ARTICLE

Growth of largemouth bass in a dynamic estuarine environment: an evaluation of the relative effects of salinity, diet, and temperature

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Abstract: Some freshwater fishes occur regularly in estuarine areas that experience spatial and seasonal variation in marine influence. These dynamic abiotic and biotic conditions potentially influence food consumption and growth. We found that effects of an estuarine environment on the growth of largemouth bass (*Micropterus salmoides*) in Alabama's Mobile–Tensaw River Delta depended on body size, distance from the marine source, and amount of freshwater inflow. Incremental growth analyses demonstrated that young largemouth bass (<age-3) grew more rapidly downstream in the estuarine environment declining with distance upstream; this relationship was reversed for older fish with faster growth in fresher, upstream areas. The magnitude of freshwater inflow influenced the relationship between age-specific growth and proximity to Mobile Bay. Bioenergetics simulations suggest that interactions among size-specific metabolic cost of salinity, maximum water temperature, and spatial differences in both salinity and prey energetic content can explain these growth patterns. The cost–benefit of the estuarine environment to largemouth bass is not only dynamic seasonally, but also changes ontogenetically because of shifts in salinity tolerance and prey use.

Résumé : Certains poissons dulçaquicoles sont régulièrement présents en zones estuariennes dans lesquelles l'influence de la mer varie dans l'espace et en fonction de la saison. Ces conditions abiotiques et biotiques dynamiques peuvent avoir une incidence sur la consommation d'aliments et la croissance. Nous avons constaté que les effets d'un milieu estuarien sur la croissance de l'achigan à grande bouche (*Micropterus salmoides*) dans le delta des rivières Mobile et Tensaw, en Alabama, dépendaient de la taille du corps, de la proximité de la source marine et de l'ampleur de l'apport en eau douce. Des analyses de la croissance différentielle ont démontré que la croissance des jeunes achigans à grande bouche (<3 ans) était plus rapide dans les zones aval du milieu estuarien, diminuant avec la distance vers l'amont; cette relation était inversée pour les poissons plus vieux, qui présentaient une croissance plus rapide dans les zones amont caractérisées par de l'eau plus douce. L'ampleur des apports en eau douce influait sur la relation entre la croissance par âge et la proximité de la baie de Mobile. Des simulations bioénergétiques suggèrent que les interactions entre le coût métabolique par taille de la salinité, la température maximum de l'eau et des différences spatiales de salinité et de contenu énergétique des proies peuvent expliquer une telle répartition des taux de croissance. Le rapport coûts–bénéfices du milieu estuarien pour l'achigan à grande bouche présente non seulement une dynamique saisonnière, mais change ontogénétiquement en raison de variations de la tolérance à la salinité et de l'utilisation des proies. [Traduit par la Rédaction]

Introduction

Estuaries are composed of a mosaic of abiotic conditions that occur along a generally predictable spatial gradient (upstream to downstream), serving as an initial physiological template influencing the spatial distribution of fish species and community structure zonation (Remmert 1983; Kimmerer 2002; Peterson 2003). Biotic interactions, both within and among estuarine zones, further refine the community resulting from this abiotic template (Sanders 1968; Martino and Able 2003; Peterson et al. 2004). As such, many stenohaline fishes within an estuary may persist or even thrive near the edge of their physiological tolerance; the realized niche for these species may be increased or decreased through biotic interactions. For example, freshwater tidal rivers and oligohaline portions of estuaries are often dominated by stenohaline freshwater fish species (Swingle and Bland 1974; Peterson and Meador 1994; Wagner and Austin 1999), and estuarine- or marine-derived prey subsidies can play an important role in offsetting apparent costs imposed by ionoregulation of salinity (Guier et al. 1978; MacAvoy et al. 2000; Peer et al. 2006).

Centrarchid species, in particular, are abundant in estuarine systems along the Gulf of Mexico and have been observed to occupy brackish habitats that presumably would hinder their growth (Swingle and Bland 1974; Peterson 1991; Peterson and Ross 1991). However, these species often maintain high body condition (Meador and Kelso 1990*a*; Peterson 1991; Norris et al. 2010), which could be the result of physiological adaptations that limit the effects of salinity exposure (Peterson 1988; Meador and Kelso 1990*b*; Glover et al. 2012), the result of estuarine and marine subsidies (Guier et al. 1978; VanderKooy et al. 2000; Peer et al. 2006), or both. Thus, quantifying how biotic interactions play a role in demographic responses of these fishes in relation to the abiotic conditions may facilitate modeling endeavors attempting to predict distributional shifts in fish assemblages as a result of climate change or other community ecology approaches (Dunson and Travis 1991).

Relative to inland freshwater populations, largemouth bass (*Micropterus salmoides*) in estuarine systems along the US Atlantic Ocean and Gulf of Mexico have slower growth, smaller maximum size, and lower annual survival rates (Colle et al. 1976; Meador and

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Kelso 1990*a*; Norris et al. 2010), suggesting these populations may be persisting at the edge of their physiological tolerances. Previous studies have hypothesized that high metabolic costs associated with ionoregulation could constrain net energetic intake and limit scope for growth of largemouth bass in estuarine systems (Meador and Kelso 1990*a*, 1990*b*; Susanto and Peterson 1996; Glover et al. 2012). Glover et al. (2012) found that specific rates of respiration for a wide size range of largemouth bass did not increase linearly with salinity, but rather exhibited a cubic relationship with salinity that interacted with temperature. Specifically, maximum effects of salinity on routine metabolism at temperatures >20 °C occurred at 3.2 and 12 ppt and were lowest at 0 and 9.7 ppt; the effect of salinity increased with temperature but had little effect on metabolism at temperatures ≤20 °C. The effect of salinity was also found to increase with body size, such that an increase in salinity from 0 to 3.2 ppt at 30 °C was predicted to increase metabolism 63% and 129% for a 50 and 800 g largemouth bass, respectively (Glover et al. 2012). The increasing energetic costs of salinity with size may help explain observed decreases in growth rates of older individuals in brackish habitats. However, the cubic effect of salinity and interactive effects with mass and temperature on metabolism may lead to counterintuitive, nonlinear effects on growth and may have contributed to past efforts having not found effects of salinity on growth of coastal largemouth bass (Meador and Kelso 1990*a*, 1990*b*; Norris et al. 2010). Moreover, salinity is only one of many factors in a dynamic estuarine environment that can influence the growth of fishes. Factors such as temperature, dissolved oxygen, and pH, as well as potential prey quantity and quality, may covary with salinity (Wheatly 1988; Jassby et al. 1995; Kimmerer 2002), confounding the specific effect of salinity on population characteristics.

Despite the costs of salinity on growth, largemouth bass in low salinity portions of estuarine systems are typically abundant (Guier et al. 1978; Tucker 1985; Krause 2002), suggesting that biotic interactions may be important for refining the estuarine abiotic template. For example, in the Mobile–Tensaw River Delta, Alabama (hereafter the Mobile Delta), the availability of small, energy-rich fish prey in habitats closest to or within brackish habitats allowed an earlier shift to and a higher degree of piscivory for age-0 largemouth bass relative to those in upstream freshwater areas (Peer et al. 2006). This conferred a growth advantage to age-0 largemouth bass in brackish habitats through their first summer of growth compared with largemouth bass in upstream areas that remained fresh, where they switched to piscivory later in life, and suggests that the metabolic cost of salinity was outweighed by prey quantity and quality. Despite switching to piscivory earlier in life, as adults, downstream largemouth bass in this system consumed a greater amount of energy-poor macroinvertebrates (e.g., blue crabs (*Callinectes sapidus*)), which may contribute to their slower growth rates relative to largemouth bass in the upstream region that consumed high proportions of fish prey (mostly sunfish (*Lepomis* species); Farmer 2008; Norris et al. 2010). Consumption of energy-poor macroinvertebrates, rather than energy-rich fish prey, has also been suspected as being responsible for the slow growth of adult largemouth bass observed in several other coastal systems (Colle et al. 1976; Lorio et al. 1982; Meador and Kelso 1990*a*), but has not been fully investigated in an energetics context. Growth rates of adult largemouth bass in downstream, brackish habitats may therefore be hindered both by increasing metabolic costs of salinity and consumption of energy-poor prey. This also suggests that the cost:benefit ratio of an estuarine environment likely changes throughout the life of largemouth bass because of ontogenetic shifts in both the magnitude of salinity effects and prey use on growth potential.

Freshwater inflow is one of the most important factors controlling the magnitude of salinity within an estuary and the extent to which salinity moves upstream (Schroeder 1978; Braun and Neugarten 2005). The upstream influx of saline water strongly influences the quantity and species composition of estuarine-dependent fish and invertebrates along the estuarine–freshwater gradient (Jassby et al. 1995; Kimmerer 2002). During years of low freshwater inflow, age-0 largemouth bass in downstream, brackish habitats may experience higher availability of energy-rich, estuarine-dependent prey, leading to increased growth rates. This increased salinity, however, would cause greater salinity-related metabolic costs and thus decreased growth rates in adult largemouth bass (Glover et al. 2012). Because precipitation patterns and temperature both vary seasonally, the magnitude of freshwater inflow is also negatively correlated with temperature. As such, periods of low freshwater inflow can coincide with temperatures surpassing the optimal temperature for largemouth bass consumption (i.e., 27.5 °C; Niimi and Beamish 1974; Rice et al. 1983), resulting in reduced consumption and elevated metabolic costs due to both temperature and salinity. To date, no studies have evaluated the influence of peak summer temperatures on largemouth bass growth in coastal environments despite the fact that temperatures can reach 32–35 °C in coastal Florida (M. Allen, personal communication, 2012, University of Florida, 7922 NW 71st Street, Gainsville, FL 32653, USA), Alabama (K. Major, personal communication, 2012, University of South Alabama, LSCB 51, Mobile, AL 36688, USA), Mississippi (M. Peterson, personal communication, 2012, Southern Mississippi University, 703 East Beach Drive, Ocean Springs, MS 39564, USA), and Louisiana (J. Cowan, personal communication, 2012, Louisiana State University, 2247 Energy, Coast and Environment Building, Baton Rouge, LA 70803, USA). As such, largemouth bass in estuarine systems are faced with a number of interacting abiotic and biotic factors that influence their growth and ability to persist at the edge of their physiological tolerance.

The purpose of this study was to determine how salinity, diet, temperature, and their interactions influence lifetime growth of largemouth bass in spatially and temporally dynamic estuarine systems. We compared growth increments derived from back-calculated length-at-age to assess the indirect effects of freshwater inflow (e.g., changes in salinity, diet composition, and temperature) on growth of largemouth bass along a salinity gradient within the Mobile Delta. Similarly, we used estimated caloric content consumed by largemouth bass from field observations to assess the indirect effects of freshwater inflow on prey quality. We also used a bioenergetics model to simulate the impacts of varying levels of freshwater inflow and correlated effects on lifetime growth trajectories of largemouth bass. Specifically, we first incorporated the metabolic costs of salinity developed by Glover et al. (2012) into the standard metabolism component of a bioenergetics model for largemouth bass, representing the first bioenergetics model for a freshwater fish that incorporates effects of salinity; this extension of the bioenergetics model can facilitate our understanding of how the freshwater fish community that often dominates oligohaline portions of estuaries respond ontogenetically to salinity. The results of this study are relevant to understanding how performance of fishes changes in response to abiotic and biotic stresses.

Materials and methods

Study area

This study was conducted in the Mobile Delta, located in Mobile and Baldwin counties, Alabama (Fig. 1). The Mobile Delta is expansive (55 km long, 8224 ha), supporting a diverse freshwater and brackish water fish assemblage (Swingle et al. 1966; Swingle and Bland 1974; Loyacano and Busch 1980). Saltwater intrusion into the Mobile Delta is generally seasonal, occurring in late summer and fall, and is negatively correlated to rainfall in the Mobile River watershed (Bault 1972; Swingle and Bland 1974; Swingle et al. 1966).

Fig. 1. Map of study area indicating sampling sites within the Mobile–Tensaw River Delta, Alabama. Tensaw Lake, McReynold's Lake, Dennis Lake, and Gravine Island were grouped into the upstream region, and Big Bayou Canot, Crab Creek, Bay Minette, and D'Olive Bay were grouped into the downstream region for analyses.
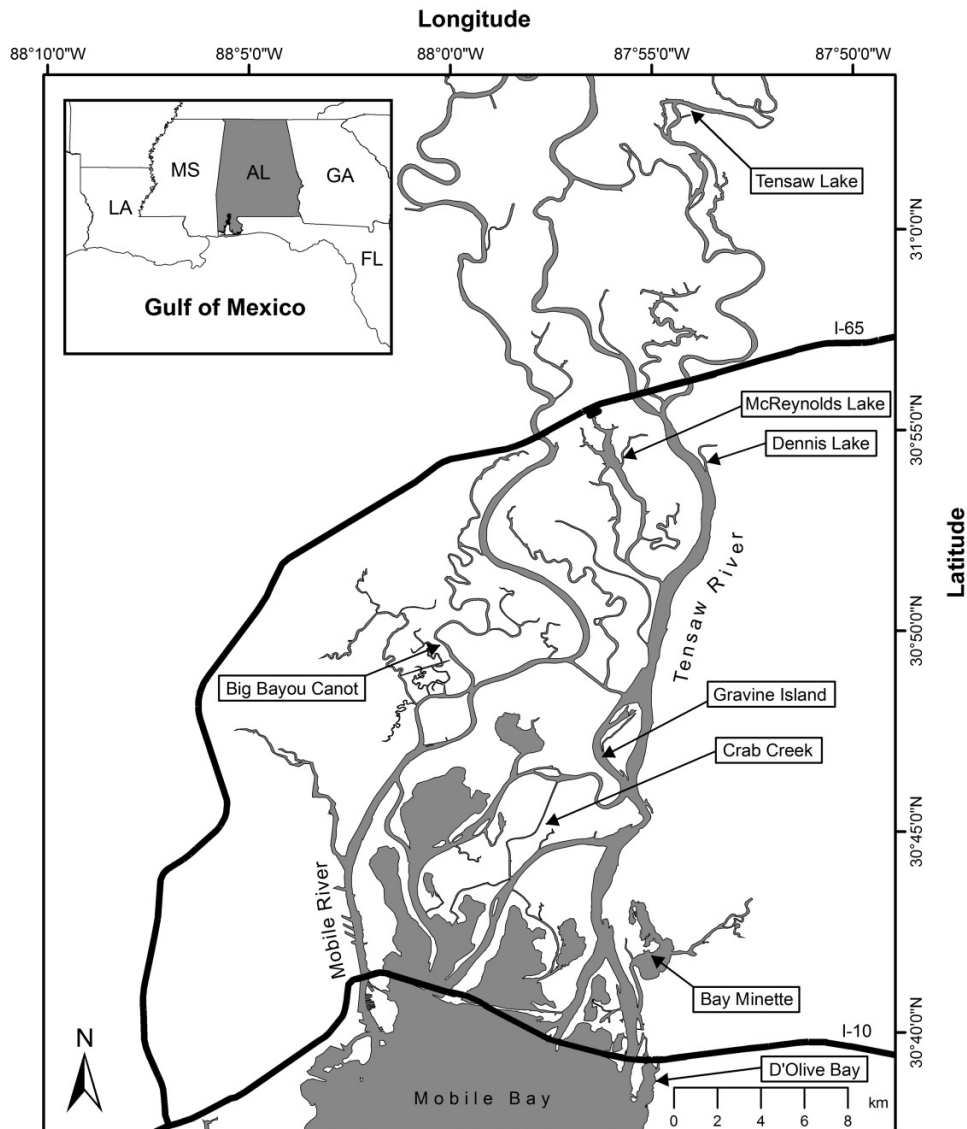
We sampled eight sites in the Mobile Delta once per month through December 2008 to capture the spatial and temporal variability of abiotic and biotic characteristics of the Mobile Delta. Six of the sites were established in January 2002 along a physicochemical gradient and were chosen to encompass the predominant habitat types of the region (from upstream to downstream: McReynolds Lake, Dennis Lake, Gravine Island, Crab Creek, Bay Minette, and D'Olive Bay; Fig. 1). Two sites were added in 2006 to increase the range of observed abiotic and biotic characteristics potentially influencing largemouth bass growth. Tensaw Lake is upstream of Highway I-65 (Fig. 1) and is a tidal-influenced fresh-water river that receives little influence from salinity and marine-derived prey. The second site, Big Bayou Canot, is located off of the Mobile River on the west side of the Mobile Delta (Fig. 1) and tends to experience higher salinity than the eastern, Tensaw River side (Valentine et al. 2004). From north to south, the habitat shifts from seasonally flooded, dense bottomland hardwood forest to a treeless marsh habitat (Swingle et al. 1966).

Largemouth bass collection

Pulsed-DC electrofishing was conducted once per month from 2002 to 2008 (Smith-Root DC electrofisher, 7.5 generator powered pulsator, 7500 W) to collect largemouth bass. Boat-mounted boom electrofishing was used to target adult largemouth bass and was conducted in two 15 min transects per site. To target juvenile largemouth bass, three 10 min transects were conducted at each site using a 3.5 m telescoping electrode prod pole, which consists of a 27 cm circular anode fitted with 4 mm mesh (Peer et al. 2006). The electrode prod pole is superior to seining in the Mobile Delta because of steep drop-offs in some areas, soft sediments, and various obstructions (e.g., bald cypress (*Taxodium distichum*) knees).

Up to 10 adult largemouth bass (≥age-1) per site across a size range at ~25 mm intervals were collected from the field each quarter (January, April, July, and October) from 2005 to 2008 to estimate whole-body energy density, as well as once per month throughout the spawning period (February–June) to determine gonad energy density for estimating spawning costs in the bioen-

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ergetics model. In the fall of each year (October and November), all largemouth bass were collected and analyzed in the laboratory for age and growth estimates. Fish with lengths that indicated they could be either age-0 or age-1 were returned to the laboratory each month for age verification using otoliths. Fish that were not euthanized were measured (nearest mm; total length, TL), weighed (nearest g), and released in the field at the transect site. Stomach contents of up to 25 individuals were removed using acrylic tubes (Van Den Avyle and Roussel 1980) prior to release, placed in individual plastic bags, placed on ice, and returned to the laboratory for analysis.

Laboratory processing of largemouth bass

Largemouth bass collected from the field and returned to the laboratory each quarter were measured (nearest mm TL), weighed (nearest g), and their sagittal otoliths removed and stored dry for age and growth determination. Stomach contents were removed and stored in 95% EtOH for diet analysis. Gonads were removed, weighed (nearest 0.01 g), and frozen in water for later caloric analyses. After processing was complete, the whole fish (minus gonads) was frozen for later caloric analysis.

Field-derived largemouth bass growth estimates

We estimated largemouth bass annual growth rates using incremental growth analysis derived from back-calculated length-at-age from otoliths to examine how annual growth varied along a longitudinal salinity gradient and how annual variation in salinity levels impacted growth. Sagittal otoliths of all fall-collected largemouth bass were examined whole under a dissecting microscope for age determination. Otolith annuli formation for largemouth bass has been verified using multiple lines of evidence (Taubert and Tranquilli 1982). The age of each fish was estimated by two independent readers. If there was disagreement between readers or if a fish was estimated to be >age-4, the otolith was sectioned with a Beuhler diamond-blade isomet saw and age determined; fish were omitted from analyses if agreement on age could not be reached. After age determination, the otolith radius and annuli radii were measured with an ocular micrometer under a dissecting microscope (nearest 0.001 mm). Length-at-age for each individual was back-calculated using the direct proportion method (Schramm et al. 1992), and annual growth increments were estimated for each individual by determining the change in back-calculated length for all previous years.

To examine the spatial variation in largemouth bass growth rates, we evaluated whether age-specific growth rates were related to distance from Mobile Bay using separate linear regressions for each age (linear regression; PROC REG; SAS Institute, Inc. 2008). The Mobile Bay Lighthouse (30°26.250′N, 88°00.683′W) was used as a reference point to measure river distance from Mobile Bay to each sampling location. To determine potential effects of freshwater inflow and correlated effects (salinity, diet, and temperature) on largemouth bass growth, we tested whether year-specific annual freshwater inflow was related to annual growth increments and whether this effect differed among sampling sites using analysis of covariance (ANCOVA), where annual freshwater flow specific to the year in which incremental growth was estimated was treated as the covariate (ANCOVA; PROC GLM; SAS Institute, Inc. 2008). If the slope between annual freshwater flow and annual growth increments was not different among sites as indicated by the interaction effect between freshwater inflow and sites, it was omitted from the model and the main effects of site and freshwater flow on annual growth increments was tested; if slopes were unequal we tested which sites had a significant relationship between annual freshwater flow and annual growth increments by determining if the site-specific slopes were different from zero using post hoc t tests. We used the combined mean daily freshwater inflow from the Alabama River at Claiborne Lock and Dam near Monroeville, Alabama (USGS stream gage No.

02428400) and from the Tombigbee River at Coffeeville Lock and Dam near Coffeeville, Alabama (USGS stream gage No. 02469761) from 1996 to 2007 (http://waterdata.usgs.gov/nwis/dv) to encompass the period in which growth increments were back-calculated. Separate analyses were conducted for each age up to age-4; too few observations precluded analyses for older fish ($N ≤ 12$ per site). A significance level ($α$) of 0.05 was used for all statistical tests. For these analyses, we assumed that the location of capture was the lifetime location of that largemouth bass (i.e., movement of largemouth bass was negligible with respect to accurately estimating the independent variable of distance from Mobile Bay up to 6 years prior to the time of collection). Multiple lines of evidence, including otolith microchemistry, radio telemetry, and external tagging, has indicated that juvenile and adult largemouth bass move little within the Mobile Delta despite seasonal elevations in salinity (Norris et al. 2005; Farmer 2008; Lowe et al. 2009).

Diet composition and energetic quality of consumed prey

Stomach contents of largemouth bass were identified to the lowest practical taxonomic level (e.g., species for fish, order or family for insects and gastropods). Size of prey ingested was measured and biomass of prey was estimated using allometric relationships determined from this study and published literature values (see Glover 2010). Broad categories of diet proportions (i.e., freshwater fish, estuarine fish, marine fish, blue crabs, shrimp, and aquatic insects) were identified for each individual fish and then averaged across fish by season and region for each age class (Krebs 1998). Energetic density values of prey groupings were based on species that dominated the prey category by percent biomass over the course of the study and were averaged among species when information was available either from the literature (i.e., Thayer et al. 1973; Irwin et al. 2003; Sammons and Maceina 2006) or this study (Table 1). To determine energetic densities of prey taxa not derived from the literature (Table 1), all samples were oven-dried at 70 °C and standard methods were used to determine caloric content (Rand et al. 1994) using a semimicro bomb calorimeter (Parr Instrument Co., Model 1425 and Model 6725). Bomb calibration occurred at 150-run intervals using a benzoic acid standard.

The mean energetic density of consumed prey (ED_{prey}; cal·g^{-1}; 1 cal = 4.185 kJ) for each individual largemouth bass was determined using

$$ED_{prey} = \sum_{i=1}^{j} P_{prey(i)} \cdot ED_{prey(i)}$$

where $P_{prey(i)}$ is the proportion of the ith prey category consumed on a wet mass basis, and $ED_{prey(i)}$ is the estimated energetic density of the ith prey category consumed (cal·g^{-1}). Using this information, we tested whether age, region (i.e., upstream and downstream), season, season-specific freshwater inflow, as well as all possible interactions affected the caloric density of consumed prey (ANCOVA; PROC GLM; SAS Institute, Inc. 2008) via an AIC$_c$ model selection procedure (Burnham and Anderson 2002). A $ΔAIC_c > 2$ was used as the threshold to determine the best model following Burnham and Anderson (2002), which is indicative of a more parsimonious model (i.e., the decrease in information lost by using a more complex model must be justified after being penalized by the addition of more explanatory variables).

Bioenergetics model

We developed a bioenergetics model to examine the potential effects of elevated salinity and its associated effects (e.g., temperature and diet composition) on growth of largemouth bass. Structurally, the model was similar to the published Fish Bioenergetics Model 3.0 (Hanson et al. 1997) with the exception of the inclusion

Table 1. Dominant prey taxa (by biomass) found in the diets of largemouth bass in the Mobile Delta across all seasons and years (2002–2008) listed for each prey category used in bioenergetics models along with the caloric density and source of the information energetic value.

Category	Prey taxon	Caloric density (cal·g wet mass⁻¹)	Source
Freshwater fish	Bluegill (*Lepomis macrochirus*) Redear sunfish (*Lepomis microlophus*) Redspotted sunfish (*Lepomis miniatus*) Threadfin shad (*Dorosoma petenense*) Warmouth (*Lepomis gulosus*)	1122.56	Present study; Sammons and Maceina 2006
Estuarine fish	Fat sleeper (*Dormitator maculates*) Gulf killifish (*Fundulus grandis*) Highfin goby (*Gobionellus oceanicus*)	1191.98	Present study; Thayer et al. 1973
Marine fish	Gulf menhaden (*Brevoortia patronus*) Spot (*Leiostomus xanthurus*) Striped mullet (*Mugil cephalus*)	1108.49	Present study; Thayer et al. 1973
Blue crabs	Blue crab (*Callinectes sapidus*)	594.57	Present study
Shrimp	Grass shrimp (*Palaemonetes* spp.) White shrimp (*Litopenaeus setiferus*)	816.67	Present study
Freshwater crayfish	Cambaridae	827.50	Irwin et al. 2003
Aquatic insects and other organisms	Coleoptera, *Neritina* spp.	874.84	Irwin et al. 2003

of a respiration function that incorporates the interactive effects of temperature, body size, and salinity as determined by Glover et al. (2012). Bioenergetics models are based on the energy mass balance equation:

$$C = R + A + S + F + U + G + \Delta B$$

where C is the amount of energy acquired through consumption, R is respiration cost via standard metabolism, A is activity cost, S is apparent specific dynamic action, F is unassimilated energy lost through egestion, U is the energy lost through excretion, G is the energetic losses due to spawning, and ΔB is the energetic equivalent of the change in whole-body mass (Hanson et al. 1997). The daily change in mass of largemouth bass can then be determined by rearranging the energy mass balance equation to solve for ΔB and dividing this result by predator energy density (ED_{pred}).

Consumption

The specific consumption rate C (cal·g⁻¹·day⁻¹) of largemouth bass was estimated using

$$C = CA \cdot M^{CB} \cdot r_c \cdot P_{C_{max}} \cdot ED_{prey}$$

where CA and CB are species-specific constants that define the maximum consumption rate (C_{max}; g·g⁻¹·day⁻¹) as a function of predator wet mass M (g), r_c is a temperature-dependent multiplier that increases at a rate defined by CQ from 0.04 at 0 °C to a maximum of 1 at the optimal temperature for consumption (CTO) and rapidly drops to zero as temperature approaches the thermal maximum for consumption (CTM; Rice et al. 1983; Table 2), $P_{C_{max}}$ is the proportion of temperature-compensated C_{max} required to grow at observed rates determined through an iterative process as described below, and ED_{prey} is the mean energetic density of consumed prey (cal·g⁻¹) as defined above. Total energy consumed (cal·day⁻¹) was then determined by multiplying C by M.

Respiration and activity

Respiration (R; cal·g⁻¹·day⁻¹) was estimated using

$$R = RA \cdot M^{RB\{RS[s(s-S_{min})^2] + RQS[t \cdot s(s-S_{min})^2]\}} e^{RQ} \cdot 3.24$$

where RA is the intercept of the allometric mass function, RB is the slope of the allometric mass function, RQ is the scaled effect of temperature t (°C), RS is the scaled effect of salinity s (ppt), RQS is

the scaled effect of the interaction between s and t, S_{min} is the salinity value at which R is similar to that in fresh water (Glover et al. 2012), 3.24 is the oxycaloric constant that converts oxygen consumed (mg O_2·day⁻¹) to calories (Elliott and Davidson 1975). Activity (A; cal·g⁻¹·day⁻¹) was estimated using

$$A = (ACT - 1) \cdot R$$

where ACT is the proportional increase in respiration costs due to activity (Table 2). We assumed that ACT was similar to that used previously for largemouth bass bioenergetics modeling (Rice et al. 1983), which represents an approximate 2% increase in standard metabolism due to activity (Table 2). Total energetic losses due to R and A (cal·day⁻¹) were determined by multiplying each by M.

Egestion, excretion, and apparent specific dynamic action

Losses due to egestion (F; cal·g⁻¹·day⁻¹), excretion (U; cal·g⁻¹·day⁻¹), and specific dynamic action (S; cal·g⁻¹·day⁻¹) were estimated using

$$F = FA \cdot C$$
$$U = UA \cdot (C - F)$$
$$S = SDA \cdot (C - F)$$

where FA is the proportion of consumed prey lost through egestion, UA is the proportion of assimilated prey lost through excretion, and SDA is the proportion of assimilated prey lost through apparent specific dynamic action (Table 2). Total energetic losses due to F, U, and S (cal·g⁻¹) were determined by multiplying each by M.

Largemouth bass energy density and spawning costs

Energetic densities of somatic tissue (i.e., whole body minus gonads) and gonads were determined separately using bomb calorimetry to allow for inclusion of spawning costs in bioenergetics simulation. Somatic tissue samples were thawed, their wet mass recorded (nearest 0.01 g), and an autoclave procedure was used to obtain a 40 to 60 g subsample (Glover et al. 2010). Gonads were thawed, their wet mass recorded (nearest 0.0001 g), and dried whole. Whole-body predator energy density (ED_{pred}; somatic + gonads) in the bioenergetics model was a function of body mass M (ANCOVA; cal·g wet mass⁻¹ = $874.98 \cdot M^{0.057}$; $F_{[1,339]}$ = 57.79, $P < 0.001$). A separate equation was fit for summer, which had a lower intercept compared with the rest of the year (ANCOVA; cal·g wet mass⁻¹ = $828.94 \cdot M^{0.057}$; $F_{[3,339]}$ = 5.12, $P < 0.001$).

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Table 2. Parameter values used in the bioenergetics model, along with their definition and source of information.

Parameter	Definition	Value	Source
Consumption			
CA	Intercept for maximum consumption	0.33	Rice et al. 1983
CB	Mass dependence exponent for maximum consumption	−0.325	Rice et al. 1983
CQ	Slope for temperature dependence of maximum consumption	2.65	Rice et al. 1983
CTO	Optimal temperature for consumption	27.5	Rice et al. 1983
CTM	Maximum temperature for consumption	37	Rice et al. 1983
Respiration			
RA	Intercept of the allometric mass function	9.3273	Glover et al. 2012
RB	Slope of the allometric mass function	−0.2527	Glover et al. 2012
RQ	Slope for temperature dependence on respiration	−0.0033	Glover et al. 2012
RS	Slope for salinity dependence, on respiration	0.0097	Glover et al. 2012
RSQ	Slope for the interactive dependence, of temperature and salinity on respiration	−0.0005	Glover et al. 2012
S_{min}	Salinity value at which respiration is similar to that at fresh water	9.7143	Glover et al. 2012
ACT	Activity multiplier	1.0198	Rice et al. 1983
Specific dynamic action, egestion, and excretion			
SDA	Proportion of assimilated energy lost to apparent specific dynamic action	0.142	Rice et al. 1983
FA	Proportion of consumed energy lost to egestion	0.104	Rice et al. 1983
UA	Proportion of assimilated energy lost to excretion	0.079	Rice et al. 1983

We were primarily interested in determining consequences of the estuarine environment for the average largemouth bass rather than sex-specific comparisons and thus did not differentiate males and females in our bioenergetics model. The energetic cost of ovaries has been suggested to be similar to the energetic expenditure of nesting males (Heidinger 1975). As such, a general spawning-cost function was used to represent both the female's size-specific energy allocation to ovaries and the energy used by males for nest building and parental care. Energetic losses due to spawning (G) was estimated in the bioenergetics model using

$$G = (G_{max} \cdot ED_{gonads}) - (G_{min} \cdot ED_{gonads})$$

where G_{max} is the maximum gonad mass as a function of body mass, G_{min} is the residual gonad mass after spawning as a function of body mass, and ED_{gonads} is the gonad mass-specific energetic density. Size-specific constraints in ovary size (G_{max} and G_{min}) were determined using quantile regression (PROC QUANTILE; SAS Institute, Inc. 2008). To define G_{max}, we used ovaries collected monthly throughout the spawning period (March–May) and determined the 95th percentile of ovary mass as a function of total female mass M (quantile regression: $G_{max} = -1.52 + 0.07 \cdot M$; $N = 298$). We used ovaries collected after spawning (June–August) to define G_{min} by estimating the 5th percentile of ovary mass as a function of female mass (quantile regression: $G_{min} = -0.28 + 0.003 \cdot M$; $N = 118$). Energetic densities of pre- and post-spawn ovaries were estimated from the relationship between ovarian energy density (ED_{gonads}; cal·g wet mass^{-1}) and ovary mass (G_{mass}) (linear regression using $\log_{10}$-transformed ED_{gonads} and G_{mass}: $ED_{gonads} = 694.64 \cdot G_{mass}^{0.24}$; $F_{[1,422]} = 624.82$; $P < 0.001$; $R^2 = 0.60$). Spawning in the simulation occurred on 31 March and was assumed to occur only in fish ≥age-2 given that 83% of females and 97% of males were predicted to be mature within the Mobile Delta at this age (DeVries and Wright 2010; Glover 2010).

Bioenergetics simulations

We conducted bioenergetics simulations for age-1 and older largemouth bass within the upstream and downstream regions of the Mobile Delta to examine potential factors affecting growth at a broad spatial scale at varying levels of freshwater inflow. The downstream region included D'Olive Bay, Bay Minette, Crab Creek, and Big Bayou Canot because elevated salinity and estuarine prey are consistently present during the summer and fall seasons at these sites (DeVries and Wright 2010). The upstream region included Gravine Island, McReynold's Lake, Dennis Lake,

and Tensaw Lake, which rarely experience high salinity except during severe droughts (Peer et al. 2006; Norris et al. 2010). We used the combined mean daily freshwater inflow from the Alabama and Tombigbee rivers from 2002 to 2008 to select years for low and high freshwater inflow years for bioenergetics simulations. Daily salinity records were available beginning in 2004, and this represented the year with the highest annual freshwater inflow during which daily salinity was recorded; therefore, we chose 2004 to represent the high freshwater inflow year. The 20-year minimum freshwater inflow for the Mobile Delta was 2007, so we chose data from this year to simulate the low freshwater inflow year. In addition, all data (i.e., salinity, temperature, and diet proportions) were averaged over the study (2002–2008) to represent average conditions experienced by largemouth bass in the Mobile Delta.

The general procedure for determining the relative impacts of temperature, salinity, and prey use on largemouth bass growth involved first determining the consumption rates necessary to grow at observed rates under the three simulation scenarios (i.e., low, average, and high freshwater inflow using the associated data for salinity, temperature, and diet). Specifically, the proportion of temperature-adjusted maximum consumption $P_{C_{max}}$ required to grow at observed annual rates from 1 April to the following 31 March was determined iteratively for each cohort until observed and predicted end masses were within ±0.001%. To determine the separate effects of salinity, temperature, and diet on spatial and temporal variation in largemouth bass growth patterns, we conducted a sensitivity analysis by using the average freshwater inflow data as a baseline, and then substituted salinity, temperature, or diet values from another freshwater inflow level (i.e., low or high) while using average freshwater inflow data for all other factors. Sensitivity analyses were conducted for lifetime growth by determining the final mass attained through age-5 for each simulation and for each region. This set of simulations was used to determine the potential impact of factors on largemouth bass growth within the bounds of observed temperature, salinity, and diet in both upstream and downstream regions.

To examine the overall potential influence of salinity on lifetime growth of largemouth bass, simulations using observed conditions and one in which salinity was set to 0 ppt were compared through age-10 for each freshwater inflow level; temperature regimes and diet proportions were not changed for this simulation. Consumption rates and diet proportions were assumed to remain constant after age-5. Similarly, we examined the potential effects on growth of consuming energy-poor prey over a lifetime by sub-

Fig. 2. Mean daily temperature (°C) and salinity (ppt) for the upstream (*a* and *c*, respectively) and downstream (*b* and *d*, respectively) regions used in bioenergetics simulations for low (black line), average (light gray line), and high (dark gray line) freshwater inflow scenarios.
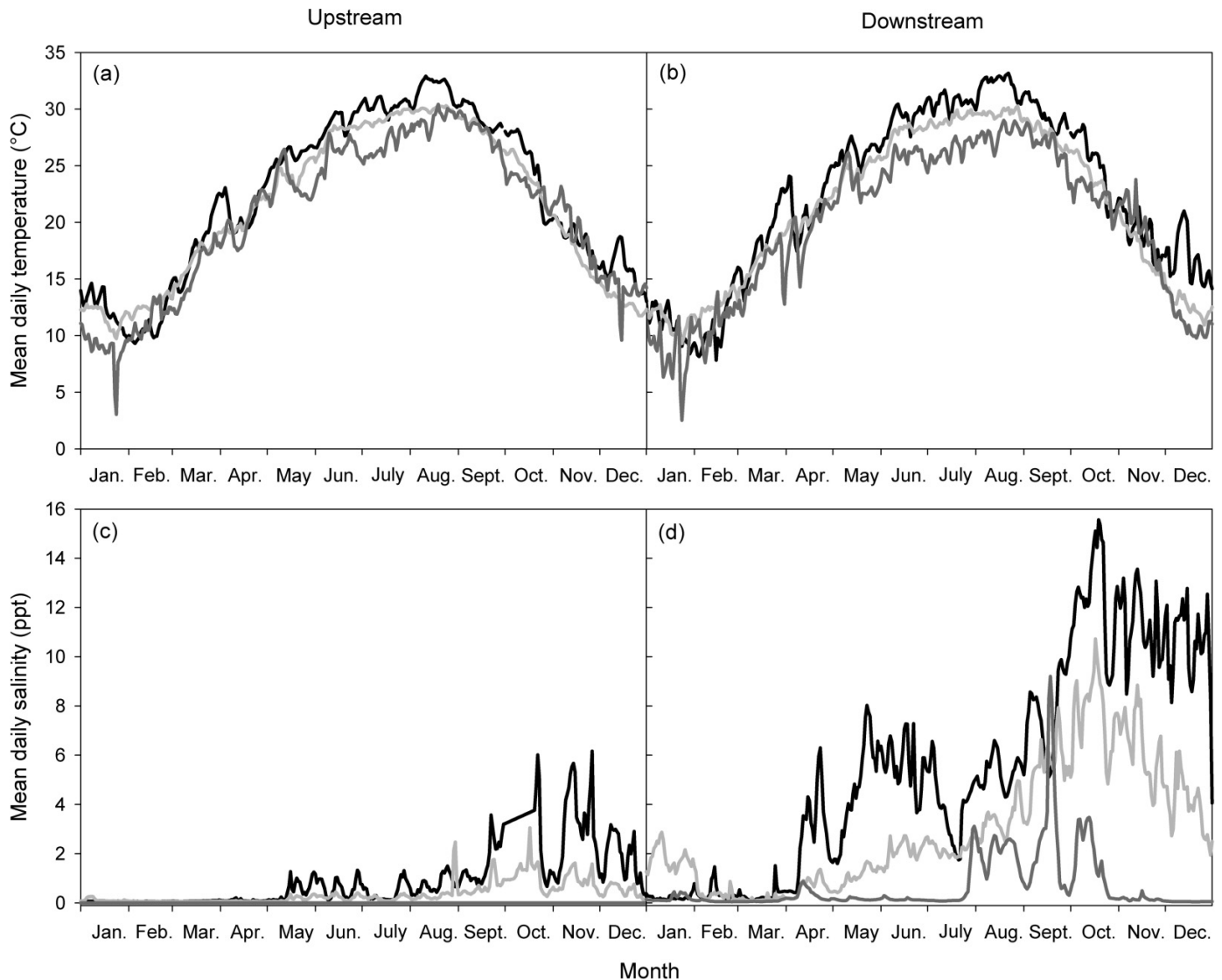
stituting the energetic value of blue crabs with an average value for fish prey (i.e., average across marine, estuarine, and freshwater fish energetic densities; Table 1) and assumed that activity costs due to foraging on other prey items did not change; salinity and temperature were not changed for this simulation. The potential effects of salinity and consumption of energy-poor prey were evaluated in terms of the time required to reach 2.3 kg (5 lb; a size commonly considered a "large" fish by anglers), the number of largemouth bass out of 1000 expected to reach 2.3 kg in the required time based on estimated survival rates from weighted catch-curve analysis (Maceina 1997), and the total mass attained by age-10. Survival rates were estimated separately for upstream and downstream using fish from fall collections (2002–2008).

Start and end mass

Start and end mass for the bioenergetics simulations were determined by first constructing von Bertalanffy growth curves for each region using observed mean TL from each age class from all fall collections (2002–2008) using nonlinear regression (PROC NLIN; SAS Institute, Inc. 2008). Growth curves were then used to estimate length-at-age corresponding to the time of annulus formation during spring (Taubert and Tranquilli 1982). Mass-at-age

was estimated by converting length-at-age estimates to mass using region-specific length–mass regressions determined from all largemouth bass collected throughout this study.

Water temperature and salinity

Water temperature was recorded at 2 h intervals at each site using HOBO temperature loggers (Onset, Inc.) set at ~1 m depth from 2002 to 2008 (2006–2008 in Big Bayou Canot and Tensaw Lake). Mean daily temperature values for 2004, 2007, and 2002–2008 were averaged from all available site-specific temperature logger data by region to simulate temperature regimes from high, low, and average freshwater inflow years, respectively (Figs. 2*a* and 2*b*).

Specific conductance (mS·cm⁻¹ at 25 °C) was recorded at 30 min intervals with loggers (Solinst Model 3001 LTC levelogger) during May 2005 through December 2008 at the most downstream site (i.e., D'Olive Bay) and a site in the middle of the spatial range (i.e., Gravine Island) and was converted to salinity (ppt) using standard formulas (APHA 1998). Logger failure resulted in gaps in the salinity record for the downstream site. Therefore, we also obtained all available salinity readings (i.e., 2004–2008) from a nearby location, Meaher State Park (30°40.028′N, 87°56.188′W), which were

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Fig. 3. Growth increments (mm·year⁻¹ ± 1 SE) of largemouth bass for each sampling site plotted as a function of distance from Mobile Bay Lighthouse (km) from (*a*) age-0 to age-1, (*b*) age-1 to age-2, (*c*) age-2 to age-3, and (*d*) age-3 to age-4.
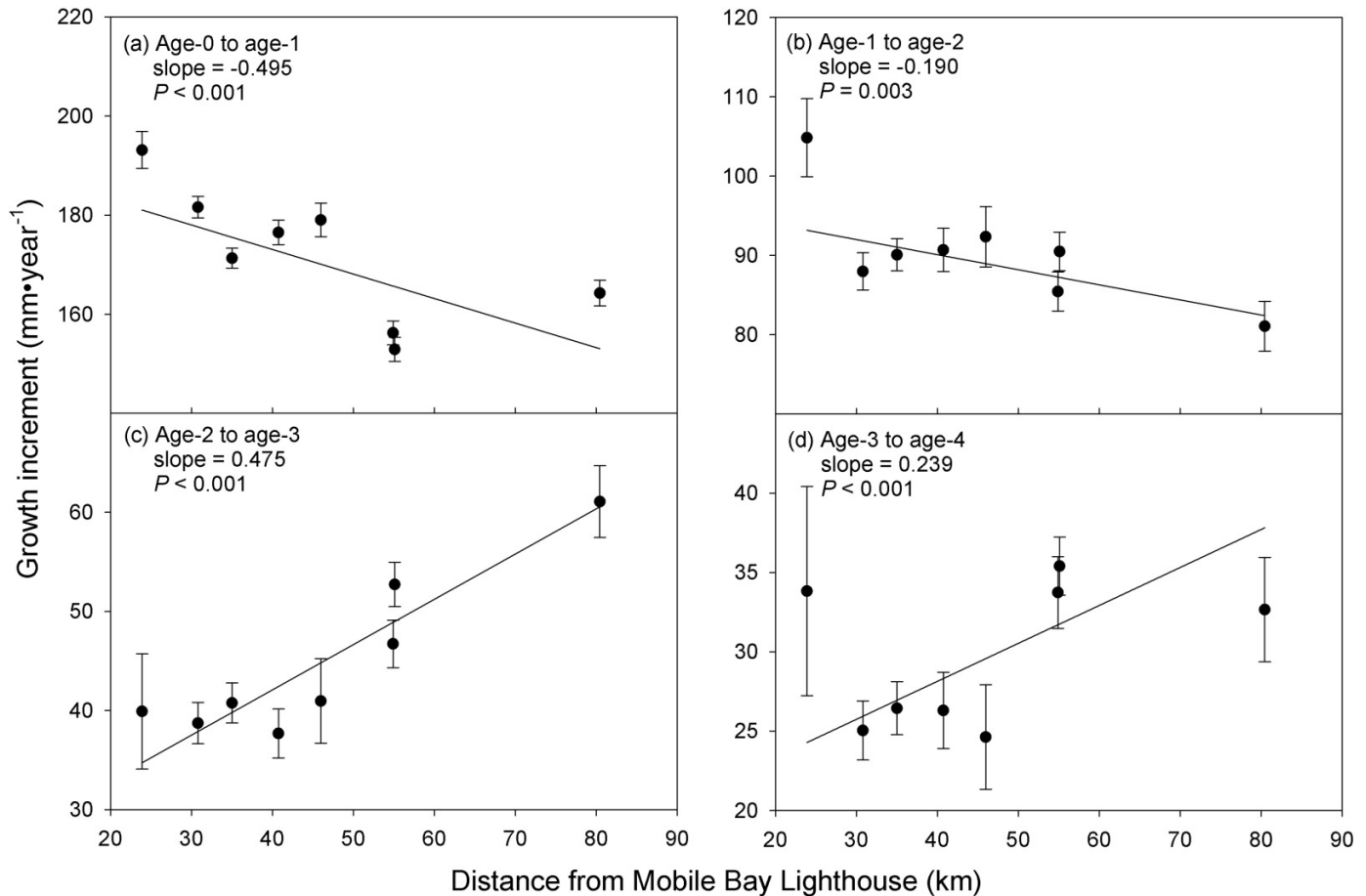
recorded by the Dauphin Island Sea Lab at 30 min intervals using a YSI model 6600 (http://www.mymobilebay.com/stationdata/) to supplement downstream salinity values. Mean daily salinity values for 2004, 2007, and 2002–2008 were averaged for the downstream region (i.e., D'Olive Bay and Meaher State Park) and the upstream region (i.e., Gravine Island) to simulate salinity regimes from high, low, and average freshwater inflow years, respectively (Figs. 2*c* and 2*d*). Salinity was not recorded in the upstream region on a daily basis in 2004, but monthly monitoring found that salinity never exceeded 0.2 ppt upstream of Gravine Island (Norris et al. 2010). Therefore, we assumed salinity in the upstream region to be 0 ppt in 2004.

Proportion of consumed prey

Seasonal diet information from 2002 to 2008 was pooled to reflect the average diet proportions consumed over the lifetime of largemouth bass, and separate diet proportions were derived for high (2004) and low (2007) freshwater inflow years. Year-specific diet information from 2002–2004, 2005–2007, and 2002–2008 can be found in Norris et al. (2010), Farmer (2008), and (Glover 2010), respectively.

Interactive effects of salinity, prey caloric content, and temperature on growth potential

We explored the potential interactive effects of salinity, prey caloric content, and temperature on growth of coastal largemouth bass by determining the net energy available for growth (cal·g⁻¹) via bioenergetics simulations at all combinations of each of these factors. Simulations were conducted at a 0.5 proportion of C_{max} for fish weighing 454 g (1 lb) and 2268 g (5 lb) to determine

how potential energetic constraints to growth vary with size. This level of consumption was found reasonable based on previous simulations with these data.

Results

Largemouth bass growth increments

Largemouth bass closer to Mobile Bay grew faster than those farther upstream in their first (regression; $F_{[1,1178]} = 73.96$, $P < 0.001$; Fig. 3*a*) and second year of life (regression; $F_{[1,586]} = 8.66$, $P = 0.003$; Fig. 3*b*). However, the site farthest downstream (D'Olive Bay) and farthest upstream (Tensaw Lake) in our sample area were most responsible for the significant relationship for growth between age-1 and age-2, as growth was similar among other sites ($t_{[580]} \le 1.52$; $P \ge 0.13$). By the third year of life, this trend was reversed such that growth rates increased with distance from Mobile Bay between age-2 and age-3 (regression; $F_{[1,275]} = 45.27$, $P < 0.001$; Fig. 3*c*.) and between age-3 and age-4 (regression; $F_{[1,130]} = 14.84$, $P < 0.001$; Fig. 3*d*).

The slope of the relationship between largemouth bass annual growth increments and the annual mean daily freshwater inflow covariate on largemouth bass growth rates was different among sites in the first year of life (ANCOVA; $F_{[7,955]} = 5.31$, $P < 0.001$). In general, increased freshwater inflow had negative effects on largemouth bass growth downstream, little to no effect midstream to upstream, and positive effects at the farthest upstream site (Fig. 4). Treating site as a continuous variable in terms of distance from Mobile Bay suggested that the point at which the effect of freshwater inflow switched from negative to positive was at 53.2 km, or 1.7 river km downstream of Dennis Lake. Neither the

Fig. 4. Site-specific effect of annual mean daily freshwater inflow ($m^3 \cdot s^{-1}$) on largemouth bass growth increments ($mm \cdot year^{-1} \pm 1$ SE) from age-0 to age-1 for (*a*) Tensaw Lake, (*b*) McReynold's Lake, (*c*) Dennis Lake, (*d*) Big Bayou Canot, (*e*) Gravine Island, (*f*) Crab Creek, (*g*) Bay Minette, and (*h*) D'Olive Bay.

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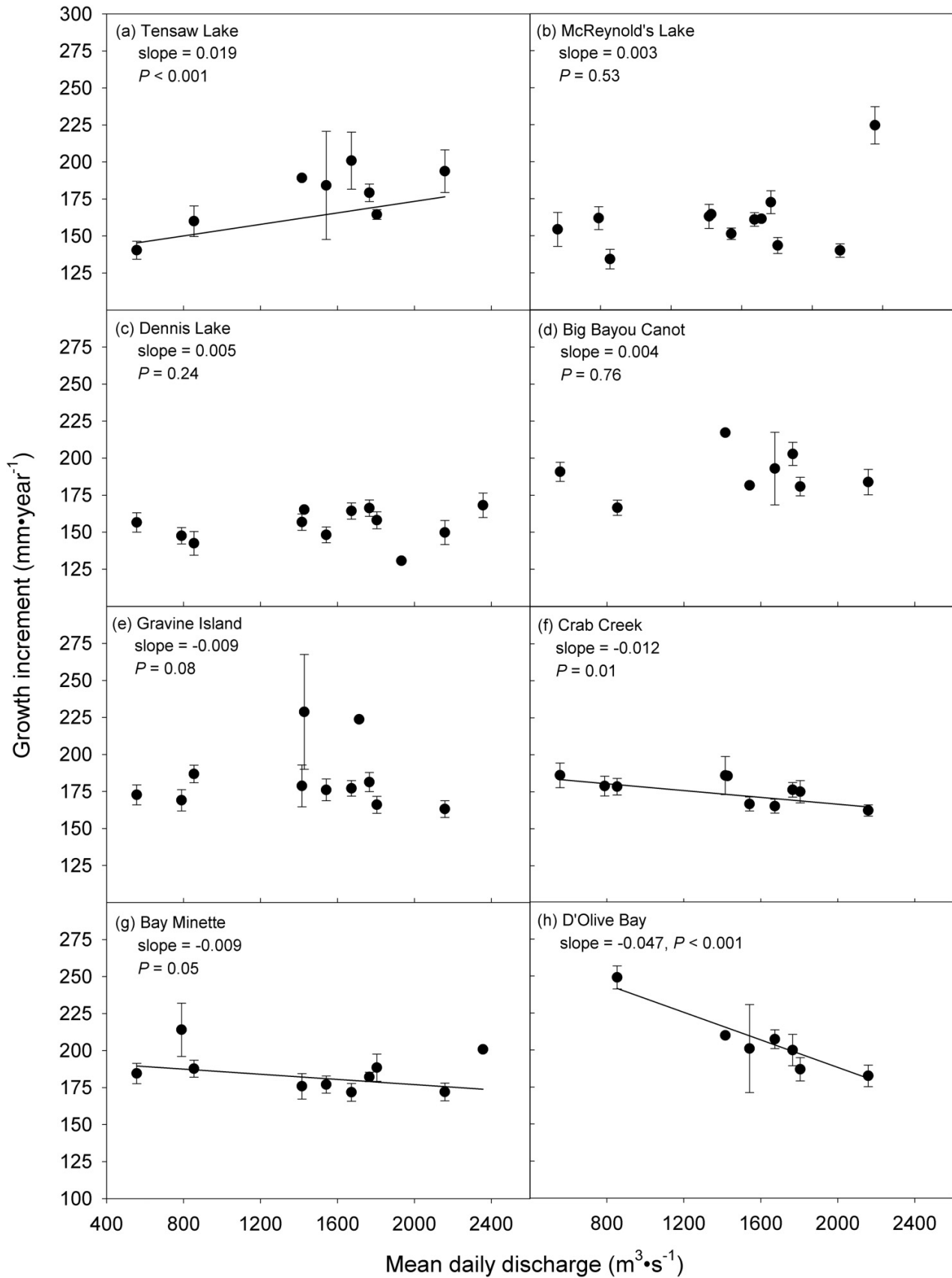
Fig. 5. The effect of salinity (*a* and *d*), temperature (*b* and *e*), and diet (*c* and *f*) on simulated mass (g) of largemouth bass through age-5 for the low (black line), average (light gray line), and high (dark gray line) freshwater inflow scenarios in the upstream (*a–c*) and downstream (*d–f*) regions. The average freshwater inflow represents simulated mass under observed conditions fit to observed mass-at-age; the change in simulated mass from either the low or high freshwater inflow scenarios is the effect from substituting the average values of salinity, temperature, or diet proportions with those from low or high freshwater inflow scenarios, respectively, while holding all other variables constant.
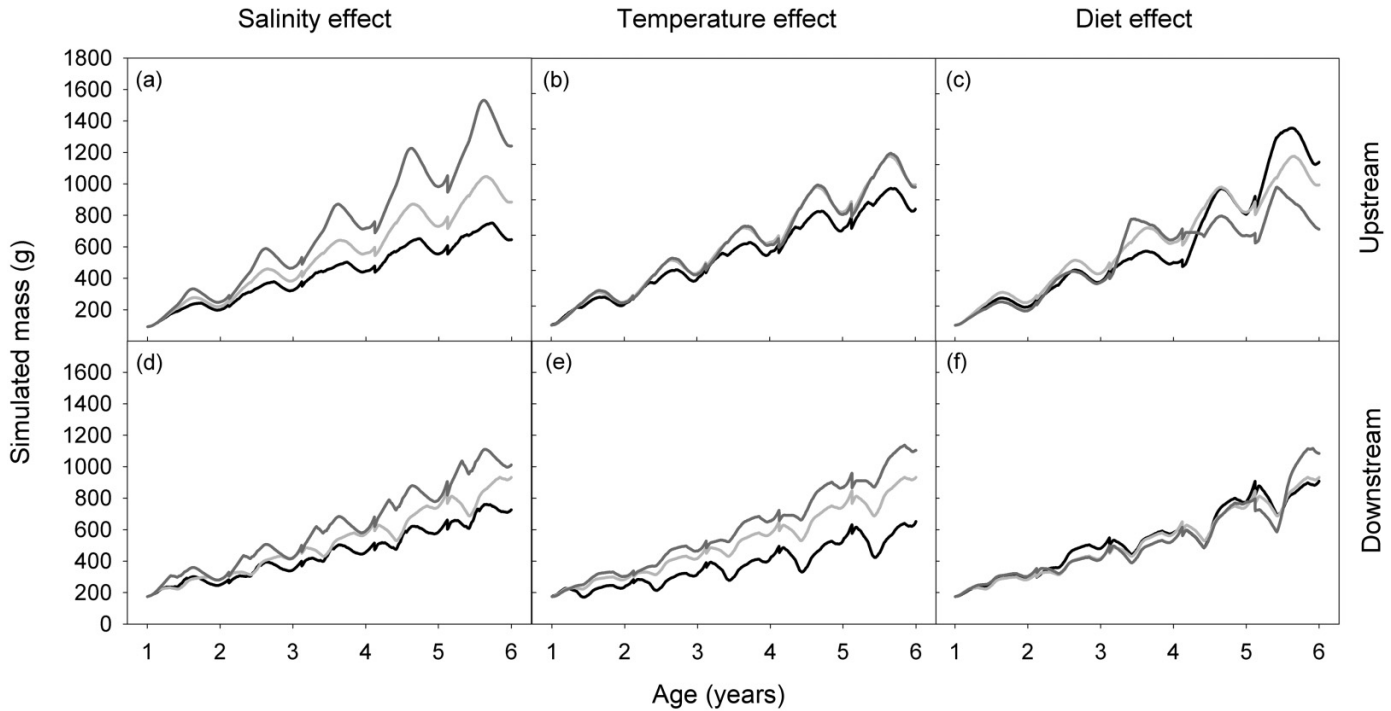
main effect of freshwater inflow (ANCOVA; $F_{[1,572]} = 1.81$, $P = 0.18$) nor the interaction with sites (ANCOVA; $F_{[7,572]} = 1.13$, $P = 0.34$) affected growth rates of largemouth bass in their second year of life. By the third year of life, the effect of the freshwater inflow covariate was again site-specific ($F_{[7,261]} = 2.98$, $P = 0.005$), with the slope of the relationship between annual freshwater inflow and annual growth increments being positive at Tensaw Lake (slope = 0.015; $t_{[261]} = 2.31$; $P = 0.02$) and McReynold's Lake (slope = 0.015; $t_{[261]} = 2.97$; $P = 0.003$), negative for Crab Creek (slope = –0.010; $t_{[261]} = -2.17$; $P = 0.03$), and no effect at all other sites ($t_{[261]} \leq 1.09$; $P \geq 0.27$). Within the fourth year of life, the main effect of freshwater inflow covariate affected growth (ANCOVA; $F_{[1,116]} = 6.51$, $P = 0.01$), and the effect of freshwater inflow on annual incremental growth was not different among sites (ANCOVA; $F_{[7,116]} = 0.86$, $P = 0.54$). After removing the interaction effect that allows for unequal effects of freshwater inflow on annual incremental growth among sites, increased freshwater inflow was found to positively influence growth at all sites (slope = 0.005; $t_{[123]} = 2.52$; $P = 0.01$).

Caloric content of consumed prey

The best model describing caloric density of consumed prey by largemouth bass as determined by AIC$_c$ included the main effects of age ($F_{[1,3379]} = 29.65$; $P < 0.001$), season ($F_{[3,3379]} = 0.81$; $P = 0.49$), region ($F_{[1,3379]} = 237.05$; $P < 0.001$), and season-specific mean daily freshwater inflow ($F_{[1,3379]} = 6.18$; $P = 0.013$), as well as the interaction between age and season ($F_{[1,3379]} = 10.64$; $P < 0.001$). All other models had ΔAIC$_c$ values > 2 and were therefore not considered. The best model indicated that caloric content of consumed prey was negatively related to age during spring (decrease of 16.85 cal·g⁻¹ of prey·year⁻¹; $t_{[3379]} = -2.66$; $P = 0.01$), summer (decrease of 42.30 cal·g⁻¹ of prey·year⁻¹; $t_{[3379]} = -5.61$; $P < 0.001$), and fall (decrease of 19.75 cal·g⁻¹ of prey·year⁻¹; $t_{[3379]} = -19.75$; $P = 0.003$), but not during winter ($t_{[3379]} = 1.48$; $P = 0.14$). Largemouth

bass in the upstream region consumed 113.51 cal·g⁻¹ of prey more than those downstream ($t_{[3379]} = 15.40$; $P < 0.001$), which was consistent across ages, seasons, and freshwater inflow levels. The caloric density of consumed prey was positively related to freshwater inflow. The caloric density increased 0.013 cal·g⁻¹ of prey with every unit increase in freshwater inflow (m³·s⁻¹).

Bioenergetics simulations

Bioenergetics simulations indicated that salinity among varying levels of freshwater inflow was most influential on lifetime growth of largemouth bass through the end of age-5 in the upstream region (Fig. 5*a*) and that variation in temperature and diet proportions among freshwater inflow levels had smaller effects on lifetime growth in relation to salinity (Figs. 5*b* and 5*c*). Variation in temperature and salinity among freshwater inflow levels had similar effects on lifetime growth of downstream largemouth bass because of the interaction between these variables on metabolic costs, and both had higher effects compared with changes in diet composition (Figs. 5*d*, 5*e*, and 5*f*). The high freshwater inflow salinity regime (i.e., lowest salinity) was the best for growth, increasing final mass attained by 40% by age-6 upstream (Fig. 5*a*) and by 9% downstream (Fig. 5*d*) in comparison with observed mass (i.e., in the average freshwater inflow simulation). The low freshwater inflow level provided the poorest environment for growth in terms of salinity, decreasing lifetime growth by 27% and 22% in relation to observed final mass in the upstream and downstream regions, respectively.

The higher summer temperatures typical of low freshwater inflow had the strongest negative impact on simulated growth at the low freshwater inflow regime in both regions, reducing final mass attained by 16% and 30% in the upstream (Fig. 5*b*) and downstream regions (Fig. 5*e*), respectively. An 18% increase in simulated final mass was observed under the temperature regime from high

Fig. 6. Age-specific largemouth bass consumption of prey (g·g⁻¹·day⁻¹) in the upstream region estimated from bioenergetics simulations for the (*a*) low, (*b*) average, and (*c*) high freshwater inflow scenarios (pink = invertebrates; blue = crayfish; yellow = shrimp; green = blue crabs; red = marine fish; white = estuarine fish; black = freshwater fish). The dashed line represents the mean caloric (1 cal = 4.185 kJ) content of consumed prey. Results were smoothed by showing daily specific consumption and caloric content estimates at 25-day intervals.
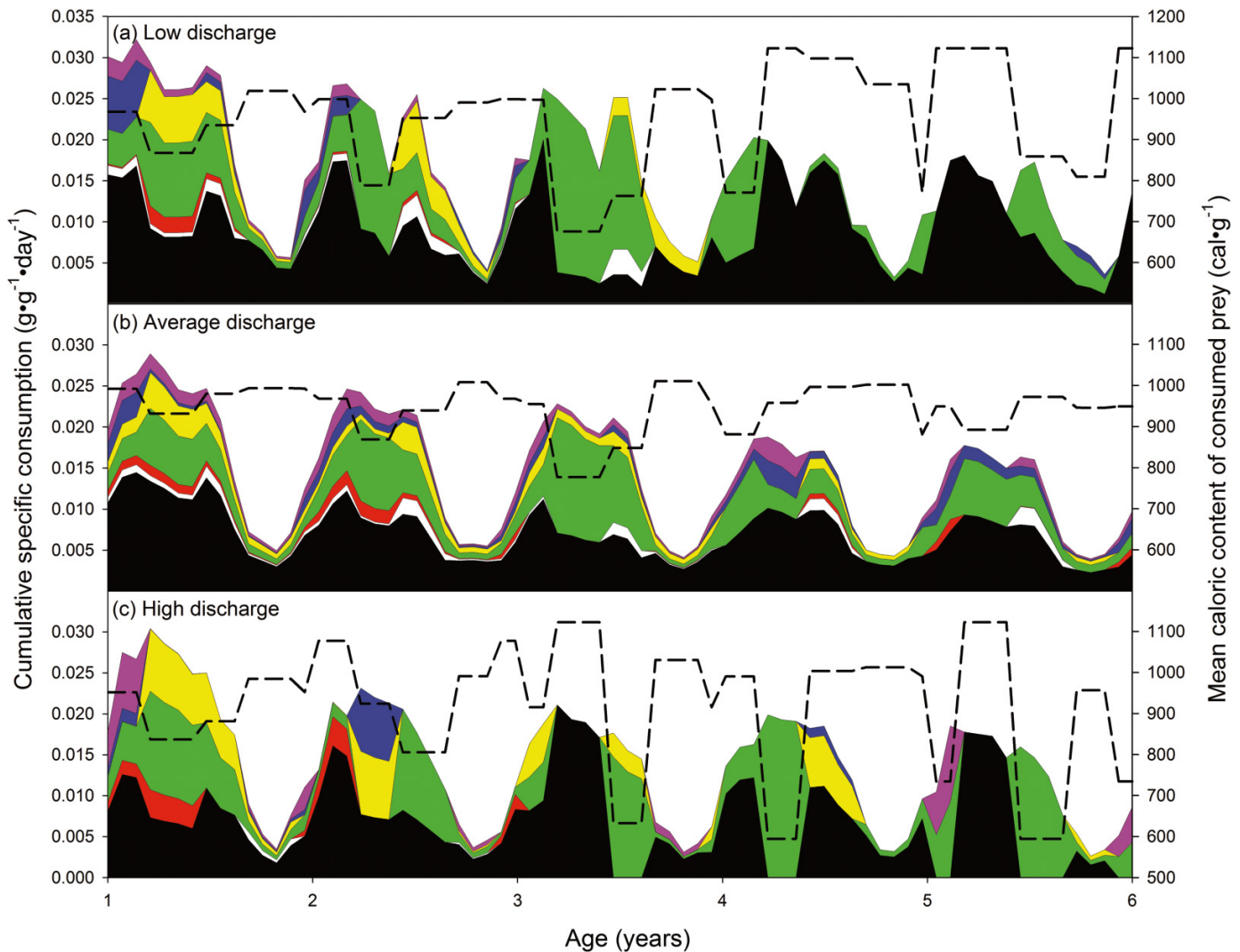
freshwater inflow years in comparison with observed final mass in the downstream region because of the interactive effects of temperature and salinity on metabolic costs, whereas simulated mass was similar between average and high freshwater inflow temperature regimes because of the relatively low salinity in both simulations. For each region, mass declined during summer at each age under the low freshwater inflow simulation, corresponding to periods when summer temperatures increased the effects of salinity and exceeded optimum temperature for consumption (i.e., 27.5 °C). Temperatures peaked at 32.9 and 33.2 °C in the upstream and downstream regions, respectively. In summary, sensitivity analyses indicated that temperature was an important determinant of growth due not only to direct temperature-related effects on respiration and consumption, but also due to the interactive effects between salinity and temperature on respiration.

Final simulated mass by age-6 was greatest using the diet composition typical of low freshwater inflow and was lowest using diets from high freshwater inflow using other conditions from in the upstream region (Fig. 5*c*). The reverse pattern was observed for the downstream region abiotic conditions, where diet composition most favorable for lifetime growth was that from the high freshwater inflow regime, and diet was similar during the low and average freshwater inflow regimes (Fig. 5*f*). It was apparent, however, that the effect of the different freshwater inflow regimes was age-specific as the growth trajectories crossed across ages.

The negative effect of diet on lifetime growth in the upstream region within the high freshwater inflow simulation was due primarily to the diet being made up entirely of blue crabs during the summer at age-4 and fall at age-5 (Fig. 6*c*), which caused a reduction in the average caloric intake per gram of prey resulting in a reduction in age-4 and age-5 growth (Fig. 5*c*). Seasonal declines in average caloric intake were evident in the average freshwater inflow simulations at all ages (Fig. 6*b*), but changes in these values were not as drastic relative to low (Fig. 6*a*) and high freshwater inflow (Fig. 6*c*). The average caloric density consumed in the downstream region was similar among the three freshwater inflow simulations (Fig. 7). By age-3, a strong seasonal pattern emerged in which the average caloric intake decreased sharply during summer and fall consistent with the increased consumption of blue crabs. There was an increase in consumption of marine fish prey with lower levels of freshwater inflow, and consequently higher mean caloric content of consumed prey (Fig. 7), which led to improved growth in the first few years of life at low freshwater inflow (Fig. 5*f*).

Fig. 7. Age-specific largemouth bass consumption of prey (g·g⁻¹·day⁻¹) in the downstream region estimated from bioenergetics simulations for the (*a*) low, (*b*) average, and (*c*) high freshwater inflow scenarios (pink = invertebrates; blue = crayfish; yellow = shrimp; green = blue crabs; red = marine fish; white = estuarine fish; black = freshwater fish). The dashed line represents the mean caloric (1 cal = 4.185 kJ) content of consumed prey. Results were smoothed by showing daily specific consumption and caloric content estimates at 25-day intervals.
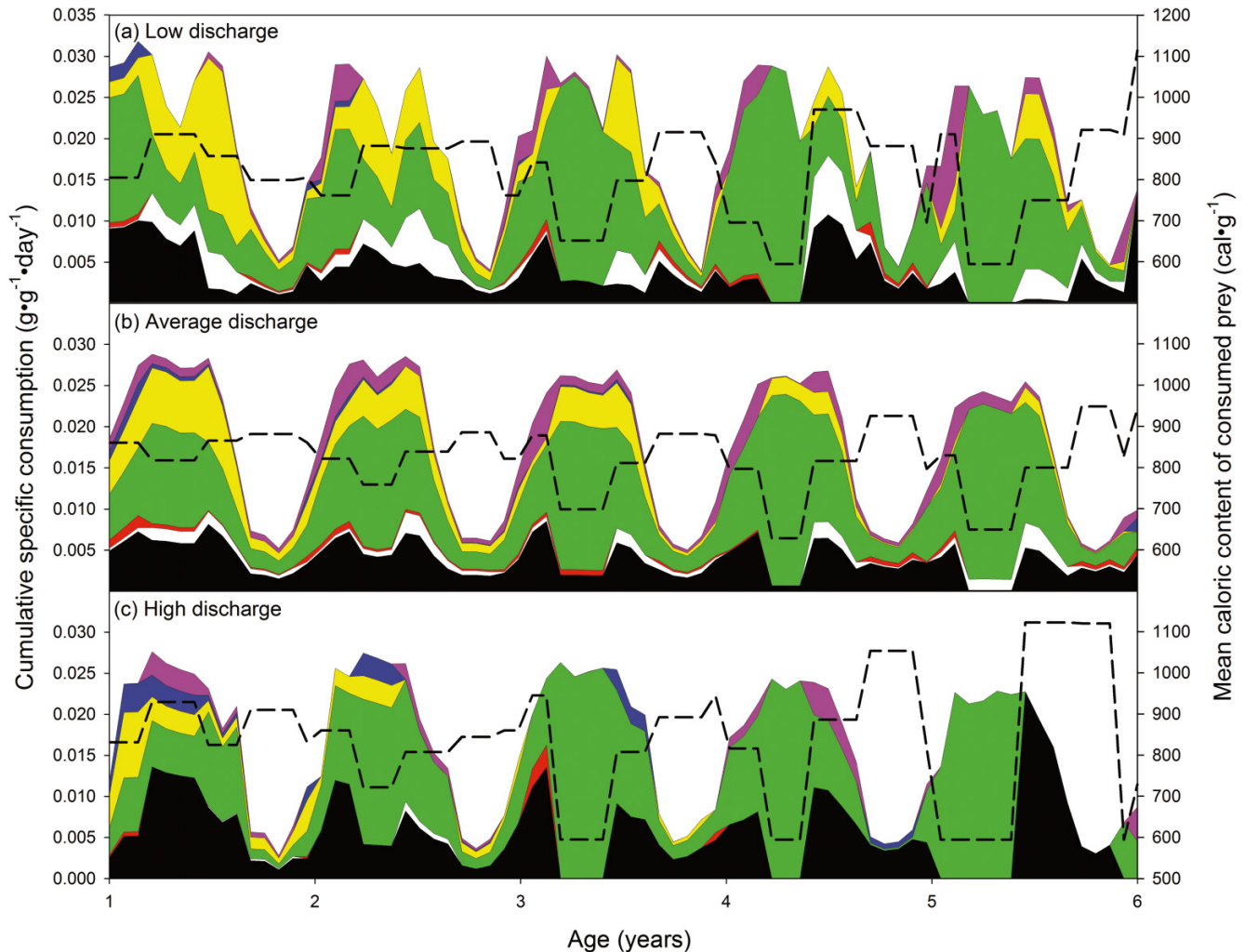
Predicted mass of age-10 largemouth bass under varying levels of freshwater inflow indicated that the average largemouth bass cannot attain a mass of 2.3 kg within this time period in either region under observed conditions (Table 3). Baseline simulations using observed conditions suggested that the high freshwater inflow conditions provided the most favorable environment for growth in the upstream and downstream regions. The simulations in which the effect of salinity was removed by setting salinity to 0 ppt suggested that largemouth bass could attain 2.3 kg within 5.41 to 8.54 and 4.48 to 6.56 years in the upstream and downstream regions, respectively. Simulated largemouth bass in the upstream and downstream regions in which lower-energy blue crabs were switched with higher-energy fish prey reached 2.3 kg within 4.55 to 5.50 and 3.47 to 4.12 years, respectively, suggesting that consumption of low-energy prey (blue crabs) has stronger negative effects on lifetime growth than salinity in both regions. Simulations indicated that growth of largemouth bass in upstream areas was likely more limited by consumption rate relative to that downstream when effects of salinity and reduced caloric intake were removed. In the upstream region, age-specific estimates of consumption rates (proportion of C_{max}) ranged 13%–33%, 13%–28%, and 7%–25% lower relative to downstream for the low, average, and high freshwater inflow simulations, respec-

tively. Therefore, it appears that lower consumption rates may have limited growth potential of largemouth bass in the upstream region more than salinity and prey caloric density.

Interactive effects of salinity, prey caloric content, and temperature on growth potential

Bioenergetics simulations in which all combinations of salinity, prey caloric content, and temperature were evaluated predicted that prey caloric content strongly influenced the effects of salinity and temperature on growth potential. Growth potential of a 454 g coastal largemouth bass consuming at an average prey energy density of 600 cal·g⁻¹ (approximate energy density of blue crabs) was positive in a fairly small range of temperatures at most salinity levels, with the exception of fresh water and near the isosmotic level (i.e., 9 ppt; Glover et al. 2012). An increase in the average caloric content of consumed prey increased the number of temperature and salinity combinations in which positive growth could occur for a 454 g largemouth bass (Figs. 8*b* and 8*c*). Although these general trends were also predicted for a 2268 g largemouth bass, the growth potential was negative for a greater number of temperature and salinity combinations relative to a 454 g largemouth bass (Figs. 8*d*, 8*e*, and 8*f*), suggesting that positive growth is much more difficult to maintain for large fish under a variety of conditions in coastal systems.

Table 3. Results of the projected growth under three different simulated scenarios showing the time (years) required to reach 2.3 kg (5 lb), the estimated annual survival rate from the weighted catch-curve analysis, number (*N*) per 1000 fish that are expected to reach this size within the required time based on annual survival rates (*S*), and the mass (kg) attained at age-10.

Region	Freshwater inflow	Time to 2.3 kg (years)	*S*	*N* per 1000	Mass at age-10 (kg)
Observed conditions					
Upstream	Low	—	0.54	—	1.27
	Average	—	0.54	—	1.34
	High	—	0.54	—	1.38
Downstream	Low	—	0.48	—	1.31
	Average	—	0.48	—	1.36
	High	—	0.48	—	1.46
Salinity removed					
Upstream	Low	5.41	0.54	36	4.35
	Average	8.54	0.54	5	2.12
	High	—	0.54	—	1.38
Downstream	Low	4.48	0.48	37	8.46
	Average	5.49	0.48	18	4.58
	High	6.56	0.48	8	3.12
Blue crabs removed (switched to fish)					
Upstream	Low	4.65	0.54	57	2.85
	Average	5.50	0.54	34	3.67
	High	4.55	0.54	61	6.37
Downstream	Low	3.47	0.48	78	8.31
	Average	4.12	0.48	49	9.61
	High	4.11	0.48	49	10.78

Note: A dash indicates that the simulated largemouth bass did not reach 2.3 kg.

Discussion

The results of this study suggest that estuarine- and marine-derived prey benefited the growth of young largemouth bass <age-3 in downstream, brackish environments of the Mobile Delta, which allowed them to not only persist at the edge of their physiological tolerances, but also to grow faster than largemouth bass found in upstream, freshwater environments. These results are consistent with previous findings for largemouth bass (Susanto and Peterson 1996; Peer et al. 2006) and may help to explain high body condition of other stenohaline centrarchids found in brackish systems (Peterson 1991). Our results also suggest, however, that ontegenetic shifts in prey use toward poorer quality prey and increasing costs of salinity of ionoregulation with size of largemouth bass (Glover et al. 2012), in combination with high peak summer temperatures, decreased the net benefit of the estuarine environment for older largemouth bass. As such, the relative costs and benefits of the estuarine environment not only changed over the life of largemouth bass, but also changed linearly with distance from the source of the marine influence. This may help to explain the small maximum size of largemouth bass observed in estuarine systems (Colle et al. 1976; Guier et al. 1978; Meador and Kelso 1990a) and may give insight into size-selective forces shaping the life history traits of this and other freshwater fishes that allow them to maintain high enough abundances in brackish environments to support economically important sport fisheries (Guier et al. 1978; Tucker 1985; Krause 2002). Moreover, ontogenetic shifts in prey use and species-specific salinity tolerance may be a key element in understanding the biotic and abiotic interactions that dictate community structure zonation along coastal rivers, thereby providing a more mechanistic viewpoint for predictive modeling with respect to climate change, such as rising sea levels and other associated effects (Meyssignac and Cazenave 2012).

Our analyses suggest that growth potential was not only affected by spatial location along the estuarine–freshwater gradient, but was also influenced by the magnitude of freshwater inflow. Specifically, bioenergetics simulations suggest that high freshwater inflow would provide the best environment for growth both upstream and downstream because of lower salinity levels, reduced peak summer temperatures, and increased caloric intake through greater consumption of fish prey. However, incremental growth analyses indicate that the age-specific effects of freshwater inflow varied along the freshwater–estuarine gradient. Specifically, freshwater inflow had a positive effect on the growth increment between age-0 and age-1 upstream and a negative effect downstream, such that growth rates at the highest freshwater inflow level were similar across sites. With decreasing levels of freshwater inflow, however, the growth advantage increased downstream relative to upstream. Although the bioenergetics simulations did not include the age-0 to age-1 cohort, lower freshwater inflow would clearly lead to increased metabolic costs through higher temperatures and salinity, particularly downstream. Previous studies on age-0 largemouth bass within the Mobile Delta found faster growth at sites closest to Mobile Bay (Peer et al. 2006), which was attributed to an earlier switch to and greater degree of piscivory downstream versus upstream likely because of the higher availability of small-bodied estuarine fish prey. Combined with results from the present study, this suggests that freshwater inflow has a negative relationship with availability of fish prey and influences the timing and degree of piscivory, ultimately dictating the growth advantage of age-0 largemouth bass downstream relative to upstream. Therefore the benefits of the estuarine environment can outweigh the costs for age-0 largemouth bass, but they clearly remain influenced by the magnitude of freshwater inflow.

By age-1, all largemouth bass were piscivorous to some degree, and while upstream largemouth bass consumed higher proportions of freshwater fish prey than they did downstream, consumption of estuarine- and marine-derived fish was evident in both regions, particularly during low freshwater inflow. Thus, the higher availability of estuarine- and marine-derived fish prey at lower freshwater inflow during summer may outweigh the negative costs associated with abiotic factors in both regions between age-1 and age-2. Freshwater inflow did not have an effect on site-specific growth rates between age-2 and age-3 and may represent the point at which the metabolic costs of salinity and high sum-

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Fig. 8. The predicted growth potential (cal·g⁻¹) of largemouth bass as a function of temperature for varying levels of salinity (0 and 9 ppt = solid line; 3 ppt = dashed line; 6 ppt = dash-dot-dash line; 12 ppt = dash-dot-dot-dash line) for a 454 and 2268 g largemouth bass plotted for an average prey energy density (ED_{prey}) of 600, 900, and 1200 cal·g⁻¹ (1 cal = 4.185 kJ). The horizontal dotted line indicates the threshold for positive growth (i.e., energy intake is equal to maintenance costs). Note that a single line represents 0 and 9 ppt because predictions were nearly identical at these salinities.
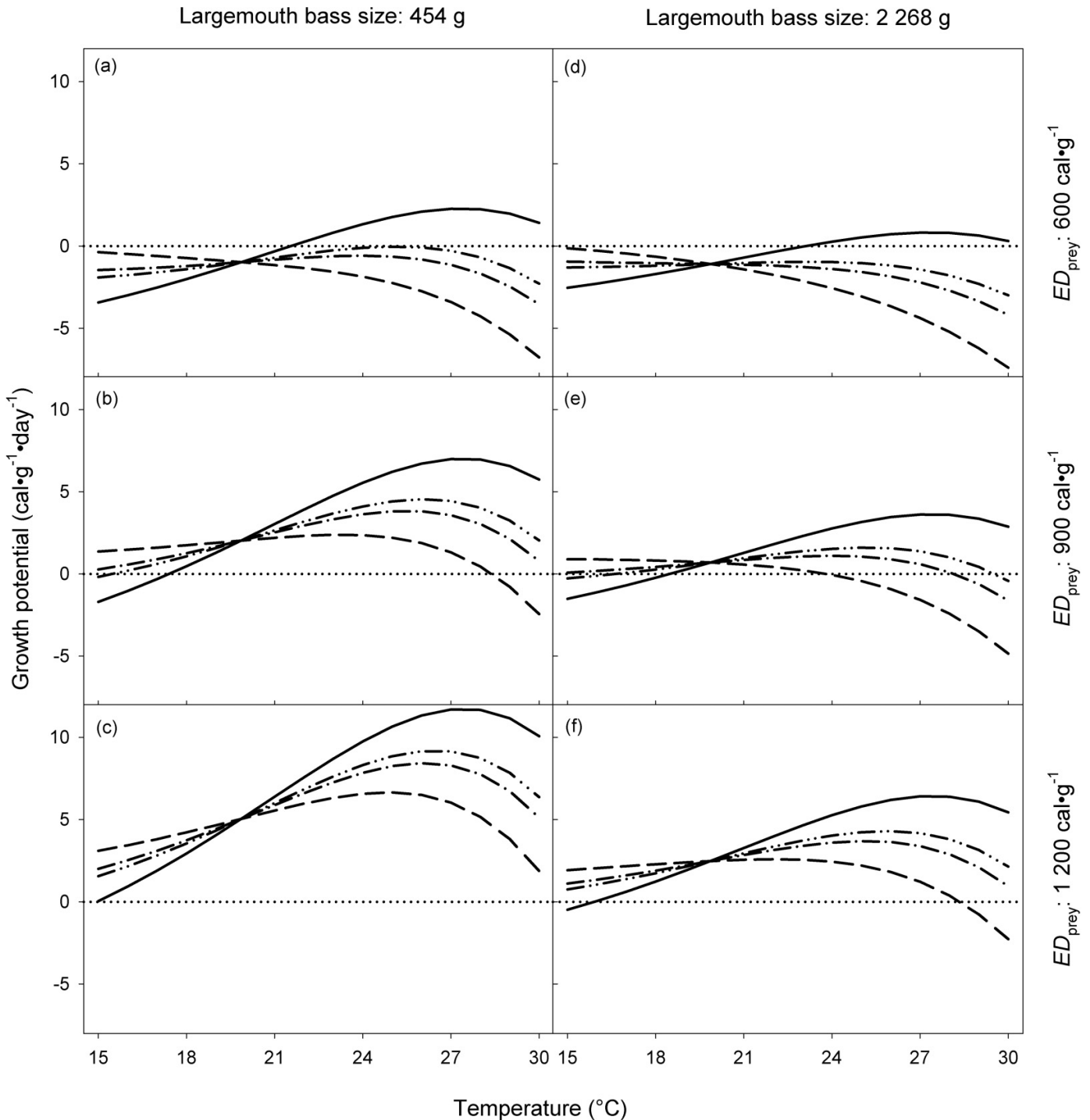
mer temperatures could no longer be offset by influx of estuarine- and marine-derived fish prey or was the result of an ontogenetic shift in prey use. In fact, the amount of blue crabs consumed by largemouth bass increased with age, resulting in reduced rates of caloric consumption in both regions, with a greater degree down-stream (Glover 2010). Further, low mean daily freshwater inflow resulted in reduced growth rates between age-3 and age-4 at all

sites within the Mobile Delta. Taken together, the influence of freshwater inflow on growth appears to change through the life of largemouth bass because of ontogenetic shifts in prey use such that young fish benefit from low freshwater inflow owing to availability of high-quality prey, whereas adults are nega-tively affected by low freshwater inflow owing to the combined effects of poor prey quality, increased salinity, and high peak

summer temperatures on their energetic intake and metabolic costs.

Previous studies suggest that this freshwater inflow-related phenomenon of controlling the degree of marine subsidies is not unique to the Mobile Delta. For example, a study on the San Francisco Bay – Sacramento–San Joaquin Delta Estuary found that 2 ppt was a critical salinity that was strongly related to the spatial and temporal distribution of a variety of marine and estuarine fish species (Jassby et al. 1995; Kimmerer 2002). The distance at which this critical salinity occurred with respect to proximity to the San Francisco Bay – Sacramento–San Joaquin Delta Estuary had an inverse relationship with freshwater inflow and could, therefore, affect abundance of small-bodied fish prey available to upstream predators. Several studies on estuarine systems have documented the contribution of marine-derived subsidies to freshwater predators, including blue catfish (*Ictalurus furcatus*; MacAvoy et al. 2000), largemouth bass (Guier et al. 1978; Yako et al. 2000; Weyl and Lewis 2006), and other centrarchid species such as redspotted sunfish (*Lepomis miniatus*), redear sunfish (*Lepomis microlophus*), and bluegill (*Lepomis macrochirus*; VanderKooy et al. 2000). In fact, among four coastal river systems in North Carolina, the greatest growth rates for largemouth bass were observed in the systems with the highest salinity (Guier et al. 1978). This pattern was attributed to a high influx and consumption of marine-derived fish prey by largemouth bass.

It is important to note that we assumed that consumption rates for largemouth bass in the Mobile Delta respond similarly to temperature as those used to derive and parameterize the published largemouth bass bioenergetics model by Hanson et al (1997), which were collected from Ontario, Canada (Niimi and Beamish 1974). The published largemouth bass consumption function peaks at 27.5 °C and declines rapidly at higher temperatures (Niimi and Beamish 1974; Rice et al. 1983). It is unknown whether largemouth bass at southern latitudes, such as the Mobile Delta, have a different functional relationship between temperature and consumption. Given that strong differences in how largemouth bass responded to temperature in the Mobile Delta compared with the standard largemouth bass respiration function have been found (Glover et al. 2012), it is possible that the consumption function may differ as well. Further, the temperature regimes used for the bioenergetics simulations were obtained at a fixed depth (~1 m), and it is possible that largemouth bass sought deeper, cooler waters during high summer temperatures. Catch rates of largemouth bass are depressed during summer months in the Mobile Delta (Norris et al. 2010), presumably because of thermoregulatory behavior. Given that the bioenergetics simulations indicated that just a few degrees change in these extreme temperatures can have profound growth consequences, additional research to evaluate the relationship of temperature to functions in bioenergetics models and the behavioral thermoregulation of largemouth bass in these extreme environments is warranted.

Bioenergetics simulations in which either the effect of salinity or consumption of energy-poor invertebrates were removed suggested that the cost of consuming blue crabs reduced growth rate to a greater degree than salinity in both regions, but to a greater extent downstream. Specifically, when the blue crab effect was removed, the final mass achieved after 10 years was 2.1 to 4.6 times higher compared with when the effect of salinity was removed, with the exception of the low freshwater inflow simulation in both regions, in which salinity had a slightly greater effect than consumption of blue crabs. Although the final masses attained in these simulations were unrealistic, this does suggest that shifts in prey use could be more influential on growth than effects of salinity; this was also evident in the simulated interactive effects of salinity, prey caloric content, and temperature. Bioenergetics simulations among the varying levels of freshwater inflow predicted that the effects of diet were greater upstream than downstream and were largely age-specific. However, analyses of consumed en-

ergy indicated that caloric density of consumed prey declined at similar rates with age in both regions, and freshwater inflow had similar effects in both regions. Therefore, it would be reasonable to assume that the effect of diet was similar between regions with respect to freshwater inflow, which was counter to what was found with bioenergetics simulations. This conflicting result was likely due to the small sample size of largemouth bass available for determining diet proportions for low and high freshwater inflow simulations (particularly for fish ≥ age-3). Therefore, it is likely that diet had similar effects on growth between regions across varying levels of freshwater inflow, but the overall negative impact of diet was higher downstream because of the greater consumption of energy-poor invertebrates there. Other studies in Gulf of Mexico coastal systems have found low piscivory by largemouth bass, with fish contributing between 5% and 48% of the diet by number (Colle et al. 1976; Lorio et al. 1982; Meador and Kelso 1990a). Although it is unclear why there is an ontogenetic shift toward lower caloric density invertebrates, Lorio et al. (1982) and Meador and Kelso (1990a) speculated that increased risk of predation from large predators, due to foraging activity, may restrict largemouth bass to submerged macrophyte beds, thereby decreasing their foraging efficiency and profitability (Savino and Stein 1982; Anderson 1984). This predator-induced change in foraging behavior has been observed in other centrarchid species as well (Mittelbach 1981; Werner and Hall 1988).

Higher caloric density of prey consumed by largemouth bass upstream and the lower salinity levels in the upstream region should combine to be more favorable for the production of large largemouth bass, yet very few large fish were present during the 7 years of this study. Specifically, out of a total of 9988 adult largemouth bass (≥age-1), only seven were ≥2268 g (5 lb), six of which were collected from the upstream region. Moreover, less than 2% of collected fish were ≥1361 g (3 lb). The bioenergetics simulations indicated that age-specific consumption rates of largemouth bass ranged from 5% to 30% lower upstream relative to downstream and generally increased with age. Thus, the growth potential of fish upstream appeared to be constrained by lower consumption rates relative to downstream as indicated by bioenergetics simulations, which was supported by low relative masses at sites farther from Mobile Bay (Norris et al. 2010). The habitat of the Mobile Delta switches from a bottomland hardwood forest in the upstream region to a marsh downstream (Swingle et al. 1966), which is a common feature of estuarine systems (Odum 1988). The greater amount of coarse woody debris and presence of bald cypress trees upstream relative to downstream (Norris et al. 2005; Peer et al. 2006) may therefore increase structural complexity and increase the availability of refuge for prey. Previous studies have demonstrated that increased structural complexity reduces foraging efficiency by largemouth bass (Savino and Stein 1982; Anderson 1984). Moreover, caloric density of consumed prey declined with age in both regions in all seasons except winter, thereby limiting the growth potential of older fish. Coupled with the fact that very few fish live past age-5 in the Mobile Delta (Norris et al. 2010), there is little potential to increase the density of memorable and trophy size largemouth bass available to anglers in the Mobile Delta using typical harvest restrictions, even under the best environmental conditions expected for this system (i.e., high freshwater inflow).

Acknowledgements

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