prey of age-1–2 red drum (%W = 61.1%) and included Atlantic croakers, spot, mullets, snake eels, and flounders. Other invertebrate taxa, including clams, insects, isopods, and other crabs, represented minor components of age-1–2 red drum diets. Similar to the diets of age-0–1 red drum, plant material (%FO = 18.2%) and other inert objects (e.g., metal, gravel, and fishing lures) were encountered routinely.

Based on the relative importance of major prey groups, the composition of red drum diets varied between the two years included in the study. In 2007, the majority of the diet for age-0–1 red drum consisted of penaeid shrimp (%W = 46.7%), whereas in 2008 penaeid shrimp only represented 13.6% of the diet by weight (Table 2). In contrast, the %W of Atlantic menhaden in the diet was only 3.4% in 2007 but increased to 59.3% in 2008. The contribution of blue crabs to the diet remained relatively consistent between the two study years: %W was 11.5% (%FO = 19.5%) in 2007 and was 8.1% (%FO = 6.5%) in 2008. Age-1–2 red drum also displayed interannual variability in the inclusion of major prey groups in their diet. In 2007, 87.1% of the diet by weight consisted of fish prey (%W = 33.2% for Atlantic menhaden; 53.9% for other bony fishes); however, in 2008 fishes only made up 50.0% of the diet by weight, primarily due to a decrease in the contribution of Atlantic menhaden prey (%W = 4.9%; Table 2). The contribution of penaeid shrimp to the diet of age-1–2 red drum was low in both years. Blue crabs were eaten consistently (%FO = 28.9–36.4%) by age-1–2 red drum, but their contribution by weight varied substantially between years (%W = 12.4% in 2007 and 48.2% in 2008), driven by higher masses of blue crab within stomachs that contained blue crab prey during 2008 (mean mass of blue crab per stomach = 9.6 g in 2008 and 6.8 g in 2007).

Seasonal patterns in food habits of age-0–1 red drum revealed a shift from a crustacean-dominated diet (%W ~ 50%) during May–October to a diet dominated by bony fishes (%W = 72.8%) during November–January (Figure 2A, B). Atlantic menhaden constituted the majority of all fish prey consumed during May–October; however, from November to January, Atlantic menhaden declined to less than 5% of fish prey (%W). Predation on blue crabs by age-0–1 red drum also displayed some seasonality: the %W of blue crabs was 8.8% (%FO = 9.0%) during May–July, increased to 15.0% (%FO = 18.6%) during August–October, and then declined to near zero (%W = 0.5%; %FO = 5.9%) during winter months. Seasonality was also evident in the feeding habits of age-1–2 red drum (Figure 2C, D). Diet analysis revealed a shift in the contribution of crustaceans (mostly blue crabs), with a %W of over 50% during February–July, decreasing to approximately 19% during fall and to nearly 8% in winter. This decline was driven mainly by predation on blue crabs, which demonstrated a high degree of seasonality in diets for age-1–2 red drum. The %W of blue crabs was 31.1% (%FO = 22.8%) from February to April, increased to 60.5% (%FO = 42.5%) during May–July, and then decreased during fall (%W = 18.2%; %FO = 19.5%) and winter (%W = 4.9%; %FO = 11.1%).

Estimation of Daily Ration

Age-0–1 red drum were captured during each of the 12 diel sampling trips and generally showed similar mean gut fullness patterns through time. Peak mean gut fullness values, representing periods of heavy feeding, typically occurred during the hours after dark; gut fullness values then declined during the overnight period and were low during the day (Figure 3). The piecewise regression model estimated a steady decline in gut fullness beginning near sunset, with modest and generally level gut fullness during daylight hours. Clear patterns of

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TABLE 1. Diet composition for two age-groups of red drum in the New River estuary, North Carolina, during 2007–2009 (%FO = percent frequency of occurrence of prey; %W = percent contribution of prey by weight). Prey items were identified to the species level whenever possible; otherwise, higher taxonomic levels (genus, family, or class) are indicated. The "other" prey category includes fishing lures, gravel, nylon rope, metal, and plant material (UID = unidentified).

	Age-0–1 red drum		Age-1–2 red drum	
Prey taxon	%FO	%W	%FO	%W
Total invertebrates	60.71	42.83	50.25	38.18
Polychaeta	0.42	0.08	0.00	0.00
Bivalvia	1.05	0.02	4.43	0.24
Gastropoda	0.21	<0.01	0.00	0.00
Isopoda	1.47	0.06	1.97	0.15
Hexapoda	0.84	<0.01	0.99	0.02
Decapoda	56.72	42.66	42.87	37.77
Grass shrimp *Palaemonetes* spp.	2.52	0.40	0.49	0.01
Total penaeid shrimp	29.20	30.65	6.40	1.11
Brown shrimp *Farfantepenaeus aztecus*	1.68	2.81	0.99	0.31
Pink shrimp *Farfantepenaeus duorarum*	0.84	0.13	0.00	0.00
White shrimp *Litopenaeus setiferus*	8.19	17.70	0.00	0.00
UID Penaeidae	18.49	10.01	5.42	0.79
Marsh crabs *Sesarma* spp.	0.42	0.01	0.00	0.00
Fiddler crabs *Uca* spp.	1.26	0.08	0.99	0.07
Harris mud crab *Rhithropanopeus harrisii*	0.63	0.10	0.00	0.00
Xanthidae (mud crabs)	0.84	0.07	0.99	0.03
Total portunid crabs	14.50	10.55	33.00	36.53
Blue crab *Callinectes sapidus*	11.97	9.60	28.57	35.08
Lesser blue crab *Callinectes similis*	0.42	0.04	0.00	0.00
Callinectes spp.	2.10	0.91	4.43	1.46
UID Decapoda	7.35	0.80	0.99	0.03
Total bony fishes	71.64	55.81	68.47	61.10
Atlantic silverside *Menidia menidia*	0.63	0.02	0.00	0.00
Bay anchovy *Anchoa mitchilli*	1.26	0.56	0.49	0.09
Bighead searobin *Prionotus tribulus*	0.21	<0.01	0.00	0.00
Blackcheek tonguefish *Symphurus plagiusa*	0.21	0.22	1.48	0.83
Atlantic croaker *Micropogonias undulatus*	0.42	2.00	5.42	7.76
Gobies *Gobiosoma* spp.	0.42	0.01	0.00	0.00
Atlantic menhaden *Brevoortia tyrannus*	24.58	27.35	8.87	15.39
Striped mullet *Mugil cephalus*	1.47	2.40	0.00	0.00
White mullet *Mugil curema*	1.05	4.48	2.46	6.95
Mullets *Mugil* spp.	3.99	3.38	1.48	1.55
Mummichog *Fundulus heteroclitus*	0.63	0.83	0.00	0.00
Pinfish *Lagodon rhomboides*	4.62	2.39	10.34	10.07
Shrimp eel *Ophichthus gomesii*	0.21	0.01	0.49	1.86
Ophichthidae (snake eels)	3.36	0.91	4.93	2.95
Speckled worm eel *Myrophis punctatus*	2.10	0.44	4.43	4.68
Spot *Leiostomus xanthurus*	4.41	2.33	7.39	1.89
Spotfin mojarra *Eucinostomus argenteus*	6.09	5.90	0.00	0.00
Southern flounder *Paralichthys lethostigma*	0.00	0.00	3.45	2.04
Summer flounder *Paralichthys dentatus*	0.00	0.00	0.49	0.32
Flounders *Paralichthys* spp.	0.00	0.00	0.99	1.87
Hogchoker *Trinectes maculatus*	0.00	0.00	0.49	0.17
UID bony fishes	15.97	2.59	15.27	1.70
Other	22.27	1.35	21.18	1.72

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TABLE 2. Interannual variation in diet composition (%FO = percent frequency of occurrence of prey; %W = percent contribution of prey by weight) for the two red drum age-groups sampled in the New River estuary. Diet information is examined for the four largest prey categories only and excludes several invertebrate prey of minor dietary importance (other bony fishes = all fish species except Atlantic menhaden; see Table 1).

	Age-0–1 red drum				Age-1–2 red drum			
	2007		2008		2007		2008	
Prey type	%FO	%W	%FO	%W	%FO	%W	%FO	%W
Blue crab	19.5	11.5	6.5	8.1	28.9	12.4	36.4	48.2
Penaeid shrimp	49.0	46.7	14.5	13.6	10.5	0.5	12.6	1.8
Atlantic menhaden	5.5	3.4	38.4	59.3	23.7	33.2	7.0	4.9
Other bony fishes	60.0	38.3	38.4	19.0	71.1	53.9	97.2	45.1

declining gut fullness in age-0–1 red drum were observed on sampling dates during July, August, October, and November 2007 and during July and August 2008 (Figure 4). Estimates of red drum G were relatively similar across these sampling periods, ranging from 0.074 to 0.154 (mean $G = 0.115$; Table 3). Mean gut fullness values (averaged over the 24-h sampling period on each date) ranged from 0.9% to 3.1% (mean = 1.5%) of red drum body mass among sample dates. The maximum gut fullness observed for a single age-0–1 red drum was 11.1% of body mass. The combination of G and mean gut fullness produced estimates of daily ration that ranged from 1.7% to 5.0% (mean = 3.4%) of red drum body mass per day. Age-1–2 red drum were captured during only 9 of the 12 diel sampling trips, and lower sample sizes hindered our ability to detect clear diurnal patterns in gut fullness on many dates. A clear declining pattern in gut fullness of age-1–2 red drum was only observed during May 2008 (Figure 4E, inset), producing a single G estimate of 0.131 (Table 3). Mean daily gut fullness values of age-1–2 red drum were low across all nine sampling dates, ranging between 0.1% and 1.3% (mean = 0.5%) of red drum body mass. The maximum gut fullness value observed for a single age-1–2 red drum was 4.8% of body mass. The daily ration estimate for the May 2008 sampling event was 1.2% of red drum body mass per day.

Quantifying Red Drum Predation

Mean prey size and the range of prey sizes consumed increased with red drum body size (Figure 5). Across the range of red drum body sizes examined, blue crabs represented many of the smaller prey eaten. Age-0–1 red drum fed on blue crabs ranging from 10 to 41 mm CW (mean = 23.5 mm CW), while age-1–2 red drum regularly preyed on blue crabs of up to 60 mm CW (mean = 40.3 mm CW). For age-0–1 red drum, Atlantic menhaden and other bony fish prey were mostly intermediate in size (~50–100 mm), and penaeid shrimp often represented the largest prey sizes eaten (>100 mm). For age-1–2 red drum, large prey were made up mostly of bony fishes, with blue crabs representing mainly smaller prey.

Using the mean daily ration estimate of 3.4%, we estimated that a single age-0–1 red drum consumed more than 200 g of blue crab prey during the rapid growth period, May–October (Figure 6A). During that same period, more than 500 g of Atlantic menhaden and nearly 600 g of penaeid shrimp were consumed by a single age-0–1 red drum. Consumption of penaeid shrimp and blue crabs increased throughout the summer, peaked during July (penaeid shrimp) or August (blue crabs), and remained at moderate levels during fall. Based on the single daily ration estimate of 1.2% for age-1–2 red drum, more than 1 kg of blue crab prey was consumed per fish during May–October (Figure 6B). Total consumption of penaeid shrimp by age-1–2 red drum was low (~40 g of shrimp eaten per individual), while consumption of Atlantic menhaden was moderate (~600 g eaten per individual). Blue crab consumption by age-1–2 red drum was concentrated during early summer, when this prey taxon represented over 60% of the diet by weight.

The 2009 stock assessment for Atlantic coast red drum (SEDAR 2009) included retrospective projections of abundance between 0.83×10^6 and 1.05×10^6 age-1–3 individuals for the northern region during the three most recent years (2005–2007). Application of von Bertalanffy and weight–length relationships enabled conversion of the numbers of individuals to biomass estimates that ranged between 1.25×10^6 and 1.88×10^6 kg. When combined with empirically derived daily ration estimates and diet composition for the New River estuary, the North Carolina red drum stock was estimated to consume between 1.3×10^6 and 2.0×10^6 kg of blue crab prey each year during May–October. Estimated consumption by the northern region stock was of similar magnitude for Atlantic menhaden (1.2×10^6 to 1.7×10^6 kg) and penaeid shrimp (0.9×10^6 to 1.4×10^6 kg) prey.

DISCUSSION

Red Drum Diet Composition

Observations in the New River estuary were closely aligned with results from previous studies of red drum food habits throughout the species' range, which have demonstrated the consistent occurrence of blue crabs, penaeid shrimp, and menhaden *Brevoortia* spp. in the diet along with ontogenetic

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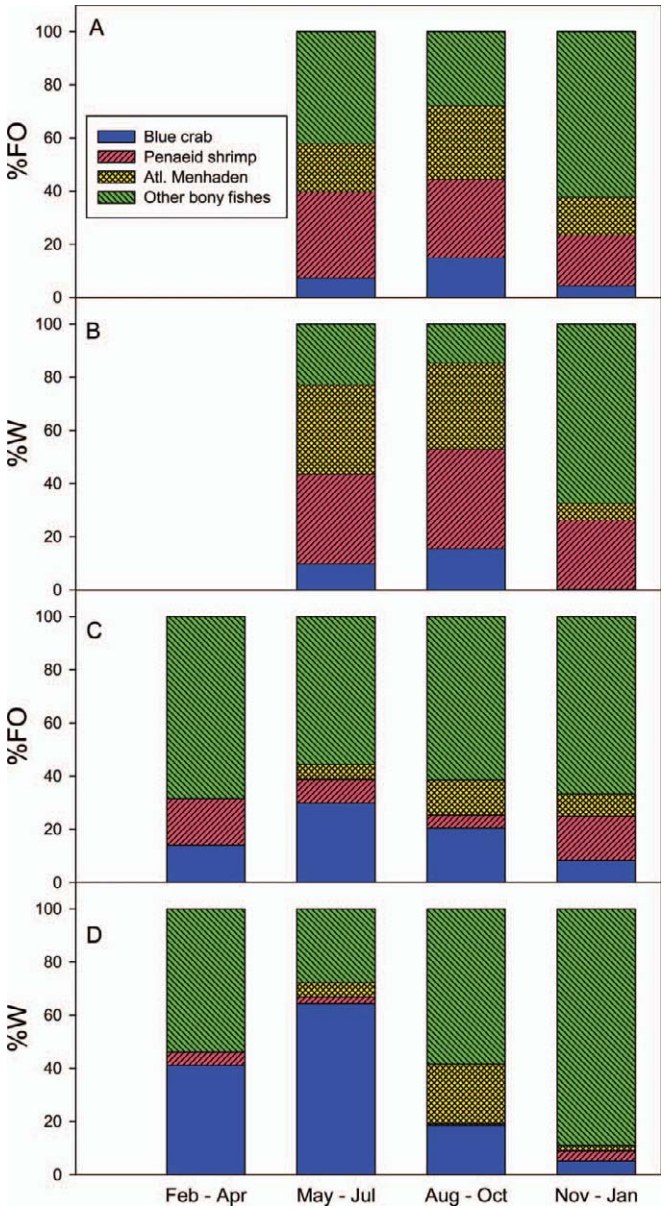


FIGURE 2. Seasonal variation in red drum diet composition in the New River estuary: **(A)** percent frequency of occurrence (%FO) of prey for age-0–1 red drum; **(B)** percent contribution of prey by weight (%W) for age-0–1 predators; **(C)** %FO of prey for age-1–2 red drum; and **(D)** %W for age-1–2 predators. Diet information is included only for the four largest prey categories (Atl. menhaden = Atlantic menhaden) and excludes several invertebrate prey types of minor dietary importance. The %FO is normalized to 100% to facilitate comparison among seasons.

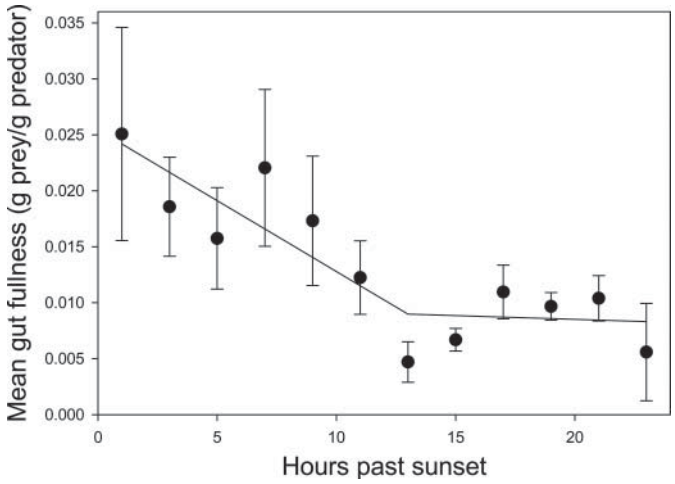


FIGURE 3. Mean (± SE) gut fullness (g of prey/g of predator) in red drum versus the number of hours past sunset during May–October in the New River estuary. Each symbol represents the mean gut fullness pooled across all dates for both age-groups (age-0–1 and age-1–2 red drum) within 2-h increments past sunset. The pattern is fitted using piecewise regression ($P = 0.0011$, $R^2 = 0.781$; constant = 0.25; segment 1 slope = −0.0013; segment 2 slope = not significant; breakpoint = 13 h past sunset).

increases in red drum reliance on larger crustaceans and other bony fishes (Pearson 1929; Boothby and Avault 1971; Bass and Avault 1975; Overstreet and Heard 1978; Wenner et al. 1990; Scharf and Schlicht 2000; Bacheler et al. 2009). In the U.S. South Atlantic, red drum food habits have generally shown this trend (Music and Pafford 1984; Wenner et al. 1990), although the diets of red drum examined in Georgia and South Carolina estuaries did not include as much blue crab or Atlantic menhaden prey as the diets of red drum in the present study. However, Bacheler et al. (2009) found that blue crabs were the dominant prey in terms of occurrence and weight for age-2 red drum in a small North Carolina estuarine creek, with fish prey becoming more important in winter. Regional differences among U.S. South Atlantic estuaries could be related to the specific habitat types or range of red drum ontogenetic stages sampled as well as to interannual fluctuations in prey availability.

During warmer periods (May–October), age-0–1 red drum diets were dominated by penaeid shrimp and Atlantic menhaden along with moderate amounts of blue crab. Winter diets included much greater proportions of other bony fishes; this was also observed for age-1–2 red drum. Bacheler et al. (2009) also reported large seasonal changes in red drum diets in a small North Carolina creek, and these changes were mostly related to the importance of fish prey during winter months. Less-extreme seasonal patterns in the relative contributions of crustacean and fish prey to red drum diets have also been noted in northern Gulf of Mexico estuaries (Guillory and Prejean 1999; Scharf and Schlicht 2000). For example, the difference between peak and minimum seasonal contributions (%W) of blue crabs to red drum diets in the New River (30-fold for age-0–1 red drum; 12.3-fold for age-1–2 red drum) was much higher than the seasonal differences in blue crab contribution reported by Scharf and Schlicht (2000; twofold) and Guillory and Prejean (1999; 2.3-fold). The greater seasonal variability in red drum food habits observed in North Carolina estuaries is likely related to changes in prey assemblages, which are driven by the larger seasonal fluctuations in estuarine water temperatures that typify the mid-Atlantic U.S. coast (Engle and Summers 1999) relative to the more tropical

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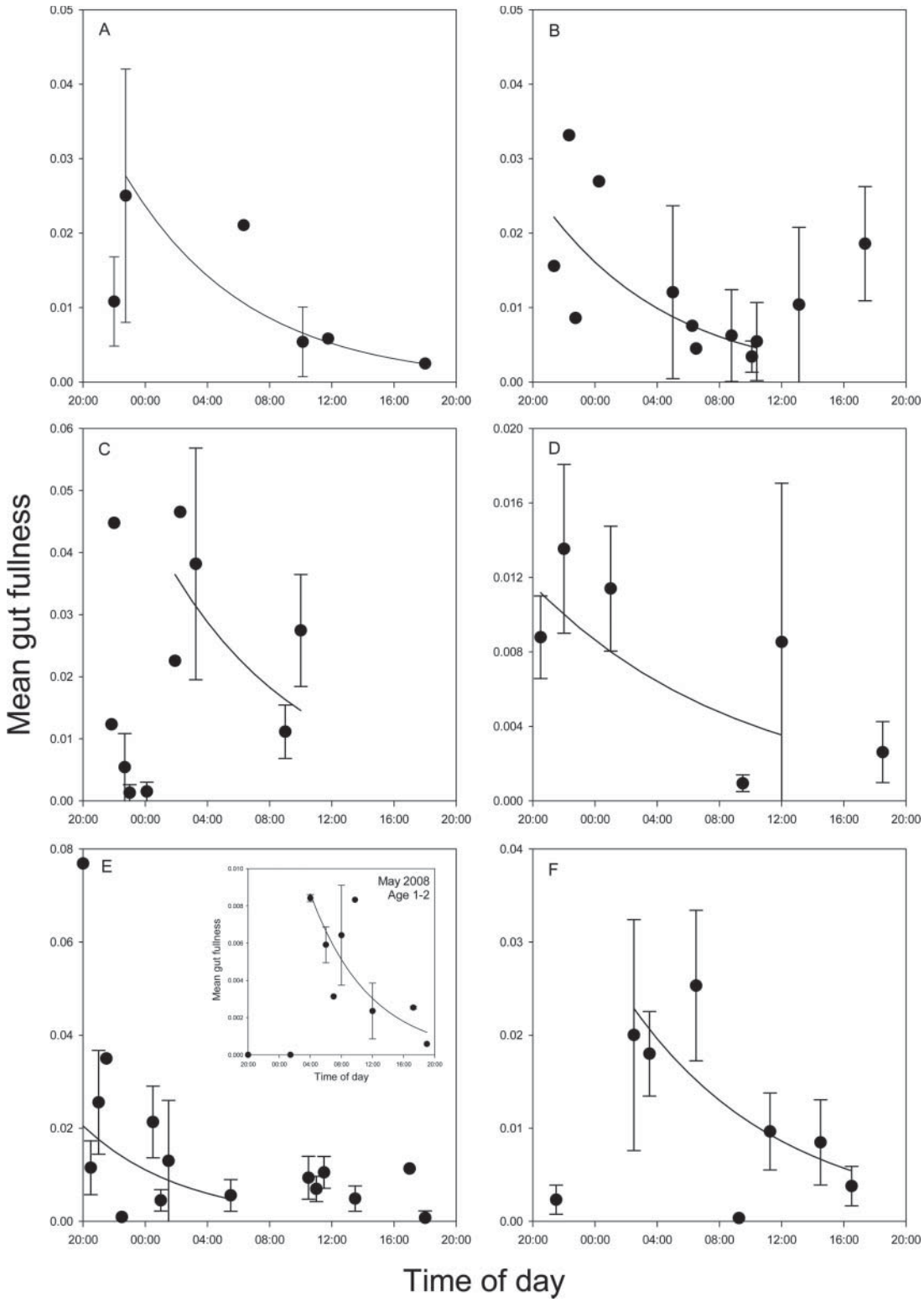


FIGURE 4. Mean (±SE) gut fullness (g of prey/g of predator) in age-0–1 red drum versus time of capture (beginning at 2000 hours [8:00 PM] in each panel) during **(A)** July 2007, **(B)** August 2007, **(C)** October 2007, **(D)** November 2007, **(E)** July 2008, and **(F)** August 2008, representing dates when declining gut fullness patterns allowed estimation of gastric evacuation rates (see Table 3). Each symbol represents the mean gut fullness per net set. Absence of error bars indicates that only one fish was captured in a given net set. Note the slight changes in scale among *y*-axes. For age-1–2 red drum, the evacuation rate could be estimated during only one time period (May 2008); the decline in gut fullness for those fish is presented as an inset in panel E.

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TABLE 3. Estimates of gut fullness, instantaneous gastric evacuation rate (G), and daily ration for red drum by age-group during each diel sampling event (Temp = daily mean water temperature; n = number of red drum captured). Gut fullness is the mean (maximum observed in parentheses) for all fish captured during each sampling event; G was calculated using the mean gut fullness values for each independent net set during a sampling event. Daily ration is expressed as grams of prey per gram of predator per day. Empty cells (–) represent dates when gut fullness data were insufficient to estimate G.

		Age-0–1 red drum				Age-1–2 red drum			
Date	Temp (°C)	n	Gut fullness	G	Daily ration	n	Gut fullness	G	Daily ration
23–24 Jul 2007	27.5	14	0.0116 (0.0420)	0.126	0.0350	2	0.0012 (0.0024)	–	–
25–27 Aug 2007	30.6	23	0.0106 (0.0331)	0.121	0.0309	8	0.0057 (0.0151)	–	–
14–16 Sep 2007	25.1	12	0.0132 (0.0268)	–	–	7	0.0029 (0.0095)	–	–
12–14 Oct 2007	22.3	23	0.0185 (0.0702)	0.114	0.0504	2	0.0131 (0.0259)	–	–
16–18 Nov 2007	12.6	63	0.0094 (0.0466)	0.074	0.0167	0	–	–	–
19–21 May 2008	25.2	10	0.0272 (0.0589)	–	–	19	0.0037 (0.0131)	0.131	0.0116
12–14 Jun 2008	27.3	14	0.0314 (0.1114)	–	–	18	0.0101 (0.0481)	–	–
24–26 Jul 2008	28.8	63	0.0111 (0.0769)	0.154	0.0411	8	0.0031 (0.0090)	–	–
28–30 Aug 2008	27.4	61	0.0120 (0.0761)	0.103	0.0297	3	0.0006 (0.0017)	–	–
22–23 Sep 2008	23.9	46	0.0101 (0.0497)	–	–	6	0.0020 (0.0062)	–	–
23–24 Oct 2008	16.2	8	0.0108 (0.0221)	–	–	0	–	–	–
26–27 Nov 2008	10.0	22	0.0108 (0.0358)	–	–	0	–	–	–

conditions and more stable seasonal temperatures in the northern Gulf of Mexico. Observations by Posey et al. (2005) support the notion that winter represents a seasonal period of low juvenile blue crab abundances in the New River estuary due to (1) the crabs' movement toward deeper waters in the vicinity of the inlet and (2) the crabs' burial in the sediment.

Changing prey availability over broader temporal scales can also generate interannual differences in diet composition. Red drum have been generally described as opportunistic predators, and observed associations between their diets and prey availability among seasonal periods (Scharf and Schlicht 2000) support the notion that red drum can adapt behaviorally to changes in prey community composition. During this study, age-0–1 red drum exhibited large interannual differences in the contributions of penaeid shrimp and Atlantic menhaden to the diet. Age-1–2 red drum also differed in the amount of Atlantic menhaden prey that was included in the diet between study years, whereas penaeid shrimp were consistently eaten at low levels. Each of these prey taxa has demonstrated a propensity for large interannual fluctuations in year-class size (e.g., Warlen 1994), which would generate considerable variation in the availability of these taxa as estuarine prey resources from year to year. In contrast, the contributions of blue crabs and other bony fishes to red drum diets were relatively consistent between study years, suggesting lower levels of fluctuation in these prey resources.

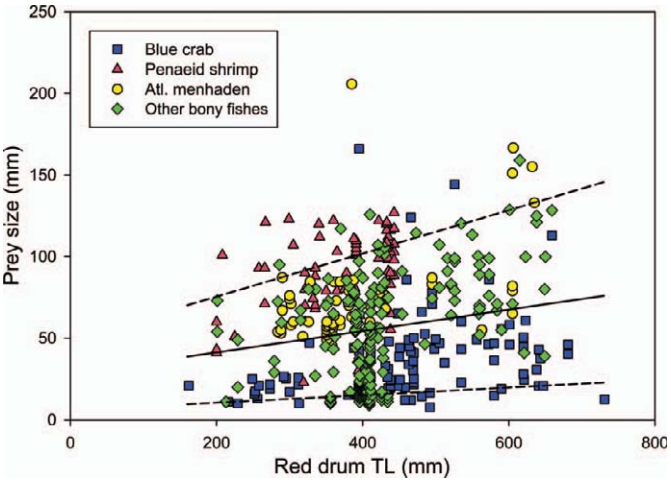


FIGURE 5. Prey sizes eaten versus total length (TL) of red drum for the four major prey categories (Atl. menhaden = Atlantic menhaden). The solid line indicates mean prey size estimated based on least-squares regression; dashed lines represent the estimated upper (95th percentile) and lower (5th percentile) bounds of the distribution based on quantile (least absolute deviation) regression (Scharf et al. 1998).

Diel Feeding Patterns and Possible Biases in Daily Ration Estimates

Patterns of red drum gut fullness, which peaked during darkness, suggest that foraging activities were most likely initiated during the evening crepuscular period around sunset. Gut fullness was generally low throughout the day, providing an indication that red drum in the New River had ceased or considerably reduced their feeding activity during daylight hours. Dresser and Kneib (2007) found that acoustically tagged juvenile red drum in a Georgia salt marsh only displayed considerable movement during daylight hours and on flood tides. Individual fish vacated structured habitat near daily high tides, presumably to take advantage of access to the flooded marsh surface to forage. Dresser and Kneib (2007) suggested that red drum may have remained stationary during nighttime flood tides to avoid predation or due to a decrease in success of visual foraging. Importantly, their

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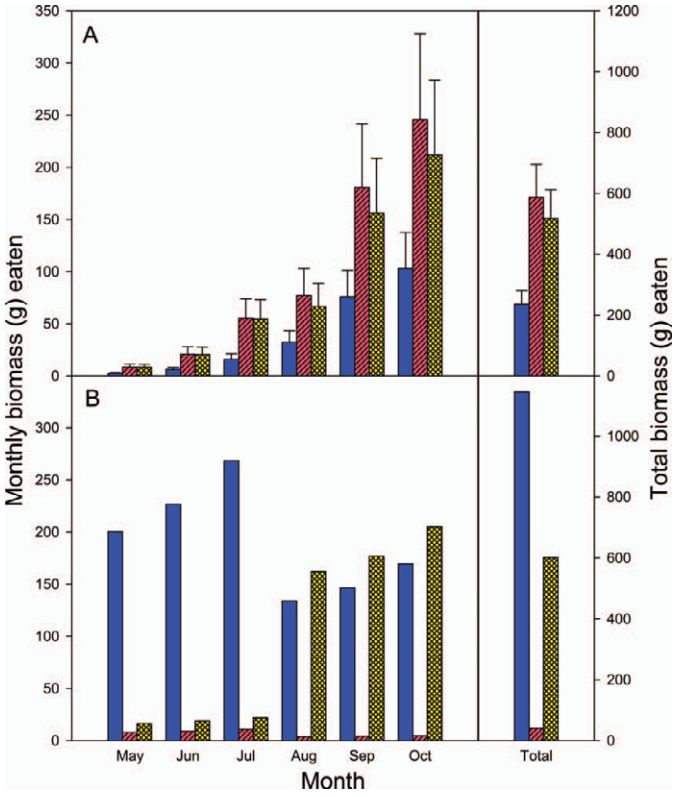


FIGURE 6. Estimated biomass of prey eaten by a single red drum in the New River estuary during each month (May–October), as calculated from field estimates of daily ration and diet composition: **(A)** biomass consumed by an age-0–1 fish; and **(B)** biomass consumed by an age-1–2 fish. Calculations were made for three major prey types (blue crabs, penaeid shrimp, and Atlantic menhaden). Total biomass eaten by a single red drum during the entire 6-month period is illustrated at the far right of each panel (secondary *y*-axis). Error bars (+SD) were calculated for each prey type and month by using the observed SD for red drum daily ration. No error bars are shown for age-1–2 red drum since only one estimate of daily ration was available. The SDs for estimates of total biomass eaten were calculated after first pooling the variance estimates for each month.

study site was located in a channelized tidal salt marsh that was subject to tidal ranges of over 2 m, which significantly altered the habitat type available to the fish during each tidal cycle. Tidal range in the New River estuary is generally less than 1 m and can be erratic depending on the prevailing winds; therefore, available shallow-water habitat is relatively homogeneous regardless of tidal stage. Both crepuscular and nocturnal feeding patterns have been documented previously for red drum (Bass and Avault 1975; Minello and Zimmerman 1983; Guillory and Prejean 1999). In addition, Bacheler et al. (2009) found that habitat use by juvenile and subadult red drum was positively correlated with an index of total prey abundance in a North Carolina creek, suggesting that red drum diel movements are strongly influenced by prey availability. In our study, passive capture techniques yielded few red drum during daylight hours, indicating reduced movement and feeding during this time (Hayward et al. 1989). Even with the use of active gear, the inability to collect large numbers of red drum during all parts of the diel cycle limited our ability to conduct a complete assessment of diel feeding patterns, and thus we cannot rule out the possibility that diurnal feeding rates of red drum are higher than those estimated here.

The field collection techniques used to capture red drum and to retrieve their gut contents can produce additional variation in gut fullness values and resulting estimates of *G* and daily ration. Strike-setting by use of a monofilament trammel net offered a minimal amount of bias while producing high catch per unit effort. Actively fishing the net reduced the amount of time during which fish were entangled and potentially stressed. Although the total gear deployment time was typically short (<40 min), large catches of target and nontarget species sometimes extended the total time of set and retrieval to 1–2 h. Fish that were still in the net or that were held in the live well were no longer able to feed, and they continued to digest the food in their stomachs; thus, digestion occurring between the time of capture and the time of gastric lavage potentially resulted in the underestimation of gut fullness. Conversely, when fish are experiencing stress (e.g., 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 that are captured in gill nets can also produce a negative bias in gut fullness estimates. Sutton et al. (2004) found that regurgitation rates of striped bass *Morone saxatilis* depended on the mode of entanglement, with the lowest rates occurring for fish that were gilled or simply entangled. Due to the design and mesh sizes of the trammel net used in this study, the majority of captured age-0–1 red drum were gilled, whereas the majority of age-1–2 red drum were entangled. Thus, potential rates of regurgitation during active sampling were likely minimized.

Gastric lavage techniques have been used to retrieve gut contents from numerous fishes and generally have proven effective (Light et al. 1983). However, the potential exists for incomplete removal of large prey items during gastric lavage (Hartleb and Moring 1995). During our study, a subset of red drum ($n < 15$) was sacrificed after lavage, and examination of these fish confirmed the complete removal of gut contents and thus a low potential for bias in gut fullness estimates. We found that it was possible to palpate the ventral surface of the red drum in order to detect the presence of any prey remaining after gastric lavage. Similar success with gastric lavage of red drum was reported by Bacheler et al. (2009). However, the use of gastric lavage could have led to another systematic bias in the estimation of evacuation rates and daily ration. Since soft-bodied prey items reach more advanced states of digestion quickly, the process of flushing prey from the stomach with water would often result in these prey items being rinsed from the gut in mostly liquid form. Portions of liquified prey were able to pass through prey sorting sieves, and thus their contributions to the diet by weight were likely underestimated. If gut fullness data had been obtained by sacrificing the fish and retaining and weighing the well-digested prey, the resulting %W estimates might have been

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higher. However, the inability to accurately measure highly digested, liquified prey may have also caused estimates of *G* to be higher, thereby producing a negligible net effect on estimates of red drum daily ration. Differential prey digestion can also bias estimates of dietary contribution (Hyslop 1980), but its effects can be lessened through evaluation of multiple diet indices (e.g., %FO and %W) and by concentrating the sampling effort during the peak feeding hours. During this study, most red drum were captured during the evening and overnight periods associated with peaks in gut fullness, which likely helped to minimize this bias.

In teleost fishes, growth efficiency is typically highest during the larval stages, when it is coupled with high ingestion rates. Houde and Zastrow (1993) reported mean larval gross growth efficiency (GGE) of 30% for a range of species, combined with ingestion rates that were mostly between 40% and 65% of body mass. Fish weight-specific consumption and growth efficiency generally decline throughout ontogeny, with noted exceptions in first-year juveniles of some species (e.g., Buckel et al. 1995; Shoji et al. 2011). Given that daily ration estimates for red drum in this study averaged between 1.2% per day (age-1–2 fish) and 3.4% per day (age-0–1 fish), GGE would have had to be approximately 50% to achieve the observed specific growth rates (0.56% per day for age-1–2 fish; 1.73% per day for age-0–1 fish). Thus, our field estimates of red drum daily ration are most likely biased low. Recent experimental results have confirmed that red drum GGE is considerably less than 50%, ranging between 13% and 16% for fish of comparable sizes held at summer and fall water temperatures (Gillum et al. 2012). When combined with observed field growth rates, this level of GGE would necessitate daily consumption rates of 11–13% per day for age-0–1 red drum and 3–4% per day for age-1–2 fish. Maximum consumption rates for red drum that were held in laboratory aquaria and that were offered unlimited prey ranged from 6% to 19% per day depending on body size and water temperature (Gillum et al. 2012), indicating that the feeding rates required to achieve the rates of growth observed in this study would still be below physiological limits. Field-based approaches will often underestimate fish daily ration, and we have discussed several possible causes of bias in our study (e.g., inability to capture large numbers of fish during the day, continued prey digestion during capture in gill nets and trammel nets, and the use of gastric lavage). Given that environmental conditions (e.g., warm temperatures and abundant prey resources) in the New River should be conducive to the high consumption rates that are necessary to achieve rapid growth during summer and fall months, we surmise that (1) red drum daily ration levels are higher than those estimated during our field study and (2) red drum may regularly approach their maximum feeding potential.

Potential Prey Impacts

As emphasis on more holistic, ecosystem-based fishery management approaches has grown, quantification of the population-level impacts of predation is becoming more frequent. Predation can be responsible for the majority of the natural mortality in juvenile prey fish within estuarine systems during some years (Buckel et al. 1999; Tuomikoski et al. 2008), can impact prey population rebuilding times (Harvey et al. 2008), and can potentially limit the effectiveness of marine reserves (Beaudreau and Essington 2009). During this study, we estimated that an individual age-0–2 red drum (i.e., both age [size] groups combined) consumed nearly 1.5 kg of blue crab, over 0.5 kg of penaeid shrimp, and over 1 kg of Atlantic menhaden (in addition to other prey) during the peak growing season. When extrapolated to the entire North Carolina coast, projections of annual aggregate consumption of these three prey types by juvenile and subadult red drum ranged from 3.4×10^6 to 5.1×10^6 kg. Commercial landings of penaeid shrimp and blue crabs in North Carolina waters during 2006–2010 averaged just over 3×10^6 and 12×10^6 kg, respectively, and landings of Atlantic menhaden were just over 0.5×10^6 kg.

Although the dominant prey taxa consumed by red drum can exhibit considerable population swings that are driven largely by oceanographic processes (e.g., Rice et al. 1999), predation on the estuarine life stages may contribute significantly to population regulation. As a case in point, Quinlan and Crowder (1999) concluded that estuarine biotic and abiotic processes during the late larval and early juvenile life stages were likely to have the greatest influence on Atlantic menhaden population dynamics. Similarly, along the northern Gulf of Mexico coast, strong associations between the abundance of juvenile blue crabs and patterns of larval supply generally dissipated less than 2 weeks after initial settlement, and apparent density-dependent declines in juvenile crab abundance suggested that predation was a structuring force (Heck et al. 2001). Given that our population-level estimates of prey consumption by red drum are likely conservative due to underestimation of daily ration, the potential for red drum to represent a significant source of mortality for estuarine prey is apparent. Further, the statewide consumption estimates were only calculated for May–October, the period during which daily ration was estimated, meaning that 6 months of feeding by overwintering red drum are not included. If red drum stock biomass increases in the U.S. South Atlantic, it may be necessary to incorporate the potential impact of this recovering predator population into fishery management plans for valuable estuarine resource species (e.g., Jurado-Molina et al. 2005; A'mar et al. 2010). Future work will require spatially explicit estimates of both red drum density and prey density over time to enable calculation of prey loss rates and the relative contribution of red drum predation to overall mortality.

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