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Consumption and gastric evacuation in juvenile red drum *Sciaenops ocellatus* (Linnaeus): Estimation of prey type effects and validation of field-based daily ration estimates

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ABSTRACT

The red drum *Sciaenops ocellatus* (Linnaeus) is a dominant member of southeastern U.S.A. estuarine systems that feeds on numerous species of commercial and recreational value. Recovering red drum stocks highlight the need for quantification of feeding habits and rates of consumption to assess predatory impact. To validate field-based estimates of gastric evacuation rates and daily ration, a series of controlled laboratory experiments was completed for juvenile and sub-adult red drum (~60–600 g). Influential factors examined included water temperature (17 °C and 27 °C), prey type (fish and crustacean prey), and red drum body size (small $\bar{x}=76.3$ g; large $\bar{x}=429.2$ g). Average maximum consumption rate varied between red drum body sizes and water temperatures. Small drum fed at a mean (±SD) rate of 18.9 ± 0.6% body mass d^{-1} at 27 °C and 9.6 ± 0.6% body mass d^{-1} at 17 °C, while large drum fed at a rate of 12.5 ± 0.8% body mass d^{-1} at 27 °C and 6.3 ± 0.4% body mass d^{-1} at 17 °C. Gross growth efficiency was generally consistent across factors, ranging between 13.2 and 16.3%, with small red drum being slightly more efficient. The rate of gastric emptying was influenced most by temperature and ranged from 4.0 to 9.4% h^{-1}. The red drum body sizes and prey types we tested demonstrated only modest effects, with slightly faster evacuation rates by smaller red drum and for anchovy prey. Among the eight factor combinations (red drum size × water temperature × prey type) tested during gastric evacuation trials, half (four) of the relationships were best described by the square root model. However, model selection approaches revealed that multiple models provided adequate fit in nearly all cases. Laboratory estimates of red drum gastric evacuation and maximum consumption confirmed that previous field-based estimates were plausible.

1. Introduction

During the past decade there has been much effort directed toward the development of frameworks for the implementation of ecosystem-based fisheries management (Fletcher et al., 2010; Francis et al., 2007; Marasco et al., 2007). A common theme found within many of these frameworks is the inclusion of trophic interactions to account for variability in natural mortality rates in addition to the impacts of harvest. Several recent examples highlight the successful incorporation of predator–prey interactions in multispecies age-structured population models and their potential to inform management (A'mar et al., 2010; Hollowed et al., 2000; Jurado-Molina et al., 2005). Analyses spanning multiple trophic levels have revealed that the population dynamics of fishery species at intermediate trophic levels will often be driven by natural mortality rates that are considerably greater than rates of fishing mortality (Buckel et al., 1999a; Gaichas et al., 2010).

Upper trophic level predators can represent dominant forces in shaping aquatic ecosystem processes. Direct mortality induced by predation can alter prey demographics and potentially limit prey recruitment when focused on early life stages (Bailey, 1994; Sheaves, 2001). Increasingly, predation has been estimated to be responsible for the majority of natural deaths within prey cohorts (Buckel et al., 1999b; Tuomikoski et al., 2008), and its incorporation into quantitative assessments has revealed predation as a regulatory mechanism capable of affecting prey population biomass and growth (Harvey et al., 2008; Hollowed et al., 2000).

The estimation of predatory impact requires detailed knowledge of prey selectivity and predator consumption rates. Traditionally, prey-specific feeding rates are either obtained empirically by combining diet information with in situ patterns of gut fullness (Eggers, 1979; Elliott and Persson, 1978) or by estimating bioenergetic parameters in a mass-balance model (Kitchell et al., 1977). When using field-based approaches, several issues can introduce bias into estimates of prey consumption, including variable rates of digestion among

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prey types, irregular predator feeding patterns, temporally variable sample sizes, and seasonal environmental changes (Beaudreau and Essington, 2009; Carpentieri et al., 2008). Controlled laboratory experiments can serve to validate field-based estimates of consumption and gastric evacuation while evaluating the influence of factors such as water temperature, prey type, meal size, and predator ontogenetic stage (Berens and Murie, 2008; Bromley, 1994; Buckel et al., 1995). Comparison of field and laboratory-based feeding rates aids in quantifying uncertainty and determining the boundaries for realistic parameter estimates (Beaudreau and Essington, 2009).

The red drum *Sciaenops ocellatus* (Linnaeus) is distributed in near shore and estuarine waters of the southeast U.S.A. Atlantic coast and throughout the Gulf of Mexico (Mercer, 1984). Adult red drum spawn during the summer and fall in near shore waters (Comyns et al., 1991; Wilson and Nieland, 1994) and, after settlement, red drum remain in estuarine and coastal ocean habitats during juvenile and sub-adult life stages, until approximately age three. Past studies have revealed that, during estuarine residency, juvenile and sub-adult red drum feed heavily on several important fishery resource species, including Penaeid shrimp, blue crab *Callinectes sapidus* (Rathbun), and several fish species (Boothby and Avault, 1971; Overstreet and Heard, 1978; Scharf and Schlicht, 2000). After a period of overexploitation, the implementation of strict harvest regulations during the 1990's has contributed to population recovery in red drum throughout their range. The most recent stock assessment (ASMFC, 2010) for Atlantic red drum concluded that overfishing is likely not occurring, with harvest rates below target levels for much of the past decade. Recovering red drum stocks could have sizeable impacts on estuarine prey populations, highlighting the need for quantitative information on trophic interactions.

This study reports on a series of controlled laboratory experiments conducted to estimate maximum consumption, gross growth efficiency, and gastric evacuation rates of red drum fed natural prey. Experiments were designed to validate previous field-based estimates of red drum gastric evacuation and daily ration, and to quantify the influence of several factors including prey type, predator body size, and water temperature on red drum feeding physiology.

2. Methods

2.1. Red drum collection and husbandry

Small ($\bar{x}=76.3$ g; SD = 12.3 g; range = 55.8–104.9) red rum were collected during early summer using a 30.2 m long × 1.8 m deep beach seine, with 6.4 mm mesh wings and a 3.2 mm mesh bag. Large ($\bar{x}=428.8$ g; SD = 115.4; range = 198.4–618.8) red drum were collected during late summer by active strike netting using a trammel net (183 m long × 2.1 m deep with 35.6 cm stretched mesh in the outer walls and a 6.4 cm stretched mesh inner panel) which was set and retrieved using a small skiff. After capture, fish were transported to the laboratory in aerated containers (142 l) containing ambient estuarine water and acclimated to captive conditions over several hours. Water temperatures (~27 °C) and salinities (15–20) within the laboratory seawater system were established to mimic ambient summer conditions typically observed in mesohaline reaches of the estuary.

Laboratory populations of red drum were held in one of two recirculating seawater systems. The larger system was approximately 5000 l in capacity and included six 700 l circular tanks maintained at a flow rate of ~60–80 l/min. The second system was about half the capacity (~2500 l) and included six 350 l circular tanks maintained at a flow rate of ~30–40 l/min. Throughout acclimation and all experimental trials, salinity was maintained between 15.9 and 21.1 through fresh and saltwater additions to compensate for evaporative loss. Water temperatures were maintained at specified levels (±1 °C) for each set of experimental trials by adjusting room air temperature and using submersible heaters equipped with digital controllers. Red drums were fed daily with a combination of live prey fishes and previously frozen fish at rations approximately equal to 5–10% of their body mass. Live prey fishes were necessary to maintain natural predator feeding behavior for subsequent consumption trials and were collected using beach seines, cast nets, and minnow traps, then acclimated to laboratory conditions. Prey fish species included pinfish *Lagodon rhomboids* (Linnaeus), striped killifish *Fundulus majalis* (Walbaum), spotfin mojarra *Eucinostomus argenteus* (Baird and Girard), Atlantic silverside *Menidia menidia* (Linnaeus), and mummichog *Fundulus heteroclitus heteroclitus* (Linnaeus). Prey fishes were fed daily with a commercially prepared food.

2.2. Experimental design — estimation of maximum consumption rate

Red drum maximum consumption rate was estimated in four separate experimental trials, each of which tested one of four red drum body size (small or large) × water temperature (17 °C or 27 °C) treatment combinations (Table 1). Each experimental trial consisted of groups of three red drum assigned to one of six replicate 700 l tanks. Prior to the start of each experimental trial, red drum were starved for 24 h to allow for gut emptying. Each fish was weighed (±0.1 g) and measured (±1 mm), then assigned to a tank to ensure no significant differences in mean red drum size among replicate tanks within any of the four experimental trials (ANOVA P-values = 0.70–0.99).

Live prey fishes were provided continuously for seven days. Only fishes of appropriate size (<25% of red drum length) were offered as prey to minimize energetic costs associated with failed capture attempts and excessive prey handing. Prey biomass was maintained at 75% and 50% of total red drum mass in each tank during warm (27 °C) and cool (17 °C) water temperature trials, respectively. Maximum consumption rates observed previously for other temperate marine fishes at similar body sizes have generally ranged between 10 and 30% body mass d^{-1} depending on temperature (e.g., Buckel et al., 1995; Hartman and Brandt, 1995). Therefore, the prey biomass levels used here were chosen to ensure that prey were never depleted during experimental trials. Tanks were monitored daily with dead prey removed and weighed, and live prey weighed and added as needed based upon visual inspection of remaining prey biomass levels. At the conclusion of each seven day trial, all remaining prey fishes were collected and weighed. After an additional 24 h to standardize gut fullness, red drum were re-weighed and measured.

2.3. Experimental design — estimation of gastric evacuation rate

Gastric evacuation rates of red drum were estimated in a series of replicate experimental trials designed to test the effects of red drum body mass (small or large), water temperature (17 °C or 27 °C), and prey type (fish or crustacean) (Table 2). Each experimental trial consisted of a single red drum assigned to one of six replicate 350 l tanks. Fish were selected randomly, with replacement, from the entire laboratory population of red drum, which was subdivided in larger holding tanks. All fish in a single holding tank were starved for 24 h, and then six individuals were selected at random, weighed (±0.1 g) and measured (±1 mm), and placed separately into one of the six experimental tanks for an additional 24 h starvation period. Each of the six tanks was then randomly assigned one of eight post-prandial times (0.5, 1, 2, 3, 4, 6, 8, or 10 h), which were replicated three times for each treatment combination.

Each red drum was fed weighed amounts of previously frozen and then thawed fish prey, either striped mullet *Mugil cephalus* (Linnaeus) or striped anchovy *Anchoa hepsetus* (Linnaeus), or crustacean prey, either northern brown shrimp *Farfantepenaeus aztecus* (Ives) or northern white shrimp *Litopenaeus setiferus* (Linnaeus). All prey species used occur naturally in red drum diets (Facendola, 2010; Scharf and Schlicht, 2000). Meal size was maintained at roughly 3% red drum body mass for

Table 1
Mean (SD) initial and final red drum body size (g), initial prey biomass (g), daily prey added (g), total prey removed (g), and total prey eaten (g) for each experimental treatment tested to estimate red drum maximum consumption rate. Initial prey biomass was on day 1; daily prey added = average during days 2–7. Total prey removed includes both daily removal of any dead prey and removal of all remaining live prey at the end of seven days. Water temperature (°C) includes the mean and the observed range; n = the number of replicate tanks. The observed mean (SD) for maximum consumption (% red drum body mass d^{-1}), gross growth efficiency (red drum growth/prey mass consumed × 100), and weight-specific growth (% d^{-1}) are presented for each treatment.

Treatment	Small × warm	Small × cool	Large × warm	Large × cool
Initial body size	79.41 (3.74)	73.13 (2.35)	414.65 (51.91)	450.19 (62.16)
Final body size	98.58 (5.01)	80.89 (2.57)	465.13 (55.63)	480.96 (66.89)
Initial prey biomass	226.10 (2.98)	217.48 (9.29)	932.45 (116.43)	688.28 (106.09)
Daily prey added	54.46 (6.23)	35.44 (18.17)	123.90 (48.01)	76.98 (36.09)
Total prey removed	199.37 (28.67)	274.85 (18.71)	532.07 (92.95)	537.87 (70.94)
Total prey eaten	353.48 (24.33)	155.28 (9.48)	1143.78 (84.47)	612.32 (72.94)
Water temperature	26.6 (26.5–26.9)	17.6 (17.4–18.2)	26.7 (26.2–27.9)	17.5 (17.0–17.9)
n	6	6	6	6
Max consumption	18.9 (0.55)	9.6 (0.61)	12.5 (0.83)	6.3 (0.37)
Gross growth efficiency	16.3 (1.61)	15.0 (2.06)	13.2 (0.41)	14.1 (1.91)
Specific growth rate	3.1 (0.28)	1.4 (0.23)	1.7 (0.13)	0.9 (0.11)

each gastric evacuation trial. Meal size averaged 3.05% with a standard deviation of 0.39% across all trials (n = 192), with only the set of trials that included large red drum feeding on shrimp prey at warm temperatures having a significantly different meal size ($\bar{x}$ = 3.45% ± 0.63%). Each red drum was observed during feeding to record the time of consumption of the entire prey item. At the designated end point time, the fish was captured and the remaining stomach contents were retrieved by gastric lavage. Stomach contents were regurgitated onto a fine mesh (100 μm) sieve and then blotted dry to remove excess water, prior to being weighed (± 0.1 mg). Previous experimental work with red drum revealed 100% prey recovery using gastric lavage techniques (Facendola, 2010). Red drums were then returned to an empty holding tank. The process of selection of fish for subsequent sets of gastric evacuation trials ensured that, after participating in a trial set, an individual red drum would not be used in the following two sets of trials. Therefore, for any of the eight treatment combinations (red drum body mass × water temperature × prey type), a single red drum individual could be used a maximum of twice. The protocol for all experiments conducted during this study was approved by the University of North Carolina Wilmington Institutional Animal Care and Use Committee (UNCW IACUC protocol #A0809-026).

2.4. Data analysis

Red drum maximum consumption rate was expressed as % body mass consumed d^{-1} on a per tank basis. Average daily biomass of prey eaten was divided by the mean size of red drum (n = 3) in each replicate tank, calculated for the duration of the trial as (mean final weight + mean initial weight)/2. Gross growth efficiency was calculated for each tank by dividing the total increase in red drum mass observed by the total prey biomass eaten during the seven day trial. Specific growth rate of red drum was calculated for each tank as the natural log of the mean final mass minus the natural log of the mean initial mass divided by seven days. The effects of red drum body mass and water temperature on maximum consumption rate, gross growth efficiency, and specific growth rate were evaluated using separate two-factor fixed effects ANOVA models. Assumptions of residual normality and homogeneity of variances were satisfied prior to running the ANOVA models.

Several models were fit to evaluate the effects of red drum body mass, water temperature, and prey type on red drum gastric evacuation rates. Linear, square root, and exponential models were fit to percent prey remaining as a function of post-prandial time for each of the eight treatment combinations. For each case, the linear (straight-line) model was tested for significant lack of fit by partitioning the residual sums of squares into pure error and error due to lack of fit. This was enabled because there were multiple (n = 3) responses at each value of post-prandial time. All candidate models were also compared using Akaike's Information Criteria (Burnham and Anderson, 2002) to determine the level of support for each model given the data. Separately, a single multivariable model was fitted to all available data to estimate the effects several factors simultaneously on the gastric evacuation rate. The model was originally presented by Temming and Andersen (1994) and includes general parameters for shape (α), the effects of predator mass (γ) the effects of water temperature (δ) and a constant (ρ). We used the reformulation of Anderson (1998), which models stomach contents remaining relative to initial meal size as a function of post-prandial time, in order to maintain homogeneity of variances. The model was expressed as:

$$S_t \Big/ S_0 = \left[1 - S_0^{(\alpha-1)} \rho (1-\alpha) t W^{\gamma} e^{(\delta T)}\right]^{(1-\alpha)^{-1}}$$

where S_0 = prey mass at time zero (initial meal size), S_t = prey mass at time t since consumption, W = predator mass, T = water temperature, α = the shape parameter, γ = the predator mass exponent, δ = the

Table 2
Red drum body mass × water temperature treatment, prey type, and mean (range) of red drum body mass (g) and water temperature (°C) used during gastric evacuation trials. n = the number of replicate tanks per trial, with each tank containing a single red drum.

Treatment	Prey type	Mean body mass (range)	Mean water temp (range)	n
Small × warm	Fish (*Anchoa hepsetus*)	79.2 (46.3–112.9)	26.6 (26.5–26.8)	24
Small × cool	Fish (*Anchoa hepsetus*)	76.6 (52.1–114.7)	17.6 (17.4–18.2)	24
Large × warm	Fish (*Mugil cephalus*)	427.5 (240.3–625.0)	26.2 (24.3–27.1)	24
Large × cool	Fish (*Mugil cephalus*)	485.2 (289.1–718.9)	16.7 (16.4–17.0)	24
Small × warm	Crustacean (Penaeid shrimp)	90.3 (52.5–133.7)	26.6 (26.5–26.6)	24
Small × cool	Crustacean (Penaeid shrimp)	103.9 (67.2–171.5)	17.6 (17.4–18.2)	24
Large × warm	Crustacean (Penaeid shrimp)	437.1 (247.8–611.3)	25.7 (24.7–27.1)	24
Large × cool	Crustacean (Penaeid shrimp)	469.8 (287.8–696.1)	17.2 (16.7–17.8)	24

water temperature exponent, and ρ = constant. Temming and Herrmann (2003) demonstrated that the specific effects on gastric evacuation of different prey types could be evaluated through estimation of ρ_i, where i = 1,2,….n to represent the number of different prey types, during subsequent model runs with other parameters fixed at values estimated during the initial full model run. For red drum, the model was first run with all available data to estimate the general parameters α, γ, and δ. In a second model run, the shape parameter (α) was fixed at a value of 0.5 and only γ and δ were estimated. Jobling (1981) and Anderson (1998) each concluded that using a gastric evacuation model with an exponent of 0.5 was most appropriate for predatory fishes. Then three separate final models were fit with the general parameters (α, γ, and δ) fixed to estimate the prey-specific parameter (ρ_i) for the three prey types used during gastric evacuation experiments (Penaeid shrimp, *A. hepsetus*, and *M. cephalus*). The two shrimp species were evaluated collectively as Penaeid shrimp. Prey-specific effects are presented graphically for a scenario that includes intermediate values, based on the range of values tested during laboratory experiments, for red drum body mass (271 g) and water temperature (22 °C), and a meal size of 3% of predator mass. All gastric evacuation models were fit with STATA (v. 10) Data Analysis and Statistical Software using the nonlinear least squares function when appropriate.

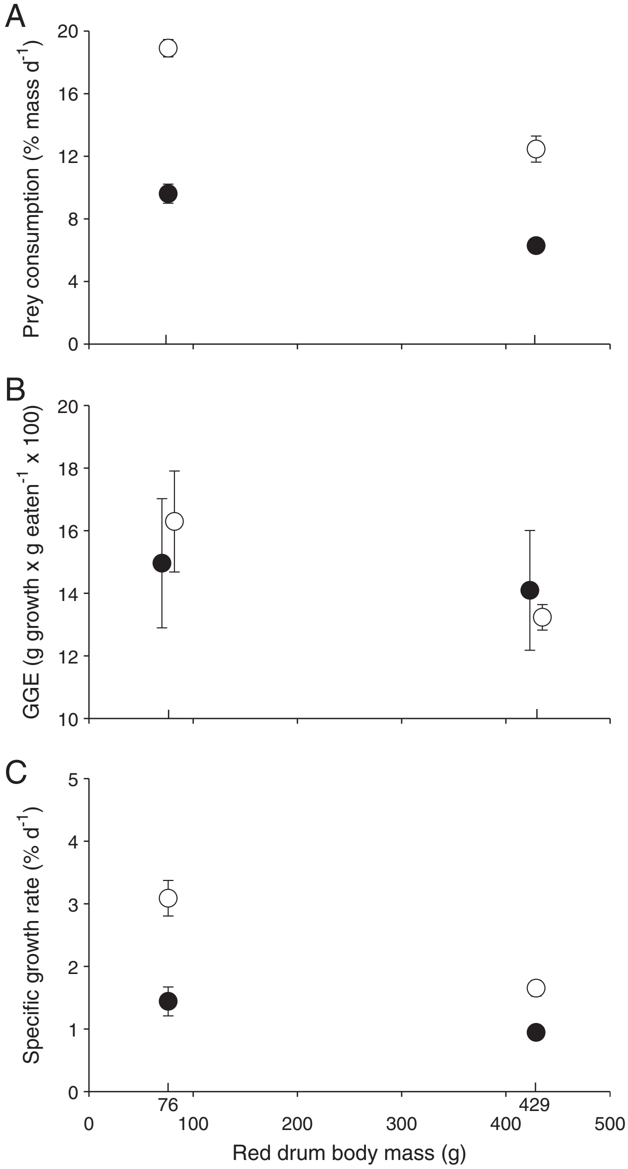

Fig. 1. Maximum consumption rates (A), gross growth efficiencies (B), and specific growth rates (C) of red drum as a function of body mass at two water temperatures (● = 17 °C; ○ = 27 °C). Response means are plotted at the mean red drum mass for each body size treatment (small = 76 g; large = 429 g). Error bars = ± 1 standard deviation.

3. Results

3.1. Maximum consumption

Both water temperature and red drum body size had considerable effects on estimates of maximum consumption rate, which ranged between 6.3 and 18.9% body mass d^{-1} (Table 1; Fig. 1A). About a two-fold difference in consumption was observed between warm (~27 °C) and cold (~17 °C) water temperatures, while differences between the body sizes tested were lower in magnitude. Larger ($\bar{x} = 429.2$ g) red drum consumed about one-third less of their mass per day compared with smaller ($\bar{x} = 76.2$ g) individuals. The results of ANOVA yielded significant main effects of water temperature and body size on consumption rate, along with a significant interaction (Table 3). Despite the interaction, both main effects could still be interpreted since the consumption response did not change direction across the range of water temperatures and body sizes tested (Fig. 1A). Additionally, the significance of the interaction was due to absolute differences in consumption between body sizes and temperature treatments. The relative differences in consumption were consistent for the temperature effect (~50% decrease at lower temperature for both body sizes) and the body size effect (~33% decrease at larger body size for both temperatures). Gross growth efficiency was fairly consistent across treatments and ranged between 13.2 and 16.3% (Table 1; Fig. 1B). The ANOVA revealed a significant effect of body size with smaller red drum achieving moderately higher gross growth efficiency on average (Table 3). Specific growth rates responded to water temperature and red drum body size similar to patterns of maximum consumption, with faster growth rates at warmer water temperatures and for smaller individuals (Table 1; Fig. 1C). ANOVA demonstrated significant effects of both water temperature and body size on red drum growth rates, with a significant interaction (Table 3). As with consumption, the growth responses did not change direction across the range of treatment factors, enabling the main effects to be interpreted despite the interaction.

Table 3
Results of three separate 2-factor fixed effects ANOVA's testing the effects of water temperature, red drum body size, and the water temperature × body size interaction on red drum maximum consumption rate, gross growth efficiency, and specific growth rate.

Source	Partial SS	df	MS	F	P
Max consumption rate					
Model	516.84	3	172.28	458.84	<0.0001
Water temperature	359.02	1	359.02	956.20	<0.0001
Body size	143.20	1	143.20	381.40	<0.0001
Temperature × Size	14.62	1	14.62	38.93	<0.0001
Error	7.51	20	0.38		
Total	524.34	23			
Gross growth efficiency					
Model	30.67	3	10.22	3.82	= 0.0258
Water temperature	0.33	1	0.33	0.12	= 0.7279
Body size	23.12	1	23.12	8.65	= 0.0081
Temperature × Size	7.22	1	7.22	2.70	= 0.1160
Error	53.48	20	2.67		
Total	84.15	23			
Specific growth rate					
Model	15.26	3	5.09	126.28	<0.0001
Water temperature	8.31	1	8.31	206.45	<0.0001
Body size	5.61	1	5.61	139.35	<0.0001
Temperature × Size	1.33	1	1.33	33.04	<0.0001
Error	0.81	20	0.04		
Total	16.06	23			

3.2. Gastric evacuation

Water temperature had the strongest effect on red drum gastric evacuation rates with moderate effects observed for body size and prey type. When feeding on crustacean (Penaeid shrimp) prey, the rates of gastric evacuation by red drum ranged from approximately 6.0–9.4%$\,h^{-1}$ (Fig. 2). The strong effect of water temperature was evident for both small (Fig. 2A) and large (Fig. 2B) red drum. Smaller red drum evacuated shrimp meals slightly faster (~7–9%$\,h^{-1}$) compared with larger red drum (~6–8%$\,h^{-1}$), but the difference was modest. Gastric evacuation relationships varied to a larger degree when red drum were fed fish prey, with rates ranging from less than 4%$\,h^{-1}$ to over 8%$\,h^{-1}$, depending on red drum mass and water temperature (Fig. 3). Similar to shrimp prey, the effect of water temperature was clearly evident for both small (Fig. 3A) and large (Fig. 3B) red drum. The body size effect was more pronounced for fish prey, with small red drum evacuating fish at faster rates than large red drum.

3.3. Gastric evacuation model selection

The model receiving the most support varied among the gastric evacuation treatment combinations and, in all but one case, two or more models could be interpreted as plausible (ΔAICc score<2 or $\omega_i \geq 20\%$; Burnham and Anderson, 2002) given the data (Table 4). Therefore, although the square root model received the highest support most often (4 treatment combinations), in each of those cases at least one other model was plausible. Interestingly, among the eight treatment combinations evaluated during gastric evacuation experiments, only one demonstrated a significant lack of fit of the simple linear (straight-line) model. With the exception of small red drum feeding at cooler water temperatures, the square root model was the most supported model for shrimp prey evacuation. In contrast, the most supported model for the evacuation of fish prey varied from an exponential model at cooler water temperatures to both linear and square root models at warmer water temperatures.

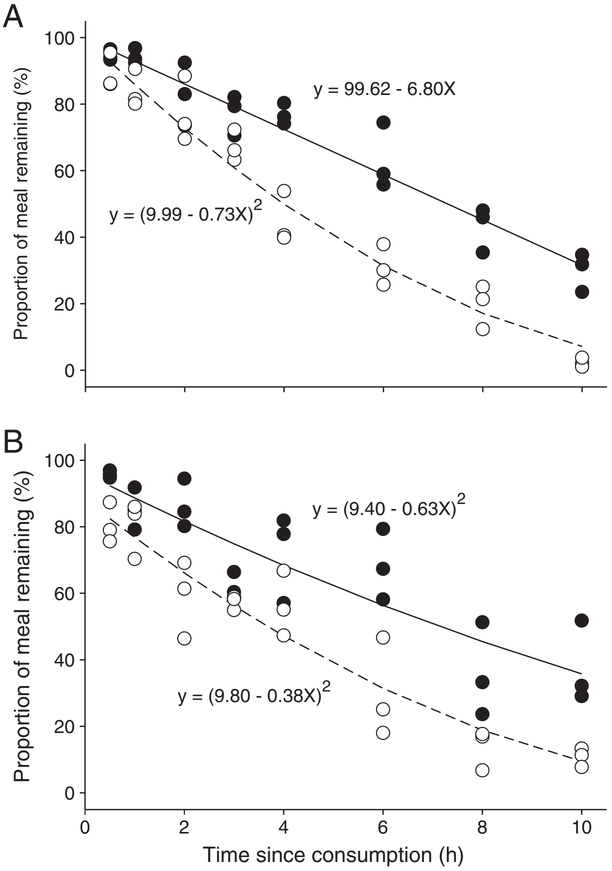

Fig. 2. Gastric evacuation of shrimp prey by small (A) and large (B) red drum at two water temperatures (● = 17 °C; ○ = 27 °C). Fitted lines and equations represent the model with the lowest AICc score in each case (presented in Table 4).

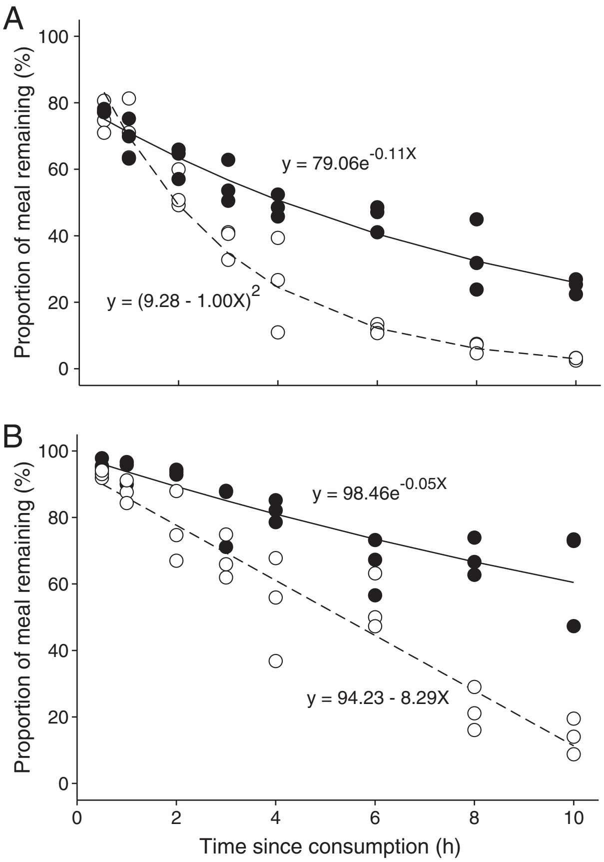

Fig. 3. Gastric evacuation of fish prey by small (A) and large (B) red drum at two water temperatures (● = 17 °C; ○ = 27 °C). Fitted lines and equations represent the model with the lowest AICc score in each case (presented in Table 4).

3.4. Prey-specific effects

When fitted to all available data, the multivariable model demonstrated good fit (residual SS = 2.336; $R^2 = 0.971$; n = 192) and generated estimates of the general parameters for shape ($\alpha = 0.684$) and the effects of water temperature ($\delta = 0.071$) that were each highly significant ($P < 0.001$). The effect of predator size was not found to be statistically significant ($P = 0.464$). When the shape parameter (α) was fixed at 0.5, the effect of predator size ($\gamma = 0.268$) was detectable ($P < 0.001$), and the effect of water temperature ($\delta = 0.069$) was relatively unchanged. Since the square root model received the most support, prey-specific effects on gastric evacuation were evaluated using the parameter estimates generated from the fixed α model. With the general parameters held constant ($\alpha = 0.5$; $\gamma = 0.268$; $\delta = 0.069$) separate model fits generated statistically significant ($P < 0.001$) estimates of the prey-specific parameter (ρ_i) for Penaeid shrimp ($\rho = 0.0142$), *A. hepsetus* ($\rho = 0.0179$), and *M. cephalus* ($\rho = 0.0123$). Confidence intervals for the prey-specific parameter did not overlap, indicating significant differences among prey types. The larger value of ρ for *A. hepsetus* prey indicated a faster rate of evacuation for this prey type, all other variables being equal (Fig. 4).

Table 4
Model selection results for gastric evacuation experiments. Fits for linear, exponential, and square root models are shown for each of the eight treatment combinations. RSS = residual sum of squares; AICc = corrected AIC score; ΔAICc = model AICc score − lowest AICc score; *L* = model likelihood; ω_i = Akaiki weight or relative weight of evidence.

Model	RSS	AICc	ΔAICc	*L*	ω_i
Large × warm × shrimp					
Linear	1930.936	109.876	2.166	0.339	0.228
Exponential	2068.268	111.525	3.815	0.148	0.100
Square root	1764.289	107.710	0.000	1.000	0.672
Large × cool × shrimp					
Linear	2921.171	119.812	0.188	0.910	0.328
Exponential	2934.669	119.923	0.299	0.861	0.311
Square root	2898.388	119.624	0.000	1.000	0.361
Large × warm × fish (*Mugil cephalus*)					
Linear	1703.348	106.867	0.000	1.000	0.507
Exponential	2024.061	111.007	4.140	0.126	0.064
Square root	1727.023	107.198	0.331	0.847	0.429
Large × cool × fish (*Mugil cephalus*)					
Linear	1294.801	100.285	1.618	0.445	0.209
Exponential	1210.406	98.667	0.000	1.000	0.468
Square root	1248.364	99.408	0.741	0.690	0.323
Small × warm × shrimp					
Linear	1165.150	97.753	2.433	0.296	0.228
Exponential	1634.245	105.873	10.553	0.005	0.004
Square root	1052.805	95.319	0.000	1.000	0.768
Small × cool × shrimp					
Linear	831.765	89.663	0.000	1.000	0.879
Exponential	1215.151	98.761	9.098	0.011	0.009
Square root	987.587	93.784	4.121	0.127	0.112
Small × warm × fish (*Anchoa hepsetus*)					
Linear	2742.138	118.294	27.095	0.000	0.000
Exponential	898.229	91.508	0.309	0.857	0.461
Square root	886.739	91.199	0.000	1.000	0.539
Small × cool × fish (*Anchoa hepsetus*)					
Linear	725.439	86.381	4.086	0.130	0.078
Exponential	611.872	82.295	0.000	1.000	0.601
Square root	644.706	83.549	1.254	0.534	0.321

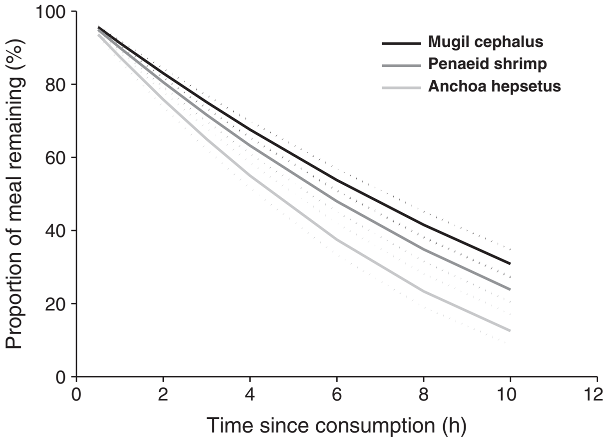

Fig. 4. The effects of prey type on red drum gastric evacuation as predicted by a multivariable model that included fixed parameters for the effects of curve shape, red drum body mass, and water temperature. Lines represent the specific effects of unique prey types on the evacuation of a meal (meal size = 3% of red drum mass) by an intermediate size (271 g) red drum at an intermediate water temperature (22 °C). Solid lines = the mean effect of each prey type; dotted lines = 95% CI.

4. Discussion

4.1. Effects of water temperature, body size, and prey type

During laboratory trials using natural prey, the physiological rates of red drum feeding and gastric emptying responded as expected, with water temperature and ontogeny explaining the majority of observed variation. Recent examples demonstrate similar responses to temperature and body size for a variety of fish species (Benkwitt et al., 2009; Griffiths et al., 2009; Petry et al., 2007). The predictable scaling of fish metabolic rate with temperature and ontogeny is believed to be the primary driver of changes in rates of feeding and gastric evacuation (Paloheimo and Dickie, 1966). Roughly two-fold increases in maximum consumption rate were observed as water temperature varied between 17 °C and 27 °C for both small and large body sizes of red drum. The effect of body size was less pronounced, however approximately 33% reductions in weight-specific consumption were evident for red drum between 76 g and 429 g mean body mass. Similarly, Hartman and Brandt (1995) demonstrated one- to four-fold increases in maximum consumption rates between approximately 5 °C and 30 °C for three temperate fish predators in Chesapeake Bay, U.S.A., with two- to three-fold variation in consumption across body sizes that ranged from roughly 10 to 1000 g.

While specific growth rates of red drum responded to water temperature and body size in a manner similar to consumption, gross growth efficiencies only responded marginally to the water temperature and body size treatments that were tested. Although gross growth efficiency was statistically greater for the smaller red drum, the difference was relatively small (~2%), and there was no effect of water temperature. Declining growth efficiency with increasing body size has been observed previously in fishes. For example, rainbow trout, *Salmo gairdneri*, being fed high ration levels showed decreased gross growth efficiencies in larger individuals (Wurtsbaugh and Davis, 1977a), as did bluefish, *Pomatomus saltatrix* (Buckel et al., 1995). Paloheimo and Dickie (1966) noted a similar relationship, but attributed declining growth efficiency at larger body size to differences in specific ingestion rate rather than to body size itself. Kiørboe et al. (1987) suggested that size-based differences in growth efficiency may be related to the potential for growth, which scales ontogenetically, and thus to size-dependent differences in the allocation of assimilated energy. In the present study, larger red drum displayed lower weight-specific ingestion rates that also may have contributed to reduced growth efficiency. Several authors have observed maximal growth efficiency within a range of optimal water temperatures, with declining efficiency at both lower and higher temperatures (Allen and Wootton, 1982, Björnsson and Tryggvadóttir, 1996, Elliott, 1976), however Wurtsbaugh and Davis (1977b) found no temperature effect on growth efficiency when fish were being fed high ration levels. In the present study, red drums were being fed maximum ration levels, which may have dampened any effect of water temperature on growth efficiency. Alternatively, the range of water temperatures that was examined may have lacked sufficient contrast to detect any such effect.

Consumption rates of carnivorous fishes can vary substantially, but have generally been observed to be between 5 and 25% body mass d^{-1}. For example, field-based estimates of consumption for age 1 striped bass in a North Carolina estuary were between 2.5 and 7.8% body mass d^{-1} (Tuomikoski et al., 2008). Maximum consumption of juvenile bluefish (3–30 g) measured in the laboratory ranged from 3 to 36% body mass d^{-1} depending on water temperature and bluefish size (Buckel et al., 1995), with field-based estimates during the warmest months between 7 and 22% body mass d^{-1}. Extremely high daily rations, above 50% predator body mass, are typically restricted to the larval or very early juvenile stages (e.g., Shoji and Tanaka, 2005), whereas lower rates are generally observed for predatory fishes approaching body sizes of 1 kg and beyond (e.g., Beaudreau and Essington, 2009). Similarly, growth efficiencies of fishes are generally highest (≥30%) during the larval period (Houde and Zastrow 1993), and fall to more modest levels at later ontogenetic stages. However, growth efficiency can often remain relatively high during the first year of life. For example, a series of laboratory experiments demonstrated that juvenile bluefish were able to maintain gross growth efficiencies between 20 and 28% during their first summer (Buckel et al., 1995). In the present study, red drum realized maximum daily consumption rates between 6 and 19% body mass, which align closely with other estuarine species at similar stages of development. Furthermore, the range of gross growth efficiencies (13–16%) achieved by red drum are in general agreement with the levels of feeding efficiency observed for other species.

Water temperature, body mass, and prey type each influenced red drum gastric evacuation rates. The effects of water temperature were strongest with red drum achieving faster rates of evacuation when held at the higher temperature tested, regardless of body mass or prey type. The influence of water temperature on fish metabolism and rates of meal processing have been studied extensively (Buckel and Conover, 1996; Persson, 1979; Wuenschel and Werner, 2004), with a general increase, often of exponential form, observed in gut evacuation rate at higher temperatures. Bromley (1994) reviewed the results of several experiments and found a range of Q_{10} multipliers (= change in the evacuation rate for each 10° temperature increase) between 2.2 and 4.3 across multiple fish species. The multivariable model that was fit in this study generated a value of $\delta = 0.069$ for the exponent of the temperature coefficient, which corresponds to a Q_{10} value of just under 2. Thus, relative to other species, the response of evacuation rates to water temperature in red drum may be low. Although the influence of body size on red drum gastric evacuation was only moderate, the smaller red drum tested did demonstrate faster rates compared to larger individuals, regardless of prey type. Similar findings were reported by Berens and Murie (2008) for gag grouper, *Mycteroperca microlepis*, which experienced faster rates of gut evacuation at smaller body sizes when fed fish or crustacean prey. Based on the allometric scaling of stomach surface area with body size, Fänge and Grove (1979) predicted that time to evacuation should increase with fish body size, however empirical evidence has often been equivocal and generally indicates a modest effect of predator body mass when detected (He and Wurtsbaugh, 1993; Jobling, 1981; Temming and Herrmann, 2003).

In contrast to the findings of other studies that have examined evacuation rates for both fish and crustacean prey (e.g., Berens and Murie, 2008; Temming and Herrmann, 2003), the effect of prey type was modest in the present study. Many authors have observed a lag in evacuation of crustacean prey that has been attributed to the resistance to enzymatic breakdown of the cuticle exoskeleton (Andersen, 1999; Bromley, 1991; Temming and Herrmann, 2003). However, in this study, parameter estimates from the multivariable model indicated that shrimp evacuation rates were intermediate relative to the two fish prey tested, yielding no clear difference between fish and crustacean prey. When prey types are structurally similar, differences in energy density can also contribute to prey-specific rates of evacuation (Temming and Herrmann, 2003). The two species of shrimp prey used in the present study (*F. aztecus* and *L. setiferus*) have been estimated to have slightly lower energy densities compared with the fish prey species tested (~21.6–24 kJ g^{-1} ash-free dry weight for shrimp versus ~23–25 kJ g^{-1} for the two fish species; Steimle and Terranova, 1985; Thayer et al., 1973), although the differences appear marginal given the variation present. The closeness in prey energy densities may partially explain the similarity among evacuation rates for shrimp and fish prey that was observed. Further, Andersen (1999) found that krill prey, which lacked a thick exoskeleton, were evacuated at similar rates to fish prey. During the present study, red drum fed shrimp prey would often reject or regurgitate the head and thoracic regions that were covered by the carapace, the thickened portion of the exoskeleton. The digestive enzymes were then focused on the muscular abdominal region of the shrimp, which is covered by a markedly thinner exoskeleton, which likely eliminated the lag in crustacean evacuation by red drum observed by previous researchers for other predators.

The fit for three mathematical models (simple linear, exponential, and square root) used to describe the red drum gastric evacuation data were compared. The most supported model varied among the gastric evacuation treatment combinations that were tested, with the square root model receiving the highest level of support most often (4 of 8 treatment combinations). However, in each of those cases, a second model was plausible (ΔAICc score < 2 or $\omega_i \geq 20\%$). Furthermore, a significant lack of fit for the simple linear (straight-line) model was detected for only one of the eight treatment combinations that were tested. Jobling (1981) first evaluated the various mathematical models used to describe gut evacuation data in fishes and subsequent contributions have highlighted the theoretical and empirical merits and drawbacks of different models (Jobling, 1986; Persson, 1986; reviewed in Bromley, 1994). In many cases, similar to the findings here, more than one plausible model can adequately describe the gastric evacuation function (e.g., Buckel and Conover, 1996). More recently, there has been widespread application of multivariable models, first developed by Temming and Andersen (1994), which can account for the influence of several factors simultaneously. The shape parameter from the multivariable model that was fitted to the red drum evacuation data was estimated to be 0.684. A value close to 0.5 is an indication that gastric emptying conforms to a power function best modeled by the square root model (Jobling, 1981; Temming and Andersen, 1994). In addition, Anderson (1998) concluded that a model with an exponent of 0.5 should be appropriate for most predatory fishes that feed on larger prey items (e.g., other fishes and macrocrustaceans). For the range of water temperatures, body sizes, and prey types that were tested, red drum gastric evacuation appeared to support this assertion.

4.2. Validation of field observations

During 2007–09, field estimation of red drum foraging habits and daily ration was completed in a southeastern estuary, North Carolina, U.S.A. (Facendola, 2010). The objectives of that study were to characterize seasonal and ontogenetic variation in red drum diet, and to estimate gastric evacuation and daily ration using measures of average gut fullness coupled with diurnal periods of declining gut fullness that represented periods of gut emptying (Elliott and Persson, 1978). The findings demonstrated that Penaeid shrimp, blue crabs, and Atlantic menhaden, *Brevoortia tyrannus*, were the principal prey of red drum. Field-based estimates of gastric evacuation rates ranged between 6.7 and 9.0% of prey mass h^{-1}, and daily ration ranged between 3 and 6% red drum body mass d^{-1} (Facendola, 2010). The laboratory estimates of gastric evacuation (4.0–9.4% prey mass h^{-1}) and maximum consumption (6.3–18.9% red drum body mass d^{-1}) generated in this study confirm that previous field-based estimates were reasonable. All estimates of red drum gastric evacuation rate obtained during the field study were contained within the boundaries of laboratory-generated estimates for a range of body sizes and water temperatures that closely matched field conditions. Field-based estimates of daily ration indicated that red drums were feeding at roughly one-third of their maximum potential feeding rate. In situ daily ration levels of carnivorous fishes should generally be expected to be lower than physiological maximums due to factors that include prey availability, prey size distributions, and environmental factors that influence predator and prey overlap. In addition, because in situ daily ration is primarily estimated through summation of discrete time point values of gut fullness, rather than continuously over 24 h, it is subject to greater variability. Thus, previous field-based estimates of red drum daily ration (Facendola, 2010) may be low.

4.3. Potential for predatory impact and management implications

Given that several managed prey species (e.g., blue crab, Penaeid shrimp, Atlantic menhaden) occur routinely in red drum diets, the estimates of consumption rate suggest that their impact on prey populations may be considerable. The juvenile stages of other estuarine predators have been shown to account for large fractions of natural mortality of their prey, depending on spatial and temporal overlap (Buckel et al., 1999b; Tuomikoski et al., 2008). Specifically, Buckel et al. (1999b) used a field-based approach to estimate the proportion of early juvenile striped bass, *Morone saxatilis*, loss rates due to predation by juvenile bluefish, *P. saltatrix*, in the lower Hudson River, U.S.A. Mortality due to bluefish predation was found to represent up to 50–100% of total striped bass loss during summer months. Similarly, Tuomikoski et al. (2008) calculated field-based and bioenergetics estimates of consumption by age-1 striped bass feeding on alosids in western Albemarle Sound, NC, U.S.A. The authors concluded that striped bass predation could be responsible for nearly all of the loss rates for certain juvenile prey fish species in shallow habitats, depending on prey selectivity which varied among study years. Relative to other age classes, the high abundance levels and metabolic rates typical of age-0 and age-1 fishes can contribute to their potential for large predatory impacts on prey populations. During their first summer, age-0 red drum growth can average 4 g d^{-1}, with fish experiencing up to 100-fold increases in mass over a 4–5 month period (Facendola, 2010). Similarly, age-1 red drums typically increase in size from ~0.5–0.6 kg to greater than 2 kg during the summer and early fall. Gross growth efficiencies of roughly 15% estimated in the present study indicate that a considerable amount of prey biomass must be consumed to fuel the observed rates of growth. To fully quantify red drum predation impacts on estuarine prey resources, future work to obtain spatially-explicit estimates of red drum density and prey-specific loss rates will be needed.

When losses due to predation are incorporated explicitly into population assessment models, estimates of natural mortality can often exceed estimates of harvest mortality, especially for species at low to moderate trophic levels (Gaichas et al., 2010). The inclusion of accurate information on predator–prey interactions in a multispecies analysis can reduce the high levels of uncertainty in predator biomass estimates characteristic of single-species models and provide fishery managers with greater insight into the potential ecosystem responses to any regulatory changes (A'mar et al., 2010; Hollowed et al., 2000; Jurado-Molina et al., 2005). Harvest and/or effort levels for resource species at low to moderate trophic levels should be set while accounting for changes in predator biomass or selectivity to increase the likelihood of meeting management objectives. For instance, Harvey et al. (2008) used multispecies age-structured models to reveal the potential effects of Pacific hake, *Merluccius productus*, predation on the rebuilding schedules of several overfished species of Pacific rockfish, *Sebastes* spp. Improvements in the fit of stock–recruit relationships have also been noted when indices of biomass for key predators are included in the model (Gjøsaeter and Bogstad, 1998; Huse et al., 2008). With the implementation of severe regulatory measures on red drum harvest beginning in the early 1990s, the U.S.A. Atlantic coastal stock has been rebuilding and has nearly reached management thresholds to indicate complete recovery (ASMFC 2010). A fully recovered red drum population will increase predatory demand on estuarine prey resources which may necessitate a more holistic approach to the management of economically important fishery resource species (e.g., blue crab, Penaeid shrimp, and Atlantic menhaden) that are shared with red drum. More careful study of the impact of red drum predation on prey populations through analysis of temporal and spatial variability in red drum density, consumption, and prey selectivity is warranted.

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References

Allen, J.R.M., Wootton, R.J., 1982. The effect of ration and temperature on the growth of the three-spined stickleback, *Gasterosteus aculeatus*, L. J. Fish Biol. 20, 409–422.

A'mar, Z.T., Punt, A.E., Dorn, M.W., 2010. Incorporating ecosystem forcing through predation into a management strategy evaluation for the Gulf of Alaska walleye pollock (*Theragra chalcogramma*) fishery. Fish. Res. 102, 98–114.

Andersen, N.G., 1999. The effects of predator size, temperature, and prey characteristics on gastric evacuation in whiting. J. Fish Biol. 54, 287–301.

Anderson, N.G., 1998. The effect of meal size on gastric evacuation in whiting. J. Fish Biol. 52, 743–755.

ASMFC (Atlantic States Marine Fisheries Commission), 2010. 2010 review of the Atlantic States Marine Fisheries Commission fishery management plan for red drum (*Sciaenops ocellatus*). ASMFC, Washington, D.C.

Bailey, K.M., 1994. Predation of juvenile flatfish and recruitment variability. Neth. J. Sea Res. 32, 175–189.

Beaudreau, A.H., Essington, T.E., 2009. Development of a new field-based approach for estimating consumption rates of fishes and comparison with a bioenergetics model for lingcod (*Ophiodon elongatus*). Can. J. Fish. Aquat. Sci. 66, 565–578.

Benkwitt, C.E., Brodeur, R.D., Hurst, T.P., Daly, E.A., 2009. Diel feeding chronology, gastric evacuation, and daily food consumption of juvenile chinook salmon in Oregon coastal waters. Trans. Am. Fish. Soc. 138, 111–120.

Berens, E.J., Murie, D.J., 2008. Differential digestion and evacuation rates of prey in a warm-temperate grouper, gag *Mycteroperca microlepis* (Goode & Bean). J. Fish Biol. 72, 1406–1426.

Björnsson, B., Tryggvadóttir, S.V., 1996. Effects of size on optimal temperature for growth and growth efficiency of immature Atlantic halibut (*Hippoglossus hippoglossus* L.). Aquaculture 142, 33–42.

Boothby, R.N., Avault Jr., J.W., 1971. Food habits, length–weight relationship, and condition factor of the red drum (*Sciaenops ocellata*) in Southeastern Louisiana. Trans. Am. Fish. Soc. 100, 290–295.

Bromley, P.J., 1991. Gastric evacuation in cod (*Gadus morhua* L.). ICES Mar. Sci. Symp. 193, 93–98.

Bromley, P.J., 1994. The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. Rev. Fish Biol. Fish. 4, 36–66.

Buckel, J.A., Conover, D.O., 1996. Gastric evacuation rates of picivorous young-of-the-year bluefish. Trans. Am. Fish. Soc. 125, 591–599.

Buckel, J.A., Steinberg, N.D., Conover, D.O., 1995. Effects of temperature, salinity, and fish size on growth and consumption of juvenile bluefish. J. Fish Biol. 47, 696–706.

Buckel, J.A., Fogarty, M.J., Conover, D.O., 1999a. Mutual prey of fish and humans: a comparison of biomass consumed by bluefish, *Pomatomus saltatrix*, with that harvested by fisheries. Fish. Bull. 97, 776–785.

Buckel, J.A., Conover, D.O., Steinberg, N.D., McKown, K.A., 1999b. Impact of age-0 bluefish (*Pomatomus saltatrix*) predation on age-0 fishes in the Hudson River estuary: evidence for density-dependent loss of juvenile striped bass (*Morone saxatilis*). Can. J. Fish. Aquat. Sci. 56, 275–287.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York, USA. 488 pp.

Carpentieri, P., Colloca, F., Ardizzone, G., 2008. Daily ration and feeding activity of juvenile hake in the central Mediterranean Sea. J. Mar. Biol. Assoc. UK 88, 1493–1501.

Comyns, B.H., Lyczkowski-Shultz, J., Nieland, D.L., Wilson, C.A., 1991. Reproduction of red drum, *Sciaenops ocellatus*, in the northcentral Gulf of Mexico: seasonality and spawner biomass. NOAA Tech. Rep. NMFS, 95, pp. 17–26.

Eggers, D., 1979. Comments on some recent methods for estimating food consumption by fish. J. Fish. Res. Board Can. 36, 1018–1019.

Elliott, J.M., 1976. The energetic of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. J. Anim. Ecol. 45, 923–948.

Elliott, J.M., Persson, L., 1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47, 977–991.

Facendola, J., 2010. 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. MS thesis, Department of Biology and Marine Biology, University of North Carolina Wilmington. 77 pp. http://dl.uncw.edu/etd/2010-1/facendolaj/josephfacendola.pdf.

Fänge, R., Grove, D.J., 1979. Digestion. In: Hoar, W.S., Randall, D.J., Brett, J.R. (Eds.), Fish Physiology. : Energetics and Growth, VII. Academic Press, New York, pp. 161–260.

Fletcher, W.J., Shaw, J., Metcalf, S.J., Gaughan, D.J., 2010. An ecosystem based fisheries management framework: the efficient, regional-level planning tool for management agencies. Mar. Policy 34, 1226–1238.

Francis, R.C., Hixon, M.A., Clarke, M.E., Murawski, S.A., Ralston, S., 2007. Ten commandments for ecosystem-based fisheries scientists. Fisheries 32, 217–233.

Gaichas, S.K., Aydin, K.Y., Francis, R.C., 2010. Using food web model results to inform stock assessment estimates of mortality and production for ecosystem-based fisheries management. Can. J. Fish. Aquat. Sci. 67, 1490–1506.

Gjøsaeter, H., Bogstad, B., 1998. Effects of the presence of hering (*Clupea harengus*) on the stock-recruitment relationship of Barents Sea capelin (*Mallotus villosus*). Fish. Res. 38, 57–71.

Griffiths, S.P., Kuhnert, P.M., Fry, G.F., Manson, F.J., 2009. Temporal and size-related variation in the diet, consumption rate, and daily ration of mackerel tuna (*Euthynnus affinis*) in neritic waters of eastern Australia. ICES J. Mar. Sci. 66, 720–733.

Hartman, K.J., Brandt, S.B., 1995. Predatory demand and impact of striped bass, bluefish, and weakfish in the Chesapeake Bay: applications of bioenergetics models. Can. J. Fish. Aquat. Sci. 52, 1667–1687.

Harvey, C.J., Gross, K., Simon, V.H., Hastie, J., 2008. Trophic and fishery interactions between Pacific hake and rockfish: effect on rockfish population rebuilding times. Mar. Ecol. Prog. Ser. 365, 165–176.

He, E., Wurtsbaugh, W.A., 1993. An empirical model of gastric evacuation rates for fish and an analysis of digestion in piscivorous brown trout. Trans. Am. Fish. Soc. 122, 717–730.

Hollowed, A.B., Ianelli, J.N., Livingston, P., 2000. Including predation mortality in stock assessments: a case study for Gulf of Alaska walleye pollock. ICES J. Mar. Sci. 57, 279–293.

Houde, E.D., Zastrow, C.E., 1993. Ecosystem - and taxon- specific dynamic and energetic properties of larval fish assemblages. Bull. Mar. Sci. 53, 290–335.

Huse, G., Salthaug, A., Skogen, M.D., 2008. Indications of a negative impact of herring on recruitment of Norway pout. ICES J. Mar. Sci. 65, 906–911.

Jobling, M., 1981. Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. J. Fish Biol. 19, 245–257.

Jobling, M., 1986. Mythical models of gastric emptying and implications for food consumption studies. Environ. Biol. Fish. 16, 35–50.

Jurado-Molina, J., Livingston, P.A., Ianelli, J.N., 2005. Incorporating predation interactions in a statistical catch-at-age model for a predator–prey system in the eastern Bering Sea. Can. J. Fish. Aquat. Sci. 62, 1865–1873.

Kiørboe, T., Munk, P., Richardson, K., 1987. Respiration and growth of larval herring *Clupea harengus*: relation between specific dynamic action and growth efficiency. Mar. Ecol. Prog. Ser. 40, 1–10.

Kitchell, J.F., Stewart, D.J., Weininger, D., 1977. Application of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34, 1922–1935.

Marasco, R.J., Goodman, D., Grimes, C.B., Lawson, P.W., Punt, A.E., Quinn II, T.J., 2007. Ecosystem-based fisheries management: some practical suggestions. Can. J. Fish. Aquat. Sci. 64, 928–939.

Mercer, L.P., 1984. A biological and fisheries profile of red drum, *Sciaenops ocellatus*. North Carolina Division of Marine Fisheries, Special Scientific Report 41, Morehead City.

Overstreet, R.M., Heard, R.W., 1978. Food of the red drum, *Sciaenops ocellata*, from Mississippi Sound. Gulf Res. Rep. 6, 131–135.

Paloheimo, J.E., Dickie, L.M., 1966. Food and growth of fishes. III. Relations among food, body size, and growth efficiency. J. Fish. Res. Board Can. 23, 1209–1248.

Persson, L., 1979. The effects of temperature and different food organisms on the rate of gastric evacuation in perch (*Perca fluviatilis*). Freshw. Biol. 9, 99–104.

Persson, L., 1986. Patterns of food evacuation in fishes: a critical review. Environ. Biol. Fish. 16, 51–58.

Petry, A.C., Agostinho, A.A., Piana, P.A., Gomes, L.C., 2007. Effects of temperature on prey consumption and growth in mass of juvenile trahira *Hoplias* aff. *malabaricus* (Bloch, 1794). J. Fish Biol. 70, 1855–1864.

Scharf, F.S., Schlicht, K.K., 2000. Feeding habits of red drum (*Sciaenops ocellatus*) in Galveston Bay, Texas: seasonal diet variation and predator–prey size relationships. Estuaries 23, 128–139.

Sheaves, M., 2001. Are there really few piscivorous fishes in shallow estuarine habitats? Mar. Ecol. Prog. Ser. 222, 279–290.

Shoji, J., Tanaka, M., 2005. Daily ration and prey size of juvenile piscivorous Japanese Spanish mackerel. J. Fish Biol. 67, 1107–1118.

Steimle, F.W., Terranova, R.J., 1985. Energy equivalents of marine organisms from the continental shelf of the temperate Northwest Atlantic. J. Northwest Atl. Fish. Sci. 6, 117–124.

Temming, A., Andersen, N.G., 1994. Modelling gastric evacuation without meal size as a variable. A model applicable for the estimation of daily ration of cod (*Gadus morhua* L.) in the field. ICES J. Mar. Sci. 51, 429–438.

Temming, A., Herrmann, J.P., 2003. Gastric evacuation in cod prey-specific evacuation rates for use in North Sea, Baltic Sea and Barents Sea multi-species models. Fish. Res. 63, 21–41.

Thayer, G.W., Schaaf, W.E., Angelovic, J.W., LaCroix, M.W., 1973. Caloric measurements of some estuarine organisms. Fish. Bull. 71, 289–296.

Tuomikoski, J.E., Rudershausen, P.J., Buckel, J.A., Hightower, J.H., 2008. Effects of age-1 striped bass predation on juvenile fish in western Albemarle Sound. Trans. Am. Fish. Soc. 137, 324–339.

Wilson, C.A., Nieland, D.L., 1994. Reproductive biology of red drum, *Sciaenops ocellatus*, from the neritic waters of the northern Gulf of Mexico. Fish. Bull. 92, 841–850.

Wuenschel, M.J., Werner, R.G., 2004. Consumption and gut evacuation rate of laboratory-reared spotted seatrout (Sciaenidae) larvae and juveniles. J. Fish Biol. 65, 723–743.

Wurtsbaugh, W.A., Davis, G.E., 1977a. Effects of fish size and ration level on the growth and food conversion efficiency of rainbow trout, *Salmo gairdneri* Richardson. J. Fish Biol. 11, 99–104.

Wurtsbaugh, W.A., Davis, G.E., 1977b. Effects of temperature and ration level on the growth and food conversion efficiency of *Salmo gairdneri* Richardson. J. Fish Biol. 11, 87–98.