

**Understanding Growth Patterns of Coastal Largemouth Bass: Integrating
Bioenergetics Modeling and Life History Theory**

by

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Abstract

Relative to inland freshwater populations, largemouth bass (*Micropterus salmoides*) in coastal systems typically have a small maximum size, high condition, and low annual survival. Much attention has focused on determining whether the size structure of largemouth bass in these systems could be enhanced. However, high condition factors of fish in coastal systems suggest not only that there may be little potential for increased growth rates, but also that these fish may possess an alternate energy allocation strategy favoring high lipid reserves. In this study, I examined the role of energetic constraints and differing life-history strategies on growth and condition of largemouth bass along a freshwater-estuarine gradient within the Mobile-Tensaw River Delta, Alabama (Mobile Delta).

Growth of age-0 largemouth bass was fastest downstream and declined linearly with distance from Mobile Bay. However, after age-2 the relationship between growth and proximity to Mobile Bay switched, with faster growth observed upstream. Bioenergetics simulations suggested that these patterns were due to a complex interaction among size-specific metabolic costs of salinity, maximum summer water temperature, and prey energy content. Additionally, freshwater riverine inputs influenced the relationship between age-specific growth and proximity to Mobile Bay, likely through its effects on prey availability, salinity, and temperature. Histological assessments revealed the probability of maturing at younger ages was greater downstream than upstream for

both sexes. Annual survival rate was similar between regions (51%), suggesting regional maturation differences were largely growth rate dependent.

A dynamic state-variable model suggested that estuarine environments should select for an increased energy allocation toward energy reserves at the cost of length when compared with a strategy suited for a freshwater environment. High lipid reserves decreased starvation risk and allowed females to switch energy allocation toward ovary development prior to spawning to ensure reproductive output in the face of poor energy availability. These results suggest slow growth and high condition of coastal largemouth bass are due to energetic constraints and an adapted energy allocation strategy. Further, it appears there is little potential to enhance the size structure of largemouth bass in the Mobile Delta, even under the best environmental conditions expected for this system.

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Table of Contents

Abstract.....	ii
Acknowledgments.....	iv
List of Tables	viii
List of Figures.....	ix
I. Introduction: Proximate and ultimate influences on body size of largemouth bass in coastal systems.....	1
II. Sample preparation techniques for determination of fish energy density via bomb calorimetry: an evaluation using largemouth bass	
Abstract.....	9
Introduction.....	10
Materials and Methods.....	11
Results.....	14
Discussion.....	15
III. The effect of a dynamic estuarine environment on the growth of largemouth bass: a bioenergetics approach incorporating metabolic costs of salinity	
Abstract.....	19
Introduction.....	21
Materials and Methods.....	24
Results.....	38
Discussion.....	45

IV. Understanding the slow-growth, high-condition paradox of coastal largemouth bass using an optimal energy allocation model	
Abstract.....	54
Introduction.....	56
Materials and Methods.....	61
Results.....	71
Discussion.....	79
Literature Cited.....	90
Appendix 1.....	160
Appendix 2.....	168
Appendix 3.....	178
Appendix 4.....	191

List of Tables

Table 2.1	Piecewise regression model selection results displaying the number of knots, sample size (N), number of parameters (k), degrees of freedom (df), sum of squared errors (SSE), and Bayesian Information Criterion (BIC) for each model tested	106
Table 3.1	Region-specific start and end mass (g) for each cohort used in bioenergetics simulations and estimated proportion of maximum consumption for the three different simulation scenarios. The upstream region included Tensaw Lake, McReynold's Lake, Dennis Lake, and Gravine Island, whereas the downstream region included Big Bayout Canot, Crab Creek, Bay Minette, and D'Olive Bay	107
Table 3.2	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 for energetic values	108
Table 3.3	Model selection results for the respirometry experiment to test for the effect of salinity on specific respiration rates, with the description of the effect of salinity on respiration, number of parameters (k) including the estimate of σ^2 , Akaike's information criterion corrected for small sample size (AIC_c), the difference in AIC_c values from the best model (Δ_i), likelihood of the model (l_i), Akaike weight of the model (w_i), and the evidence ratio for each model. Models are sorted from best to worst as indicated by AIC_c . See text for definitions of equation symbols	109
Table 3.4	Parameter estimates from the best model (model 7, Table 3.2) describing the effects of salinity on specific respiration rates ($\text{mg O}_2 \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) for largemouth bass, along with SE of the estimate, df, the t -value, and probability of having a higher absolute t -value (P) given the df. See text for definitions of parameter symbols	110
Table 3.5	Results of the projected growth under three different simulated scenarios showing the time required to reach 2.3 kg, the estimated annual survival rate from the weighted catch-curve analysis, number (N) per 1,000 fish that is expected to reach this size within the required time based on annual survival rates (S), and the mass (kg) attained at the end of age-9. A dash indicates that the simulated largemouth bass did not reach 2.3 kg	111

List of Figures

Figure 2.1	Drying time (mean number of d \pm 1 SE) for each bomb calorimetry sample preparation method. Different letters above the bars indicate statistically significant differences ($\alpha = 0.05$).....	112
Figure 2.2	Energy density (cal·g ⁻¹) on a wet mass basis for each bomb calorimetry sample preparation method plotted against percent dry mass of fish sample and associated regression lines. The estimated energy density based on percent dry mass using the relationship proposed by Hartman and Brandt (1995) is also included.....	113
Figure 2.3	Energy density (cal·g ⁻¹) on a wet mass basis (filled circles = traditional; empty circles = subsampled; triangles = autoclaved + subsampled) plotted against total wet mass (g). The solid line is the best-fit piecewise regression model for all methods combined.....	114
Figure 3.1	Map of sampling sites within the Mobile-Tensaw River Delta, AL. The gray shaded area represents water and the white area represents land	115
Figure 3.2	Summer and fall daily discharge (mean m ³ ·s ⁻¹ \pm 1 SE) combined from the Alabama and Tombigbee rivers in which growth increments were observed. The twenty-year minimum and maximum mean daily discharges for fall and summer are referenced by dotted lines.....	116
Figure 3.3	Mean daily salinity (ppt) for a) upstream and b) downstream, and mean daily temperature (°C) for c) upstream and d) downstream used in bioenergetics simulations for low (2007), average (averaged across 2002-2008), and high (2004) discharge years. The upstream region included Tensaw Lake, McReynold's Lake, Dennis Lake, and Graving Island, whereas the downstream region included Big Bayou Canot, Crab Creek, Bay Minette, and D'Olive Bay (Figure 3.1)	117

Figure 3.4	<p>(a) Ovary mass (g) plotted against total body mass (g) with the upper 95th quartile (solid line) fit to females collected during the spawning period (March-May; filled circles) and the lower 5th quartile (dashed line) fit to females collected after the spawning period (June-August; open circles). The upper and lower quartiles were used as the maximum constraint to ovary mass for spawning and the residual mass retained after spawning, respectively. (b) Regression between log₁₀-transformed ovary caloric density and log₁₀-transformed gonad-somatic index, which was used to estimate size-specific energetic losses due to spawning.....</p>	118
Figure 3.5	<p>Average proportion of diet by biomass of largemouth bass by season and age for the a) upstream and b) downstream region pooled from 2002 to 2008. Numbers above bars indicate the number of largemouth bass included in estimate. Abbreviations are SP = spring, SU = summer, FA = fall, and WI = winter.....</p>	119
Figure 3.6	<p>Average proportion of diet by biomass of largemouth bass by season and age for the a) upstream and b) downstream region from 2007, representing a low discharge year. Numbers above bars indicate the number of largemouth bass included in estimates. Abbreviations are as in Figure 3.5.....</p>	120
Figure 3.7	<p>Average proportion of diet by biomass of largemouth bass by season and age for the a) upstream and b) downstream region from 2004, representing a high discharge year. Numbers above bars indicate the number of largemouth bass included in estimate. Abbreviations are as in Figure 3.5.....</p>	121
Figure 3.8	<p>Predicted oxygen consumption (mg O₂·g⁻¹·d⁻¹) from the best model for a 450-g largemouth bass as a function of temperature and salinity.....</p>	122
Figure 3.9	<p>Predicted increase in oxygen consumption from freshwater for three salinity levels as a function of largemouth bass body mass.....</p>	123
Figure 3.10	<p>Comparison of predicted oxygen consumption (mg O₂·g⁻¹·d⁻¹) for a 450-g largemouth bass at freshwater as a function of temperature determined for the Mobile Delta and that determined for inland largemouth bass as modeled by Rice et al. (1983).....</p>	124
Figure 3.11	<p>Predicted oxygen consumption (mg O₂·g⁻¹·d⁻¹) of largemouth bass of three different sizes exposed to four different salinity treatments at (a) 15°C, (b) 20°C, (c) 25°C, and (d) 30°C (error bars represent 1 SE). Bars with the same letters indicate no statistical difference in oxygen consumption between salinity treatments for a given temperature and size (α = 0.05)</p>	125

Figure 3.12	Predicted energy density of consumed prey ($\text{cal}\cdot\text{g}^{-1}$) as a function of season-specific mean daily discharge ($\text{m}^3\cdot\text{s}^{-1}$) for a) spring, b) summer, c) fall, and d) winter for age-1 to age-5 largemouth bass in the upstream (US) and downstream (DS) region. The downstream region is also identified by thicker age-specific predicted lines.....	126
Figure 3.13	Percent change from observed to predicted mass attained over the lifetime of largemouth bass (through age-5) after substituting one variable at a time from one discharge simulation to another for the upstream (a-c) and downstream regions (d-e)	127
Figure 3.14	Age-specific percent change from observed to predicted mass of largemouth bass by substituting one variable at a time from on discharge simulation to another for the upstream (a-c) and downstream regions (d-e).....	128
Figure 3.15	Simulated mass (g) of largemouth bass in the upstream region for the low discharge (a-c), average discharge (d-f), and high discharge (g-i) simulations. The solid black lines represent simulated mass for the observed conditions and the dotted and dashed lines represent the simulated mass by substituting a single variable's values with those from one of the other discharge simulations. The gray solid line represent the observed values for that simulation that were substituted	129
Figure 3.16	Simulated mass (g) of largemouth bass in the downstream region for the low discharge (a-c), average discharge (d-f), and high discharge (g-i) simulations. The solid black lines represent simulated mass for the observed conditions and the dotted and dashed lines represent the simulated mass by substituting a single variable's values with those from one of the other discharge simulations. The gray solid line represent the observed values for that simulation that were substituted	130
Figure 3.17	Temporal consumption of prey by largemouth bass in the a) upstream and b) downstream region estimated from bioenergetics simulations for an average discharge year (2002-2008).....	131
Figure 3.18	Temporal consumption of prey by largemouth bass in the a) upstream and b) downstream region estimated from bioenergetics simulations for a low discharge year (2007).....	132
Figure 3.19	Temporal consumption of prey by largemouth bass in the a) upstream and b) downstream region estimated from bioenergetics simulations for a high discharge year (2004).....	133

Figure 3.20	Growth increments (mean \pm 1 SE mm \cdot yr $^{-1}$) of largemouth bass for each sampling site plotted as a function of distance from Mobile Bay Lighthouse 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. Means with different letters indicate significant differences at the $\alpha = 0.05$ level.....	134
Figure 3.21	Site-specific effect of summer and fall mean daily discharge on largemouth bass growth increments (mean mm \cdot yr $^{-1}$ \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.....	135
Figure 3.22	The predicted critical temperature that if exceeded by largemouth bass will result in weight loss by (a) 450-g and (b) 2268-g largemouth bass plotted as a function of salinity (ppt) and mean caloric density of consumed prey (cal \cdot g $^{-1}$). The black portions on the graphs represent undefined critical temperatures in which there was no temperature that would result in positive growth. Simulations were conducted assuming a 0.5 proportion of maximum consumption.....	136
Figure 4.1	a) Weekly temperature and b) salinity in the downstream region of the Mobile Delta averaged from 2002 to 2008. Abbreviations are SP = spring, SU = summer, FA = fall, and WI = winter; seasons are demarcated by vertical dashed lines.....	137
Figure 4.2	a) Ovary mass R plotted against total length L with the upper 95 th quartile (solid line) fit to females collected during the spawning period (March-May; filled circles) and the lower 5 th quartile (dashed line) fit to females collected after the spawning period (June-August; open circles). The upper and lower quartiles were used as the maximum constraint (R_{\max}) for ovary mass and the residual mass (R_{\min}) retained after spawning. b) Log ₁₀ -transformed ovary energy density plotted as a function of log ₁₀ -transformed total length L	138
Figure 4.3	Total lipid mass F plotted against total length L with the upper 95 th quartile defining the maximum constraint for lipid mass (F_{\max}). Data are from Barziza and Gatlin (2000).....	139
Figure 4.4	Fecundity plotted as a function of ovary mass R . Data are from Kelley (1962).....	140

Figure 4.5	Site-specific von Bertalanffy growth curve parameter estimates of the a) asymptotic length (L_{inf} [mm]), b) growth coefficient (K), c) theoretical age at which length is zero (t_0 [years]) for female and male largemouth bass as a function of distance from Mobile Bay Lighthouse (mean \pm 1 SE). Site-specific parameter estimates were solved by including the effect of distance from Mobile Bay in an extended von Bertalanffy growth curve (Kimura 2008).....	141
Figure 4.6	Site-specific mean relative weight (\pm 1 SE) across time (2002-2008) plotted against distance from Mobile Bay (km) with linear (solid line) and quadratic (dashed line) regression lines.....	142
Figure 4.7	Predicted mean monthly relative weight (\pm 1 SE) adjusted for distance from Mobile Bay. Similar letters above error bars indicate that means were not statistically different ($\alpha = 0.05$).....	143
Figure 4.8	Region-specific observed and predicted probability of maturity for females (a and b) and males (c and d) plotted as a function of age (years) and total length (mm). The horizontal dashed line references the point at which individuals have a 50% chance of being sexually mature	144
Figure 4.9	a) Gonadosomatic index and b) total ovarian energy for upstream (solid circles) and downstream (open circles) female largemouth bass collected from 2005 to 2008. Ages are demarcated by vertical dotted lines.....	145
Figure 4.10	a) Gonadosomatic index and b) total testicular energy for upstream (solid circles) and downstream (open circles) male largemouth bass collected from 2005 to 2008. Ages are demarcated by vertical dotted lines.....	146
Figure 4.11	Total energy in somatic tissue, gonads, and mesenteric fat for a) female and b) male largemouth bass collected on a quarterly basis from 2005-2008. Abbreviations are spring (SP), summer (SU), fall (FA), and winter (WI) periods.....	147
Figure 4.12	Cumulative optimal allocation of net available energy toward growth in length L , ovary development r , and energy reserves f through age-5 for a freshwater and estuarine optimal energy allocation strategy at a 50% and 60% ration. Results are shown for a 50% annual survival rate for a female largemouth bass with initial states of $L = 23$, $r = 0$, and $f = 0.1$. Results were generally consistent across survival rates	148
Figure 4.13	Optimal trajectories of length (L), ovaries (r), energy reserves (f), and resulting body condition through age-5 for a freshwater and estuarine optimal energy allocation strategy at a 50% and 60% ration within their optimal environment at a 30% annual survival rate. Initial states in the model were $L = 23$, $r = 0$, and $f = 0.1$	149

Figure 4.14	Optimal trajectories of length (L), ovaries (r), energy reserves (f), and resulting body condition through age-5 for a freshwater and estuarine optimal energy allocation strategy at a 50% and 60% ration within their optimal environment at a 50% annual survival rate. Initial states in the model were $L = 23$, $r = 0$, and $f = 0.1$	150
Figure 4.15	Optimal trajectories of length (L), ovaries (r), energy reserves (f), and resulting body condition through age-5 for a freshwater and estuarine optimal energy allocation strategy at a 50% and 60% ration within their optimal environment at a 70% annual survival rate. Initial states in the model were $L = 23$, $r = 0$, and $f = 0.1$	151
Figure 4.16	Predicted total length trajectories through age-5 for the freshwater and estuarine optimal energy allocation strategies placed in a freshwater and estuarine environment plotted at varying levels of food rations and annual survival rates. Optimal trajectories are when strategy is equal to environment; suboptimal trajectories are when strategy is not equal to environment. Initial states in the model were $L = 23$, $r = 0$, and $f = 0.1$..	152
Figure 4.17	Predicted body condition (relative weight) of female largemouth bass ≥ 150 mm TL for a freshwater and estuarine optimal energy allocation strategies placed in a freshwater and estuarine environment plotted at varying levels of annual survival rates at a 50% ration. Initial states in the model were $L = 23$, $r = 0$, and $f = 0.1$	153
Figure 4.18	Predicted proportion of maximum energy reserves (f) of female largemouth bass for a freshwater and estuarine optimal energy allocation strategies placed in a freshwater and estuarine environment plotted at varying levels of annual survival rates at a 50% ration. Initial states in the model were $L = 23$, $r = 0$, and $f = 0.1$	154
Figure 4.19	Expected lifetime reproductive output of a female largemouth bass exhibiting a freshwater or estuarine optimal energy allocation strategy when placed in a freshwater and estuarine environment at varying levels of annual survival rates and food rations. The word “optimal” above bars represents the maximum expected number of egg for that environment resulting from the optimal energy allocation strategy. Initial states in the model were $L = 23$, $r = 0$, and $f = 0.1$	155
Figure 4.20	Predicted proportion of maximum ovary mass (r) of female largemouth bass for freshwater and estuarine optimal energy allocation strategies placed in a freshwater and estuarine environment plotted at varying levels of annual survival rates at a 50% ration. Initial states in the model were $L = 23$, $r = 0$, and $f = 0.1$	156

Figure 4.21	Predicted total length trajectories through age-5 for the freshwater and estuarine optimal energy allocation strategies placed in a freshwater and estuarine environment for a 50% survival rate at two ration levels. Data points are female largemouth mean length-at-age for the upstream (solid circles) and downstream (open circles) region collected during the fall from 2005-2008. Error bars represent ± 1 SE	49
Figure 4.22	Predicted relative weights through age-5 for the freshwater and estuarine optimal energy allocation strategies placed in a freshwater and estuarine environment for a 50% survival rate at two ration levels. Data points are age-specific mean relative weights for female largemouth for the upstream (solid circles) and downstream (open circles) region collected during the fall from 2005-2008. Error bars represent ± 1 SE	50
Figure 4.23	Region-specific observed and predicted relative weights as a function of proportion of maximum energy reserves for largemouth bass collected for quarterly energetic assessments from 2005-2008. Mesenteric fat was used as an index of total lipids for determining proportion of maximum energy reserves and therefore likely represented an underestimate of total energy reserves	51
Figure A.1	Age-specific predicted probabilities of crabs dominating the diet of largemouth bass in the upstream region plotted as a function of discharge for the (a) spring, (b) summer, (c) fall, and (d) winter seasons. Predicted probabilities were derived from the best logistic regression model selected using a backward selection procedure and included the main effects of age, mean daily discharge, and season, as well as the interaction between season and mean daily discharge	85
Figure A.2	Age-specific predicted probabilities of crabs dominating the diet of largemouth bass in the downstream region plotted as a function of discharge for the (a) spring, (b) summer, (c) fall, and (d) winter seasons. Predicted probabilities were derived from the best logistic regression model selected using a backward selection procedure that included the main effects of age, mean daily discharge, and season, as well as all possible two- and three-way interactions.....	86
Figure A.3	Season-specific predicted probabilities of crabs dominating the diet of largemouth bass for the (a) upstream and (b) downstream region. Error bars represent the upper and lower 95% confidence intervals. Different letters above bars indicate significantly different odds ratio estimates at the $\alpha = 0.05$ level	87

Figure A.4 Region-specific predicted probability of largemouth bass having an empty stomach plotted as a function of age for the (a) spring, (b) summer, (c) fall, and (d) winter. Predicted probabilities were derived from the best logistic regression model selected using a backward selection procedure that included the main effects of age, season, and region, as well as interactions between age and season and between region and season.....88

I. Introduction: proximate and ultimate influences on the growth, body size, and condition of largemouth bass in coastal systems

Large body size often confers advantages that enhance individual fitness, particularly in fishes (Beverton 1959; Adams 1980; Sogard 1997). Compared to smaller individuals, larger organisms tend to have a lower risk of starvation (Kleiber 1932; Toneys and Coble 1979; Peters 1983) and predation (Miller et al. 1988; Hambricht et al. 1991; Fuiman and Magurran 1994), and also tend to have greater reproductive output through greater fecundity (Bagenal 1966; Bagenal 1978; Wootton 1990) and offspring quality or viability (Miranda and Muncy 1987; Chambers et al. 1989). It is not surprising therefore that the role of body size has been the focus of many ecological studies due to its influence on individual fitness, and “bigger is better” appears to be a pervasive phenomenon. However, there are situations in which a large body size can be disadvantageous (see Blanckenhorn 2000 for complete review). For example, while large individuals have lower metabolic costs per unit mass than small individuals (Kleiber 1932; Peters 1983), absolute energetic requirements are greater for large individuals; thus, large body size can actually be selected against in environments with unstable food resources or high energetic demands (Wikelski et al. 1997; Blanckenhorn 2000). It is clear therefore that body size has strong ecological implications (Peters 1983; Werner and Gilliam 1984), yet the roles of proximate and ultimate influences on body size are not well understood.

An obvious constraint to body size is the availability and quality of food resources and an organism's ability to acquire and use those resources. After metabolic costs are met for maintenance, organisms must then allocate remaining energy toward somatic growth, reproduction, or energy reserves. Allocation of energy toward reproduction and

energy reserves can increase fitness through greater reproductive output and enhanced survival, respectively. Yet, reproduction and energy-dense lipid reserves are energetically expensive and are traded off against somatic growth and body size, thereby potentially reducing future fitness (Bell 1980; Roff 1982; Stearns 1992; Shertzer and Ellner 2002). It is the allocation of limited energy among these pathways that ultimately dictates not only the body size of an individual at any one time, but also its lifetime fitness (Roff 1992; Stearns 1992).

Relative to inland freshwater populations, largemouth bass (*Micropterus salmoides*) in coastal systems along the U.S. coasts of the Atlantic Ocean and Gulf of Mexico have slower growth, higher body condition, and lower annual survival (Colle et al. 1976; Guier et al. 1978; Meador and Kelso 1990a; Norris et al. 2010). Previous studies have indicated that high metabolic costs associated with osmoregulation of salinity could constrain net energetic intake and limit scope for growth (Meador and Kelso 1990a; Susanto and Peterson 1996). Consumption of relatively energy-poor macroinvertebrates (e.g., blue crabs *Callinectes sapidus*), rather than energy-rich fish prey, also has been suggested as being responsible for the slower growth of largemouth bass observed in several coastal systems (Colle et al. 1976; Lorio et al. 1982; Meador and Kelso 1990a). These effects, salinity and diet, interact to determine net energy available and change not only along an estuarine to freshwater gradient within coastal systems, but also over the lifetime of an individual largemouth bass, such that larger fish may be at a greater disadvantage than small fish in estuarine environments. For example, plasma osmolality was consistently lower for age-0 largemouth bass individuals (Susanto and Peterson 1996) than for adult largemouth bass (Meador and Kelso 1990b) at all salinities,

suggesting age-0 largemouth bass are better able to maintain their plasma osmolality at increased salinity than are adults. Given that previous studies have shown that juvenile and adult largemouth bass move little in response to salinity in the Mobile Delta (Norris et al. 2005; Farmer 2008; Lowe et al. 2009) and other coastal systems (Meador and Kelso 1989), it is evident that largemouth bass endure periods of increased salinity rather than exhibiting largescale migrations upstream toward fresher water. Therefore, it is critical to understand the energetic costs of this salinity exposure in an effort to determine its effects on growth throughout the lifetime of largemouth bass.

An ontogenetic shift in quality of prey types consumed appears to exacerbate the salinity-related metabolic costs of an estuarine environment for adult largemouth bass relative to age-0 largemouth bass. For example, relative to upstream freshwater portions of the Mobile-Tensaw River Delta, Alabama, the availability of small, energy-rich fish prey in habitats closest to or within brackish habitats allowed a faster shift to and a higher degree of piscivory for age-0 largemouth bass (Peer et al. 2006). This conferred a growth advantage to age-0 largemouth bass residing in brackish habitats through their first summer of growth compared to largemouth bass in upstream areas that remained fresh, where they switched to piscivory later in life (Peer et al. 2006). However, by age-2 the growth advantage gained by largemouth bass in downstream areas of the Mobile-Tensaw River Delta diminished relative to upstream reaches (Norris et al. 2010). Despite switching to piscivory earlier in life, downstream adult largemouth bass consumed a greater amount of energy-poor macroinvertebrates (Norris et al. 2010), which may have decreased their growth rates relative to fish in the upstream region. Consumption of low

quality prey has also been observed in many other coastal systems along the U.S. Gulf of Mexico (Colle et al. 1976; Lorio et al. 1982; Meador and Kelso 1990a).

Although salinity and poor prey quality may constrain net energy for growth, coastal largemouth bass often have high condition factors (Colle et al. 1976; Guier et al. 1978; Meador and Kelso 1990a; Norris et al. 2010) and, compared to freshwater individuals, have even been found to have a stockier body form (Meador and Kelso 1990a). The high body condition of coastal largemouth bass is counterintuitive, given that slow growth in length is often coupled with low body condition (Wege and Anderson 1978; Gablehouse 1991; Willis et al. 1991). One possible explanation is that largemouth bass in coastal systems possess an alternative energy allocation strategy in which a greater amount of energy is devoted to energy-dense lipid reserves, increasing their “plumpness.” This strategy would ensure that metabolic demands are met during periods of high salinity, thereby increasing an individual’s chance of surviving to the next reproductive event. This strategy is not without costs, however, as it limits scope for growth in length and mass, thereby limiting future fecundity.

Poor survival and reduced longevity of largemouth bass in these systems, potentially the result of living in a physiologically stressful environment, could also select for earlier age-at-maturity at the cost of reduced somatic growth. Size-selective exploitation of larger individuals has resulted in early age-at-maturity and low growth rates in sport fishes (Diana 1983; Drake et al. 1997) and many commercially fished species (e.g., Ricker 1981; Rijnsdorp 1993; Olsen et al. 2005). Although it has been established that coastal largemouth bass exhibit slower growth rates than freshwater largemouth bass (reviewed by Meador and Kelso 1990a), no information exists on age-at-

maturity to determine whether growth differences are due to differences in reproductive schedules or effort.

Despite the stresses of an estuarine environment, coastal populations appear to be successful, based on their high abundance and given that they often support important sport fisheries (Nack et al. 1993; Richardson-Heft et al. 2000; Krause 2002). The small maximum body size observed in these systems relative to inland freshwater populations can lead to angler dissatisfaction, however. Basic life history understanding is necessary to determine if effective management could enhance the size structure of largemouth bass in coastal systems. Therefore, determining if and how these estuarine stressors have shaped the life-history strategy and growth patterns of coastal largemouth bass over evolutionary time is an important question from an ecological perspective as well as relative to management of these valuable recreational fisheries. As such, these systems provide a unique opportunity to examine the energetic constraints and life-history tradeoffs that ultimately shape the growth pattern of freshwater fish in an estuarine environment.

My dissertation research is focused on the role of energetic constraints and life-history tradeoffs on the growth and condition of largemouth bass along a freshwater-estuarine gradient within the Mobile-Tensaw River Delta, Alabama (hereafter referred to as the Mobile Delta). I used a bioenergetics approach to examine factors affecting growth of largemouth bass in the Mobile Delta. Consumer energy density is an essential parameter required for bioenergetics modeling because it determines the net energy required for growth. Surprisingly, there are few existing data on the energetic density of adult largemouth bass, and a constant value of $1000 \text{ cal}\cdot\text{g}^{-1}$ from Rice et al. (1983) is

generally used for this species in bioenergetics models. Energy density has been found to vary within fish species as a function of body size, geographic location, sex and reproductive status (e.g., Stewart et al. 1983; Rand et al. 1994; Anthony et al. 2000), which can bias consumption or growth estimates if not considered; therefore it was essential to determine energy density of largemouth bass specific to the Mobile Delta. Determining the energy density of fish, particularly large individuals, can be labor intensive and requires expensive equipment to homogenize and subsample tissue from an individual fish. In Chapter II, I compared three methods of homogenizing and subsampling fish tissue for bomb calorimetry: 1) homogenization after drying the whole fish, 2) drying a subsample of the fish tissue after homogenization of the whole fish using a meat grinder, and 3) drying a subsample of the fish tissue after subjecting the fish to an autoclave and homogenization. An autoclave was used to soften the hard structures of fish to facilitate homogenization and subsampling, yet it was unknown whether the extreme heat would affect estimates of fish energy density. The three methods were evaluated in terms of energy density estimates as a function of both percent dry mass and wet mass as well as the amount of time required for drying across a wide range of largemouth bass sizes.

In Chapter III, I examined the effects of an estuarine environment on the age-specific and lifetime growth of largemouth bass using a bioenergetics approach. I first determined the metabolic costs of salinity across a range of temperatures and body sizes for largemouth bass collected from the Mobile Delta and incorporated this information into the standard metabolism component of the existing largemouth bass bioenergetics model (Rice et al. 1983). I then used this modified bioenergetics model to simulate the

relative impacts of salinity and diet composition on lifetime growth trajectories of largemouth bass along a salinity gradient within the Mobile Delta. I compared growth increments derived from back-calculated length-at-age to assess the indirect effect of freshwater riverine inputs on growth of largemouth bass and compared these results to those from the bioenergetics simulations.

In Chapter IV, I determined whether observed slow growth and high condition of coastal largemouth bass could be the result of an adaptive energy allocation strategy. I quantified life-history characteristics of largemouth bass (age- and size-at-maturity, reproductive investment, energy reserves, somatic growth, and annual survival rates) in habitats along an estuarine-freshwater gradient in the Mobile Delta that vary in their abiotic (e.g., salinity) and biotic (e.g., prey quantity/quality, potential competitors, and predators) components. An optimal annual routine (OAR) model (Feró et al. 2008), also known as a state-dependent dynamic programming model (Mangel and Clark 1988), was used to determine optimal energy allocation strategies among growth in length (i.e., somatic tissue), reproduction (i.e., gonads), and energy reserves (i.e., lipid stores) that maximized expected lifetime fitness while being influenced by the expectation of an annual salinity regime, variable feeding conditions, and differing probability of survival. Observed life-history characteristics were then compared with model predictions to determine whether growth and condition factors of largemouth bass in estuarine systems could be the result of an adaptive energy allocation strategy.

The combination of these approaches allowed me to determine the proximate constraints on growth of largemouth bass in an estuarine environment as well as how largemouth bass growth patterns have been shaped by these constraints over evolutionary

time through life-history adaptations (i.e., ultimate influences). The results from this study not only provide further insights into the ecology and life-history attributes of a freshwater fish in estuarine systems, but also have broad implications towards understanding life-history adaptations and population dynamics of organisms in energetically dynamic environments.

II. Sample preparation techniques for determination of fish energy density via bomb calorimetry: an evaluation using largemouth bass

Abstract

Three homogenization and subsampling techniques for preparing fish tissue samples for bomb calorimetry were evaluated to identify differences in efficiency for estimating fish energy density. I compared: 1) drying the whole fish and homogenizing the dried fish tissue, 2) homogenization prior to drying and then drying the subsample of fish tissue, and 3) homogenization after autoclaving to soften the hard structures and then drying a subsample of the homogenized fish tissue. Sample drying time and energy density estimates were compared among techniques across a size range (32-1080 g wet mass) of largemouth bass *Micropterus salmoides*. Both subsampling techniques reduced drying time by about 40% relative to drying whole fish. All three methods provided statistically similar estimates of largemouth bass energy densities. The autoclave process was most efficient, minimizing both sample preparation time and drying time. Variance of energy density estimates was higher for both subsampling methods compared to the traditional whole-fish method. Thus, subsampling can decrease sample preparation time for bomb calorimetry, but may reduce power to detect differences among variables of interest (e.g., season). Lastly, estimates of energy density for largemouth bass were a function of body mass, suggesting that using a constant energy density in bioenergetics models is not appropriate.

Introduction

Bioenergetics models are commonly used for estimating fish consumption and growth (Chipps and Wahl 2008). Predator energy density is an essential parameter required for bioenergetic modeling because it determines the net energy required for growth. Energy density has been found to vary within fish species as a function of body size, geographic location, sex, and reproductive status (e.g.; Stewart et al. 1983; Rand et al. 1994; Anthony et al. 2000), which can bias consumption or growth estimates if not considered. However, determining the energy density of fish, particularly large individuals, can be labor intensive and require expensive equipment to homogenize and subsample an individual fish. Thus, it is common practice to borrow energy density estimates from related species or use indirect measures (Ney 1993; Hartman and Brandt 1995). Although these practices can prove expedient, it is often necessary to verify the energy density of the fish species in question with direct observation.

Determining the whole body energy density of a fish traditionally requires that the entire fish is dried, homogenized, and then replicate samples are ignited in a bomb calorimeter to determine caloric density ($\text{cal}\cdot\text{g}^{-1}$) on a dry mass basis (Rand et al. 1994). Caloric density on a wet mass basis can then be calculated by multiplying dry mass caloric density by the dry:wet mass. Grinding dry tissue permits the use of burr or centrifugal grinders that can effectively pulverize hard tissues such as scales and bone to facilitate homogenization. Depending on the biomass, drying a whole fish may be time-intensive, particularly for large-bodied fish. Drying a subsample of the whole-body fish tissue decreases the amount of drying time and allows a greater number of samples to be dried at one time in limited drying oven space. However, calcified structures (e.g.,

vertebrae) and other tough tissue (e.g., skin) may make manual homogenization of wet fish tissue difficult and can require expensive equipment for blending. The inability to completely homogenize both wet and dry samples makes proper sub-sampling a challenge and can result in additional variation in analyses within samples.

In this study, I compared 3 methods of homogenizing and subsampling fish tissue for bomb calorimetry: 1) homogenization after drying the whole fish, 2) drying a subsample of the fish tissue after homogenization of the whole fish using a meat grinder, and 3) drying a subsample of the fish tissue after autoclaving and homogenizing. An autoclave was used to soften the hard structures of fish to facilitate homogenization and subsampling. The three methods were evaluated in terms of energy density estimates as a function of percent dry mass and wet mass as well as the amount of time required for drying across a wide range of largemouth bass *Micropterus salmoides* sizes.

Materials and methods

Fish collection

Largemouth bass were collected from a pond on Auburn University's E. W. Shell Fisheries Research Station on 16 September 2008 using a boat-mounted electrofisher (Smith-Root, Inc., 7.5 GPP, 7500 W). A total of 15 largemouth bass was collected across a size range (150 to 450-mm TL at 20-mm increments) for each sample preparation treatment (i.e., traditional, subsample, and autoclave + subsample). Total length (nearest mm) and mass (nearest g) were recorded for each individual, and their stomach contents were removed.

Sample preparation

Largemouth bass from each 20-mm size class were randomly assigned to the three treatments. For the traditional method, whole fish were cut into 2.5-cm cubes and oven dried at 70°C until a constant mass was achieved for two consecutive d (± 0.01 g between d), and the final dry mass was recorded. For the subsample method, the 2.5-cm cubes were pulverized in a meat grinder (#10 LEM brand stainless steel manual meat grinder) prior to drying and the tissue was homogenized by hand. A 40 to 60-g subsample was weighed and oven-dried to a constant mass as above. For the autoclave + subsample method, whole fish were placed into oven bags that were loosely sealed, and bags were placed in a steam-generated autoclave (Barnstead Laboratory Sterilizer; Model C-1761) at 120°C and 1.4 kg·cm⁻² for 1 h. Mass was recorded before and after autoclaving to document any change in moisture content. The fish was then homogenized using a hand mixer and a 40 to 60-g subsample of the homogenate was removed and oven-dried similar to above.

Energy content determination

Dried samples were blended to a homogenous mixture using a standard coffee grinder, then re-dried to a constant mass (± 0.01 g for two consecutive d) to remove any moisture accumulated during homogenization. At least two 0.1 to 0.2-g pellets were formed and ignited in a semimicro bomb calorimeter (Parr Instrument Co., Model 1425 and Model 6725) to measure caloric content. A third pellet was analyzed when the caloric values of the first two were not within two percent of each other. Caloric values for all pellets were averaged to estimate caloric density (cal·g dry mass⁻¹) of the sample.

The caloric density per wet mass of the sample was then determined by multiplying the energy density of the dry sample by the proportion of final dry mass to original wet mass.

Statistical Analyses

Analysis of covariance (ANCOVA) was used to determine if estimates of caloric density were affected by sample preparation method (PROC GLM; SAS Institute 2008).

The percent dry mass was used as the covariate to determine the overall effect of treatments on caloric density. I used percent dry mass in lieu of total length or mass to reduce the variation in caloric density in relation to sex, maturity state, and condition.

Sample preparation method was used as a class variable to determine if elevation differences existed among treatments, percent dry mass was used to determine the effect on caloric density among all treatments, and the interaction between percent dry mass and sample preparation method was used to evaluate if slope differences existed among treatments in the regression of caloric density on percent dry mass. Residuals were assessed for normality and homogeneity of variance as a function of percent dry mass, sample preparation method, and predicted values to ensure that assumptions of ANCOVA were met. Analysis of variance (ANOVA) was used to determine if drying time differed among the three treatments (PROC GLM; SAS Institute 2008). Normality and homogeneity of variance of residuals were assessed similar to above to ensure the assumptions of ANOVA were met.

Piecewise regression was used to determine the relationship between largemouth bass energy density and total wet mass using the program Joinpoint (National Cancer Institute 2008). I fit piecewise regression models containing zero to three knot values and used Bayesian Information Criterion (BIC; Tiwari et al. 2005) to determine the best-

fit piecewise regression model. The residuals from the best model were compared among methods to examine the effect of sample preparation method while controlling for the effect of body size.

Results

Sample preparation method had a significant effect on drying time (ANOVA: $F_{2,42} = 17.73, P < 0.001$). Compared to drying whole fish (i.e., traditional method), both subsampling methods reduced the amount of time (d) required for drying by approximately 40% ($t_{43} \geq 4.65$, Bonferroni-adjusted $P < 0.001$; Figure 2.1). Wet mass energy density ($\text{cal} \cdot \text{g}^{-1}$) increased with percent dry mass of the sample (ANCOVA: $F_{1,39} = 142.51, P < 0.001$; Figure 2.2). The sample preparation method did not affect the slope (ANCOVA: $F_{2,39} = 1.98, P = 0.15$) or elevation (ANCOVA: $F_{2,39} = 1.96, P = 0.15$) of this relationship, indicating that neither the subsampling nor the autoclave process affected energy density estimates. The regression model for all methods pooled was:

$$\text{cal} \cdot \text{g wwt}^{-1} = -376.56 + 60.41 \times \text{dwt} (\%),$$

and explained 83% of the variation in energy density ($F_{1,43} = 204.53, P < 0.001$). Additionally, the mean coefficient of variation within each fish (i.e., measurement precision) for the traditional, subsampling, and autoclave + subsampling method was 2.3, 2.3, and 1.1%, respectively. However, within fish variance was similar among methods (Levene's test: $F_{2,42} = 0.61, P = 0.55$), indicating sample homogenization was equal among the three techniques.

The relationship between energy density of largemouth bass and wet mass was best explained by a two-piece regression model with a single knot value (Table 2.1;

Figure 2.3). The mass (M) at which the trend in energy density changed (i.e., the knot value) for all methods pooled was 174 g, resulting in the following model:

$$\text{cal} \cdot \text{g wwt}^{-1} = \begin{cases} 816.54 + 3.55M & \text{for } M \leq 174 \text{ g} \\ 1489.44 - 0.31M & \text{for } M > 174 \text{ g} \end{cases}$$

Residuals from the two-piece regression model had unequal variances among the sample preparation methods (Brown and Forsythe's test: $F_{2,42} = 5.23$, $P = 0.009$). Equality of variance tests on residuals indicated that variance of caloric estimates for the traditional method was approximately seven times smaller compared to both subsampling methods ($Folded-F_{14,14} \geq 7.69$; $P < 0.001$), but was similar between subsampling methods ($Folded-F_{14,14} = 1.11$; $P = 0.85$). Controlling for heterogeneous variances, residuals from the two-piece regression model were similar among all methods (Welch's ANOVA: $F_{2,22.46} = 1.70$; $P = 0.21$), indicating that caloric density values were equal among methods when accounting for the effect of body size.

Discussion

I found that the relationship between caloric density ($\text{cal} \cdot \text{g wet mass}^{-1}$) and percent dry mass was similar among all sample preparation methods in terms of elevation and slope, suggesting that preparation method did not affect caloric estimates. Residuals from the two-piece regression model were similar among all methods, also indicating that caloric density values were not statistically different among methods when accounting for the effect of body size. In addition, both subsampling techniques took 40% less drying time compared to the traditional method, increasing the efficiency of the sample preparation process. However, variance of residuals was smaller using the traditional method compared to both subsampling methods, but was similar between subsampling methods. These results suggest that subsampling can decrease the time required for

determination of energy density, but will reduce the power to detect differences among a variable of interest (e.g., season). Despite the higher variability in energy density estimates, subsampling techniques may increase the number of samples that can be processed, which would offset the loss in power due to increases in degrees of freedom. Additionally, it is possible that a larger subsample may decrease the variability in energy density estimates, but this was not tested in this study. In future studies, it may be advantageous to determine an optimal proportion of fish tissue to subsample that minimizes the variance of energy density estimates while maintaining the benefits of increased efficiency.

Caloric density as a function of body mass (g) was best explained by a two-piece regression model. Energetic density increased rapidly up to 174 g, at which point the energy density declined gradually and may represent the rapid accumulation of lipids up to a given threshold as largemouth bass increase in size (Ludsin and DeVries 1997; Garvey et al. 1998). This suggests that the common use of a single fixed value for largemouth bass energy density (i.e., $1000 \text{ cal}\cdot\text{g}^{-1}$ or $4.184 \text{ kJ}\cdot\text{g}^{-1}$) is not appropriate (e.g., Rice et al. 1983). Although estimates of energy density for largemouth bass from this study represent an improvement over using a fixed value, it is only a point estimate in time; thus caution should be used in incorporating this function across annual bioenergetics simulations. I also found that predicted estimates of energy density from percent dry mass using an empirically derived relationship pooled across 22 species (Hartman and Brandt 1995) produced energy density estimates 5 to 45% higher than those derived in the laboratory (Figure 2.2). The resulting slope between energy density and percent dry mass was significantly different from bomb calorimetry-derived

estimates ($F_{3,86} = 610.68$; $P < 0.001$). This suggests caution should be used in estimating energy density from the relationship provided by Hartman and Brandt (1995), and predictions should be verified with direct observation.

There are a number of techniques that can be used for estimating whole-body energetic density of fish, such as component analyses (see review by Paine 1971), but bomb calorimetry remains the most direct and widely used technique. In this study I identified that some time-saving subsampling techniques can be used for preparing samples for bomb calorimetry to estimate energy density for large-bodied fish. Despite providing similar estimates of largemouth bass energy density to other methods, the meat grinder method was the most labor intensive and required the greatest amount of time in terms of the sample preparation prior to drying. Although the amount of labor required for this method could be reduced by using an electric meat grinder, the whole fish would still need to be cut into pieces small enough to feed through the grinder. While I did not quantify the consistency of the final dried and homogenized tissue among sample preparation techniques, the autoclave process resulted in a very fine powder that facilitated the formation of pellets prior to bomb calorimetry. Scales from the fish still remained in the other samples, which made it more difficult to form pellets. Although the within fish variation was statistically similar among methods, the lower coefficient of variation observed using the autoclave method resulted in fewer fish that required a third pellet to be analyzed (i.e., a third pellet was bombed when the first two deviated more than 2% from each other). Only 20% of the fish from the autoclave method required a third pellet to be bombed in comparison to 47 and 60% with the traditional drying and subsampling methods, respectively. While the high temperature of an autoclave (i.e.,

120°C) may affect the fatty-acid profile of fish, the results of this study clearly indicate that the gross energy was not significantly affected by the process. Therefore, the autoclave process offered the most efficient alternative of the methods that I compared by minimizing both sample preparation time and drying time, while not affecting caloric density estimates.

III. The effect of a dynamic estuarine environment on the growth of largemouth bass: a bioenergetics approach incorporating the metabolic cost of salinity

Abstract

Relative to inland populations, largemouth bass *Micropterus salmoides* in Alabama's Mobile-Tensaw River Delta (Mobile Delta) exhibit slow growth, high condition, and low annual survival, similar to many other coastal populations. To examine how salinity influences largemouth bass growth in these systems, I first quantified the metabolic cost of salinity as a function of mass and temperature. Salinity had a nonlinear effect on oxygen consumption, with predicted respiration highest at 3 and 12 ppt, and lowest at 0 and 9 ppt. Further, the metabolic cost of salinity increased with mass. Incorporating this cost into a bioenergetics model revealed that the combined effect of salinity, high peak summer temperature, and consumption of energy-poor macroinvertebrates reduced growth of age-1 and older largemouth bass. Incremental growth analyses demonstrated that the downstream environment was beneficial for growth of age-0 largemouth bass, and these benefits declined linearly with distance from Mobile Bay. After age-2, the relationship between growth rates and proximity to Mobile Bay switched, such that faster growth was observed in fresher areas. These patterns were due to complex interactions among the size-specific metabolic cost of salinity, maximum summer water temperatures, and prey energy content. In addition, discharge influenced the relationship between age-specific growth and proximity to Mobile Bay, likely through its effects on prey availability, salinity, and temperature. Growth rates of older fish were higher upstream, but bioenergetics simulations indicated that consumption rates were 6 to 54% lower than downstream, and these differences increased with age. The results of this study suggest that there is little potential to enhance the size structure of largemouth

bass in the Mobile Delta, even under the best environmental conditions expected for this system.

Introduction

Coastal populations of largemouth bass *Micropterus salmoides* occur in brackish to freshwater tidal-influenced environments along the North American coasts of the Atlantic Ocean and Gulf of Mexico (Bailey et al. 1954; Renfro 1960; Keup and Bayless 1964; Swingle and Bland 1974; Guier et al. 1978; Davies 1981). These populations are typically abundant and support important sport fisheries (Guier et al. 1978; Tucker 1985; Krause 2002). They are characterized by smaller length-at-age and slower growth rates than their freshwater counterparts, but they have higher condition factors (Colle et al. 1976; Guier et al. 1978; Meador and Kelso 1990a; Norris et al. 2010). The resulting small maximum size observed in these systems relative to inland freshwater populations can lead to angler dissatisfaction. Basic understanding of what drives growth rates in these systems is necessary to determine if effective management can change the size structure of largemouth bass populations in coastal systems.

One hypothesis to explain the relatively slow growth of coastal largemouth bass is that salinity reduces the scope for growth via increased metabolic demands for osmoregulation (Meador and Kelso 1990a; Susanto and Peterson 1996). Age-0 largemouth bass generally increased their routine oxygen consumption with increasing salinity to maintain osmotic balance (Susanto and Peterson 1996), although the implications for growth were not determined. Meador and Kelso (1990a) compared growth between freshwater and brackish populations of adult largemouth bass exposed to a range of salinities under controlled laboratory conditions. Growth decreased with salinity up to 8 ppt for the freshwater population, but there was no effect of salinity for the brackish population, suggesting that the brackish population possessed a

physiological adaptation to alleviate salinity stress. At 12 ppt, fish from both populations stopped feeding within 1 week, and no fish survived the experiment at this salinity, suggesting an upper threshold of salinity tolerance (Meador and Kelso 1990a).

Salinity tolerance of largemouth bass appears to change with life stage, and may lead to varying effects on survival and growth at different life stages. Egg and larval stages appear to be most sensitive and were previously found to be unable to survive in salinity > 3.6 ppt (Tebo and McCoy 1964). Survival of age-0 largemouth bass, on the other hand, was not reduced significantly until > 12 ppt (Susanto and Peterson 1996). Further, median 96-h salinity tolerance limits increased with body size for age-0 largemouth bass, indicating that large body size confers an osmoregulatory advantage within this life stage (Tebo and McCoy 1964). However, large body size does not appear to translate to higher salinity tolerance for adult largemouth bass. Osmolality values reported by Susanto and Peterson (1996) were consistently lower for age-0 than values reported by Meador and Kelso (1990b) for older largemouth bass at all salinities, suggesting juveniles are better able to maintain their plasma osmolality at increased salinity. Other fishes, such as striped mullet *Mugil cephalus* (Nordlie et al. 1982), spotted seatrout *Cynoscion nebulosus* (Banks et al. 1991), and spot *Leiostomus xanthurus* (Moser and Miller 1994), display similar ontogenetic shifts in salinity tolerance.

Despite the apparent cost of salinity on growth, estuarine systems may offer advantages to age-0 largemouth bass. For example, relative to upstream freshwater portions of the Mobile-Tensaw River Delta, Alabama, the availability of small, energy-rich fish prey in habitats closest to or within brackish habitats allowed a faster shift to and a higher degree of piscivory for age-0 largemouth bass (Peer et al. 2006). This conferred

a growth advantage to individuals residing in brackish habitats through their first summer of growth compared to largemouth bass in upstream areas that remained fresh. By age-2, however, the growth advantage gained by fish in downstream areas of the Mobile-Tensaw River Delta diminished (Norris et al. 2010). The lack of differences at these later ages may have been due to an ontogenetic shift toward energy-poor macroinvertebrates (i.e., blue crabs *Callinectes sapidus*) by individuals downstream and a greater degree of piscivory (mostly sunfish) in the upstream, freshwater reaches (Norris et al. 2010). Limited piscivory by adult largemouth bass has also been observed in other U.S. Gulf Coast systems (Colle et al. 1976; Lorio et al. 1982; Meador and Kelso 1990a) and may help explain the slower growth observed in these systems compared to inland freshwater systems.

It has been suggested that the physiological effect of salinity increases with largemouth bass size (Susanto and Peterson 1996), yet previous experiments did not find significant differences in growth among 3 salinity levels for adult largemouth bass collected from a brackish environment (Meador and Kelso 1990a). However, the age-0 largemouth bass used by Susanto and Peterson (1996) were collected from a different population than those used by Meador and Kelso (Meador and Kelso 1990a), and it is unknown whether there are differences in salinity tolerance among populations. Therefore, it is necessary to evaluate the ontogeny of salinity tolerance across a wide size range of largemouth bass collected from a single coastal population to determine the lifetime growth implications. Further, it is unknown how, or if, salinity, diet, and temperature interact to influence growth. The purpose of my study was to examine the effects of estuarine environments on lifetime growth of largemouth bass using a

bioenergetics approach. I first determined the metabolic costs of salinity across a range of temperatures and body sizes for largemouth bass collected from the Mobile-Tensaw River Delta, AL, and incorporated this information into the standard metabolism component of a bioenergetics model. I then used this model to simulate the relative impacts of salinity and diet composition on lifetime growth trajectories of largemouth bass along a salinity gradient within the Mobile-Tensaw River Delta showing a range of freshwater discharge. Lastly, I compared growth increments derived from back-calculated length-at-age to assess the indirect effect of discharge on growth of largemouth bass and compared these results to those of bioenergetics simulations.

Materials and methods

Study area

This study was conducted in the Mobile-Tensaw River Delta (hereafter called the Mobile Delta), located in Mobile and Baldwin counties, AL (Figure 3.1). The Mobile Delta begins at the confluence of the Alabama and Tombigbee rivers and extends ~55 km south to the mouth of Mobile Bay. Containing approximately 8,224 ha of surface water comprising a tidal-influenced network of braided creeks, rivers, lakes, wetlands, marshes, bays, and bayous (Crance 1971; Armstrong et al. 2000), the Mobile Delta is a highly productive system and supports a diverse freshwater- and brackish-water fish assemblage (Swingle et al. 1966; Swingle and Bland 1974; Loyacano and Busch 1980; Tucker 1985). Saltwater intrusion into the Delta is generally seasonal, occurring in late summer and fall, and has been recorded 33.8 km upstream on the Mobile River (Swingle et al. 1966; Swingle and Bland 1974). During winter and early spring, salt intrusion in the tidal rivers is minimal because of high discharge associated with rainfall (Bault 1972).

Eight sites were sampled along the Mobile Delta. Of those, 6 sites were established in 2002 along a latitudinal physicochemical gradient, chosen to encompass the predominant habitat types of the region. From upstream to downstream, sites were at Dennis Lake, McReynolds Lake, Gravine Island, Crab Creek, Bay Minette, and D'Olive Bay (Figure 3.1). These sites were sampled monthly from 2002-2008 to capture the spatial and temporal variability of abiotic and biotic characteristics of the Mobile Delta. Two sites were added in 2006 to increase the range of abiotic and biotic characteristics. Tensaw Lake is upstream of I-65 (Figure 3.1) and is a tidal-influenced freshwater 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 (Figure 3.1) 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).

Fish collection and water quality sampling

Electrofishing was conducted monthly from 2002 to 2008 (Smith-Root DC electrofisher, 7.5 GPP, 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-minute 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).

Up to 10 adult largemouth bass (\geq age-1) per site were chosen across a size range at ~25-mm intervals and returned to laboratory each quarter (Jan, Apr, July, and Oct) from 2005 to 2008 to estimate whole-body energy density, and throughout the spawning

period (Feb – Jun) to estimate gonad energy density. In the fall of each year (Oct, Nov, or both), all largemouth bass were returned to the laboratory for age-and-growth estimates. Fish that were of intermediate size between age-0 and age-1 were returned to the laboratory for age verification. Fish not returned to the laboratory were measured (nearest mm; TL), weighed (nearest g), and released. Stomach contents of up to 25 individuals were removed using acrylic tubes (Van Den Avyle and Roussel 1980), placed in individual plastic bags, and returned to the laboratory for diet analysis.

Laboratory processing of largemouth bass

Largemouth bass returned to the laboratory were measured (nearest mm TL), weighed (nearest g), and their saggital otoliths were 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.

Metabolic costs of salinity

I conducted a respirometry experiment to determine routine metabolic rates at four salinities (0, 4, 8, and 12 ppt) and four temperatures (15, 20, 25, and 30°C) for inclusion in a bioenergetics model. These salinity and temperature treatments were chosen to encompass the range of conditions typically experienced by largemouth bass in the Mobile Delta. To capture the effect of body size, eight largemouth bass ranging from 120 to 400-mm TL were used in each treatment combination. Fish used in the respirometry experiment were collected from Bay Minette, one of the routine sampling sites in the Mobile Delta, from 16 July 2008 to 5 January 2009. At the time of collection,

temperature and salinity at 1-m depth ranged from 14.4 to 30.7 °C and 0.1 to 5.2 ppt, respectively. All fish were transported to the laboratory in an aerated hauling tank and then placed in two outdoor 5000-l fiberglass holding tanks.

Eight largemouth bass within predefined 30-mm length classes were randomly selected and transferred into one of two recirculating acclimation systems. Temperature and salinity treatments were randomly assigned throughout the respiration trials. Salinity concentration was increased 2‰ per day using Crystal Sea Bioassay MarineMix (Marine Enterprises International, Inc.) simultaneously with temperature at a rate of 2°C per day. Water temperature was maintained $\pm 1^\circ\text{C}$ with a combination of an aquarium heater and a flow-through water chiller (1/3 hp Aqua Logic® Delta Star® Research Chiller). Once the appropriate salinity and temperature combination was achieved, fish were acclimated for 2 wk. Largemouth bass were fed maintenance rations of fathead minnows *Pimephales promelas* as determined from a bioenergetics model (Hanson et al. 1997) until 48 h prior to oxygen consumption evaluation to allow for complete gut evacuation (Beamish 1964). A 12L:12D photoperiod was maintained throughout the acclimation procedure.

To determine routine metabolism, oxygen consumption was quantified using an open, flow-through respirometer. Once acclimated, individual fish were placed in one of four appropriately sized acrylic respirometer chambers (inside diameter x length (mm) = 73 x 300, 98 x 375, 124 x 450, and 149 x 550), submersed in a 400-L polyethylene tank. After air bubbles were removed, chambers were sealed with end caps fitted with a silicon rubber gasket. A fishless control chamber was used to measure background oxygen consumption. All respirometers were shielded with black acrylic dividers to reduce

visually induced stress. Flow rates were adjusted with a pinch valve to maintain an oxygen difference between inflow and outflow water of 0.5-1.0 mg·L⁻¹ and to maintain an oxygen level > 5 mg·L⁻¹ (Cech 1990). Oxygen concentration of the inflow and outflow water from each respirometry chamber was monitored with microcathode oxygen electrodes (Strathkelvin Instruments, model 1302) fitted in a flow cell (Strathkelvin Instruments, model FC100). The final oxygen concentration of in-flowing and out-flowing water for each chamber was measured with a dissolved oxygen meter (YSI Model 51B) after at least 1 h of stable oxygen consumption was achieved. After each trial, all fish were measured (TL nearest mm), weighed (nearest g), and euthanized by immersion in 300 ppm tricaine methanesulfonate (MS-222).

Routine oxygen consumption was calculated from the formula:

$$MO_2 = [(CO_2)_I - (CO_2)_O] \times V_w$$

where MO_2 is oxygen consumption rate (mg O₂·min⁻¹), $(CO_2)_I$ is the oxygen concentration of in-flowing water, $(CO_2)_O$ is the oxygen concentration of out-flowing water corrected for background oxygen consumption, and V_w is the water flow rate (L·min⁻¹) through the respirometer chamber (Cech 1990). The effect of temperature, salinity, and body mass on the specific rate of respiration (mg O₂·g⁻¹·d⁻¹) was analyzed using non-linear regression (PROC NLMIXED; SAS Institute 2008). The specific rate of respiration (R) was first fit as a function of body mass and temperature using

$$R = RA \cdot M^{RB} \cdot e^{RQ \cdot t}$$

where RA is the intercept of the allometric mass function, M is fish mass, RB is the slope of the allometric mass function, and RQ is the scaled effect of temperature (t). I then tested whether the effect of salinity was additive to temperature or interacted with

temperature by multiplying this equation by $e^{SQ \cdot s}$ or $e^{SQ \cdot s + SQT \cdot t \cdot s}$, where SQ scales the effect of salinity (s) and SQT scales the effect of the interaction between temperature and salinity. I also tested whether the effect of salinity changed with body size or if there was a three-way interaction among salinity, temperature, and body size by multiplying the mass coefficient RB by $e^{SQ \cdot s}$ or $e^{SQ \cdot s + SQT \cdot t \cdot s}$, respectively. I also tested polynomial forms for the effect of salinity. Parameters were estimated using a dual quasi-Newton algorithm and starting values were provided using a grid-search procedure to minimize the chance of converging on local minima in the sum-of-squares surface (SAS Institute 2008). Akaike's second order information criterion corrected for small sample size (AIC_c) was used to determine the best fit model (Akaike 1973; Hurvich and Tsai 1989; Burnham and Anderson 2002).

Differences in R values were compared among salinities within each temperature treatment for 3 body sizes (50, 300, and 550 g) using contrast statements from the best model. These body sizes were chosen to encompass the size range of fish used in all treatment combinations. Standard errors were approximated using the delta method (Billingsley 1986) and $\alpha = 0.05$ was used.

Bioenergetics simulations

I used the combined mean daily discharge from the Alabama River at Claiborne Lock and Dam near Monroeville, Alabama (USGS stream gage #02428400) and from the Tombigbee River at Coffeenville Lock and Dam near Coffeenville, Alabama (USGS stream gage #02469761) from 2002-2008 (URL: <http://waterdata.usgs.gov/nwis/dv>) during summer through fall (i.e., June through November) to select years for low and high discharge years, and therefore salinity levels (Schroeder 1978; Braun and Neugarten

2005) for bioenergetics modeling simulation purposes (Figure 3.2). The first year daily salinity records were available was 2004 and represented the highest summer and fall discharge period in which salinity was recorded and thus was chosen to represent a high discharge year. The 20 y minimum discharge for the Mobile Delta was 2007 and was therefore chosen to simulate a low discharge year. In addition, all data were averaged over the study (2002-2008) to represent the average conditions experienced by largemouth bass in the Mobile Delta.

Bioenergetics simulations were conducted for the upstream and downstream region of the Mobile Delta to examine potential factors affecting growth at a broad spatial scale. The downstream region included D'Olive Bay, Bay Minette, Crab Creek, and Big Bayou Canot because salinity and estuarine prey are consistently present during the summer and fall seasons at these sites (unpublished data). 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).

The general procedure for determining the relative impact 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 discharge; Table 3.1). To determine which factors influenced spatial and temporal variation in largemouth bass growth patterns, I conducted a sensitivity analysis by varying salinity, temperature, and diets in the various levels of discharge. Sensitivity analyses were conducted for both age-specific and lifetime growth. To examine the overall potential impact of salinity on lifetime growth, simulations using

observed conditions and one in which salinity was removed were compared through age-10 (i.e., 9 cohorts). Consumption rates and diet proportions were assumed to remain constant after age-5. Similarly, I examined the potential effects of consuming energy-poor prey over a lifetime growth by changing the energetic value of blue crabs with an average value for fish prey (i.e., average across marine, estuarine, and freshwater fish energetic densities). The potential effects of salinity and consumption of energy-poor prey were evaluated in terms of the time required to reach 2.3 kg (a size commonly considered a “large” fish by anglers in the Mobile Delta), 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 for each region separately using fish from all fall collections (2002-2008).

Start and end mass for the simulations were determined by first constructing von Bertalanffy growth curves for each region using observed mean TL from each age class up to age-6.5 from all fall collections (2002-2008) using nonlinear regression (PROC NLIN; SAS Institute 2008). These were used to estimate length-at-age corresponding to the time of annulus formation during spring (Taubert and Tranquilli 1982). Weight-at-age was then estimated by converting length-at-age estimates to weight using region-specific length-weight regressions determined from all largemouth bass collected throughout this study.

Bioenergetics model components

The upper limit of specific consumption ($\text{g}\cdot\text{g}\cdot\text{d}^{-1}$) was constrained by maximum consumption (C_{max}):

$$C_{\text{max}} = 0.33M^{-0.325}r_c$$

where M is wet mass (g) and r_c is a temperature-dependent multiplier (Niimi and Beamish 1974; Rice et al. 1983). If temperature exceeded 37°C , consumption was set to zero (Niimi and Beamish 1974; Rice et al. 1983). Daily energetic losses from specific dynamic action (SDA), egestion (F), and excretion (U) were estimated as 14.2% (Beamish 1974; Rice et al. 1983), 10.4% (Beamish 1972; Rice et al. 1983), and 7.9% (Beamish 1974; Niimi and Beamish 1974; Rice et al. 1983) of consumed energy. The best model describing oxygen consumption as a function of body mass, temperature, and salinity determined from the respirometry experiment was used to estimate standard metabolism in bioenergetics simulations (see above). Oxygen consumed was converted to calories using $3.24 \text{ cal}\cdot\text{mg O}_2^{-1}$ (Elliott and Davidson 1975). Activity costs were assumed to be similar for that found previously for largemouth bass (Rice et al. 1983; Trebitz 1991). The proportion of C_{max} required to grow at observed rates from 1 April to 31 March was determined iteratively for each cohort until observed and predicted end masses were within $\pm 0.001\%$.

Water temperature and salinity

Water temperature was recorded at 2-h intervals at each site using temperature loggers set at $\sim 1\text{-m}$ depth from 2002-2008. Specific conductance ($\text{mS}\cdot\text{cm}^{-1}$ at 25°C) was recorded at 30-min intervals with loggers (Solinst Model 3001 LTC levelogger) placed at the most downstream site (i.e., D'Olive Bay) and a site in the middle of the spatial range

(i.e., Gravinge Island) from May 2005 to December 2008. Conductivity readings were converted to salinity (ppt) using standard formulas (APHA 1998). Logger failure resulted in gaps in the salinity record for the downstream site. Therefore, I also obtained all available salinity readings (i.e., 2004-2008) from Meaher State Park (30° 40.028' N, 87° 56.188' W) recorded at 30-min intervals using a YSI model 6600 by the Dauphin Island Sea Lab (URL: <http://www.mymobilebay.com/stationdata/StationInfo.asp?jday=&property=&chartyear=&StationID=703>).

The first year daily salinity records were available was 2004 from Meaher State Park and represented the highest summer and fall discharge period when salinity was recorded (Figure 3.2). Therefore Meaher State Park mean daily salinity from 2004 was used as the salinity regime during a high discharge year (Figure 3.3b). 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 Gravinge Island (Norris et al. 2010). Therefore I assumed that salinity in the upstream region was 0 ppt in 2004 (Figure 3.3a). Bi-hourly data from Meaher State Park and D'Olive Bay were averaged each day for the low discharge year (i.e., 2007) to compensate for missing values in the downstream region (Figure 3.3b). The Gravinge Island salinity readings were divided by 2 for the low discharge year, assuming that values further upstream were close to 0 ppt throughout 2007 (Figure 3.3b). All available salinity values were averaged for Meaher State Park and D'Olive Bay to simulate an average salinity year in the downstream region (Figure 3.3a), whereas the upstream salinity was an average between Gravinge Island values and a freshwater value (Figure 3.3b). 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 discharge years, respectively (Figure 3.3c and 3.3d).

Largemouth bass energy density

Energetic density of somatic tissue (i.e., whole body minus gonads) and gonads was determined using bomb calorimetry. For somatic tissue, samples were thawed, their wet mass recorded (nearest 0.01 g), and an autoclave procedure was used to aide in obtaining a 40- to 60-g subsample (Glover et al. 2010). Gonads were dried whole except during spring, when half of the gonad lobe was kept for maturity assessments (see Chapter IV). All samples were oven-dried, 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.

Whole body energy density (somatic + gonads) in the bioenergetics model was a function of body mass M ($874.98 \cdot M^{0.057}$; $F_{1,339} = 57.79$, $P < 0.001$), as determined above. A separate equation was fit for summer, which had a lower intercept compared to the rest of the year, as indicated by analysis of covariance ($828.94 \cdot M^{0.057}$; $F_{3,339} = 5.12$, $P < 0.001$).

Spawning costs

I was primarily interested in determining average consequences of the estuarine environment for individual largemouth bass rather than sex-specific comparisons and used one set of bioenergetic model parameters for both males and females. 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.

The energetic cost of ovaries has been shown to be similar to the energetic expenditure of nesting males (Heidinger 1975).

Size-specific constraints in ovary size were determined using quantile regression (PROC QUANTILE; SAS Institute 2008). To define the maximum constraint to gonad mass I used gonads collected throughout the spawning period (March-May), and determined the upper 95th percentile of gonad mass as a function of total female mass (Figure 3.4a.). Because gonad mass does not return to zero after spawning, I used gonads collected after spawning (June-August) to define the minimum constraint of gonad mass by estimating the lower 95th percentile of gonad mass as a function of female mass (Figure 3.4a.). The total energetic losses due to spawning were then estimated by subtracting residual ovarian tissue energy from the maximum expected energy devoted to ovaries. Caloric density of pre- and post-spawn ovaries was estimated from the relationship between gonad-somatic index (GSI; Strange 1996) and energy density developed in this study (Figure 3.4b). Spawning in the simulation occurred on 31 March.

Prey consumption and energetic content

Stomach contents of largemouth bass were identified to the lowest practical taxonomic level (e.g., species for fish, order and family for insects and gastropods). Size of prey ingested were measured and biomass of prey was converted using allometric relationships determined from this study and published literature values (Schoener 1980; Smock 1980; Pace and Orcutt 1981; Sage 1982; Culver et al. 1985; Benke et al. 1999; Sabo et al. 2002; Peer 2004; Norris 2007; Farmer 2008). Broad categories of diet proportions were determined for each individual fish (i.e., freshwater fish, estuarine fish,

marine fish, crabs, shrimp, and aquatic insects) and then averaged across fish by season and region for each age class (Krebs 1998). Seasonal diet information from 2002-2008 were pooled to reflect the average diet proportions consumed over the lifetime of largemouth bass (Figure 3.5a and 3.5b) and separate diet proportions were derived for high (Figure 3.6a and 3.6b) and low discharge (Figure 3.7a and 3.7b). Year-specific diet information from 2002-2004 and 2005-2007 can be found in Norris et al. (2010) and Farmer (2008), respectively. 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 (Table 3.2).

The average energetic density of consumed prey for individual largemouth bass was estimated using the diet proportions and energetic values above. Using this information, I tested whether age, region (i.e, upstream and downstream), season, season-specific discharge, as well as all possible interactions affected the caloric density of consumed prey (PROC GLM; SAS Institute 2008). Backward model selection was used to eliminate insignificant terms in the model to determine the most influential variables on consumed energy.

Field-derived largemouth bass growth

In addition to bioenergetic simulations, I compared growth rates of largemouth bass using incremental growth analysis derived from back-calculated length-at-age from otoliths. Sagittal otoliths of all fall-collected largemouth bass were examined whole under a dissecting microscope for age determination (Taubert and Tranquilli 1982). The age of each fish was estimated by two independent readers. If there was any disagreement between readers or if a fish was estimated to be > age-4, the otolith was

sectioned transversely with a low-speed diamond blade Isomet® saw (South Bay Technologies, San Clemente, California), mounted on a slide with thermoplastic cement, and polished smooth to the nucleus for age determination. After final age was determined, otolith radius and annuli radii were measured from whole otoliths with an ocular micrometer under a dissecting microscope for fish \leq age-4 and sectioned otoliths for fish \geq age-5 were measured with a digital micrometer mounted on a compound microscope (nearest 0.001 mm; Schramm et al. 1992). 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 length.

To examine the spatial variation in largemouth bass growth rates, I evaluated whether age-specific growth rates were a function of distance from Mobile Bay (PROC REG; SAS Institute 2008) and also used ANOVA to determine if there were differences in site-specific growth rates (PROC GLM; SAS Institute 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. Pairwise *t*-tests were used to determine which sites were different when the *F*-test was significant. To determine potential effects of salinity on largemouth bass growth, I tested 1) whether year-specific discharge (a surrogate for salinity) was related to annual growth increments, and 2) whether this effect differed among sample sites using analysis of covariance (ANCOVA; PROC GLM; SAS Institute 2008). I used the combined mean daily discharge from the Alabama and Tombigbee rivers during summer and fall (i.e., June through November) as a surrogate of salinity from 1996 to 2007 to encompass the period in which growth

increments were back-calculated. Separate analyses were conducted for each age up to age-4 because there were too few observations for older fish and $\alpha = 0.05$ was used in all cases.

Results

Respirometry experiment

The effect of salinity was best described by a cubic function in which the cost of salinity increased with body mass (Table 3.3), as supported by ΔAIC_c and improved evidence ratio compared to the next best model (Burnham and Anderson 2002). This model explained 84% of the variance in specific respiration rates. Predicted respiration increased with salinity up to a peak at 3 ppt and then declined as salinity approached 9 ppt (Figure 3.8). The model predicted that the specific respiration rate at 9.3 ppt (95% CI = 8.48 to 10.12 ppt) was similar to that observed at freshwater, which is approximately the isosmotic level of largemouth bass (Peterson and Meador 1994). Respiration increased with salinity past the isosmotic level up to 12 ppt, which was still slightly below the effects predicted at 3 ppt. The percent increase in respiration due to salinity increased with body mass (Figure 3.9). The salinity level that had the highest increase in respiration in the respirometry trials, 4 ppt, showed a 25% increase for a 50-g largemouth bass compared to respiration at freshwater, whereas an 800-g largemouth bass had an estimated 45% increase in respiration. The effect of temperature on respiration had a reduced slope but higher intercept than previously published inland largemouth bass populations (Beamish 1970; Rice et al. 1983; Figure 3.10).

Size-specific comparisons from the best model indicated that the effect of salinity on oxygen consumption was highest at 4 ppt across all body sizes and temperatures,

which was significantly different from the 0 and 8 ppt treatments ($t_{120} \geq 2.41$, $P \leq 0.018$; Figure 3.11), but was similar to 12 ppt ($t_{120} \leq 0.54$, $P \geq 0.587$). Oxygen consumption was similar between 0 and 8 ppt ($t_{120} \leq 1.33$, $P \geq 0.186$) and between the 8 and 12 ppt treatments ($t_{120} \leq 1.74$, $P \leq 0.084$), but was higher at 12 ppt compared to 0 ppt ($t_{120} \geq 2.16$, $P \leq 0.033$). These trends were similar across all body sizes and temperatures (Figure 3.11).

Caloric content of consumed prey

The best model describing caloric density of consumed prey by largemouth bass included the main effects of age ($F_{1,3340} = 27.54$; $P < 0.001$), season ($F_{3,3340} = 2.29$; $P = 0.08$), region ($F_{1,3340} = 236.22$; $P < 0.001$), and season-specific mean daily discharge ($F_{1,3340} = 8.96$; $P = 0.003$), as well as the interactions between age and season ($F_{1,3340} = 10.37$; $P < 0.001$), and discharge and season ($F_{1,3340} = 4.41$; $P = 0.004$). Age had a negative effect on mean caloric content of consumed prey across all seasons ($t_{3340} \geq 2.37$; $P \leq 0.02$) except for winter when there was no relationship with age ($t_{3340} = 1.39$; $P = 0.17$; Figure 3.12). Largemouth bass in the upstream region consumed ~ 113.82 cal·g⁻¹ of prey more than those downstream ($t_{3340} = 15.37$; $P < 0.001$), which was consistent across ages, season, and discharge levels. The only season when discharge affected caloric intake of largemouth bass was during the summer ($t_{3340} = 4.20$; $P < 0.001$), when mean caloric content of consumed prey increased with discharge at similar rates between upstream and downstream regions ($P > 0.05$). Discharge did not affect caloric consumption during any other season ($t_{3340} \leq 1.27$; $P \geq 0.20$). Correcting for effects of age, region, and discharge, the highest and lowest caloric intake was during winter (t_{3340}

≥ 2.73 ; $P \leq 0.006$) and summer ($t_{3340} \geq 3.71$; $P < 0.001$), respectively, whereas fall and spring values were not different ($t_{3340} = 0.015$; $P = 0.99$).

Bioenergetics simulations

Bioenergetics simulations indicated that salinity was most influential on lifetime growth through the end of age-5 in the downstream region and that variation in temperature and diet proportions among discharge levels had smaller effects on lifetime growth (Figure 3.13d-f). In the upstream region, changes in diet proportions and salinity regimes impacted lifetime growth more than temperature (Figure 3.13a-c). The substitution of salinity regimes between simulations indicated that the average salinity regime negatively impacted lifetime growth to a greater degree than salinity regimes from either the low or high discharge years in the downstream region, and that the high discharge year was best for growth in terms of salinity (Figure 3.13d). In the upstream region, however, average and low salinity regimes had similar negative impacts on lifetime growth (Figure 3.13a).

Despite the increased specific metabolic costs of salinity with mass in the respiration function I determined, proportional differences in the effects of salinity on age-specific growth were negligible in both regions (Figure 3.14a and 3.14d). This apparent lack of an effect was due to a faster decrease in respiration rates with mass relative to increases due to salinity. Considering total changes in mass, the negative effect of salinity increased with age and size. The upstream simulation indicated strong negative effects of salinity on age-specific (Figure 3.14a) and lifetime growth (Figure 3.13a, 3.15a, 3.15d, and 3.15g) during average and low discharge years. Declines in mass over time did not appear to be correlated with seasonal changes in salinity, but

rather appeared to be cumulative over time (Figure 3.15a, 3.15d, 3.15g, 3.16a, 3.16d, 3.16g).

In both regions, temperature had its greatest negative impact on growth during the low discharge year, but was similar during the average and high discharge years (Figure 3.13c and 3.13f). For each region, sharp decreases in mass were observed at each age under the low discharge simulation, which corresponded to periods when summer temperatures began exceeding optimum temperature for consumption (i.e., 27.5°C) and peaked at 32.9 and 33.2 °C in the upstream and downstream region, respectively (Figure 3.15c, 3.15f, 3.15i and Figure 3.16c, 3.16f, 3.16i). The effects of temperature tended to decrease with age, particularly for the downstream region due to lower specific respiration of larger largemouth bass (Figure 3.14c and 3.14f).

Diet composition was most favorable for growth in the upstream region during the low discharge year and was considerably worse during the high discharge year (Figure 3.13b). The reverse was observed for the downstream region, where diet proportions were most favorable for growth during the high discharge year, and similar during the low and average discharge years (Figure 3.13e). The large negative effect of diet on lifetime growth in the upstream region was due primarily to the diet being made up entirely of crabs during the summer at age-4 and fall at age-5 in the high discharge year (Figure 3.7), which caused the average caloric intake per gram of prey to be low and caused a drastic reduction in age-4 and age-5 growth (Figure 3.15h and 3.15e). Seasonal declines in average caloric intake were evident in the average discharge simulations at many ages (Figure 3.15e), but changes in these values were not as drastic relative to high and low discharges, likely due to the greater sample size for determining diet proportions

during the average discharge years (Figure 3.6). The average caloric density consumed in the downstream region was strikingly similar among the three discharge simulations (Figure 3.16b, 3.16e, 3.16h). By age-3, a strong seasonal pattern emerged in which the average caloric intake decreased sharply during summer and fall seasons consistent with the consumption of crabs (Figure 3.7). Age-specific effects of diets in the downstream region (Figure 3.14b) were due mostly to diet shifts between blue crabs and freshwater fish, causing an increase in the average caloric intake per gram of prey consumed (Figure 3.16b, 3.16e, 3.16h). The smaller age-specific changes in the downstream region among simulations compared to the upstream region indicate that diet composition was more stable across the range of discharges, at least in terms of average caloric density of consumed prey.

Predicted mass through age-10 under the various observed discharge conditions indicated that the average largemouth bass cannot attain a mass of 2.3 kg within this time period in either region (Table 3.5). Simulations suggested that the high discharge conditions provided the most favorable environment for growth in the upstream and downstream region, attaining a mass of 1.41 and 1.50 kg within 10 y, respectively. 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 8.3 to 8.6 and 4.6 and 6.6 y in the upstream and downstream region, respectively. However, final mass after 10 y in the upstream region after removing salinity were < 2.3 kg, indicating that they do not maintain this mass for a long period due to weight loss. Simulated largemouth bass in the upstream and downstream region that were provided an all fish diet reached 2.3 kg within 5.2 to 5.5 and 3.5 to 4.1 y, respectively, suggesting that consumption of low-energy prey

(crabs) have higher negative effects on lifetime growth than salinity. Simulations indicated that growth potential of upstream largemouth bass was not as high relative to 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 from 17-54%, 23-46%, and 6-22% lower relative to downstream for the low, average, and high discharge simulations, respectively (Table 3.1). Therefore, while the estuarine environment is not as detrimental to lifetime growth of largemouth bass upstream with respect to salinity and caloric density of consumed prey, it appears that lower consumption rates may have limited growth potential of largemouth bass in the upstream region.

The bioenergetics simulations predicted higher largemouth bass consumption rates downstream than upstream among all discharge simulations, yet regional differences in terms of caloric intake was more variable among discharge simulations. For example, the average discharge simulation indicated similar patterns of higher consumption rates downstream compared to upstream (Figure 3.17), whereas the low discharge simulation indicated that largemouth bass upstream consumed approximately 1.5 to 3 times more energy through age-3 (Figure 3.18). At older ages, energetic intake was fairly similar between regions in the low-discharge simulation. At high discharges, simulations suggested that age-1 and age-5 fish consumed up to 1.75 times more energy per gram of body mass upstream compared to downstream, whereas age-2 through age-4 energetic intake was similar (Figure 3.19).

Largemouth bass growth increments

Largemouth bass growth rates differed among the 8 sites for all ages (ANOVA; $P < 0.001$; Figure 3.20a). Largemouth bass closer to Mobile Bay grew faster than those farther upstream in their first (Regression; $F_{1, 973} = 80.03$, $P < 0.001$; slope = -0.619; Figure 3.20a.) and second year of life (Regression; $F_{1, 482} = 15.92$, $P < 0.001$; slope = -0.295; Figure 3.20b.). However, the site farthest downstream (D'Olive Bay) and farthest upstream (Tensaw Lake) were most responsible for the significant relationship, as growth was similar among other sites (Figure 3.20b). 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; $F_{1, 216} = 22.54$, $P < 0.001$; slope = 0.394; Figure 3.20c.) and between age-3 and age-4 (Regression; $F_{1, 103} = 12.77$, $P < 0.001$; slope = 0.254; Figure 3.20d).

The effect of summer and fall mean daily discharge on largemouth bass growth rates was site-specific in the first year of life (ANCOVA; $F_{7, 955} = 5.31$, $P < 0.001$; Figure 3.21). In general, increased discharge had negative effects on largemouth bass growth downstream, little to no effect mid- to upstream, and positive effects at the farthest upstream site. In their second year of life, largemouth bass were negatively affected by increased summer and fall discharge (ANCOVA; $F_{1, 468} = 7.70$, $P = 0.006$, slope = -0.010), and this effect was similar among all sites (ANCOVA; $F_{7, 468} = 1.21$, $P = 0.296$). Neither the main effect of discharge ($F_{1, 202} = 0.45$, $P = 0.452$) nor the interaction with sites ($F_{7, 202} = 1.35$, $P = 0.230$) affected growth rates of largemouth bass in their third year of life. By the fourth year of life, summer and fall discharge had a positive effect on

largemouth bass growth at all sites throughout the Mobile Delta ($F_{1, 89} = 4.81, P = 0.031$, slope = 0.015) and this effect was similar across all sites ($F_{7, 89} = 1.45, P = 0.197$).

Discussion

The results of the bioenergetics simulations suggested that the combined effects of metabolic costs of salinity, high peak summer temperatures, and low prey caloric density negatively impacted growth of age-1 and older largemouth bass in the Mobile Delta. The growth potential of large fish was severely hampered by high metabolic costs of salinity combined with diets heavily weighted toward energy-poor invertebrates (i.e., blue crabs), particularly downstream. The growth potential of fish upstream appeared to be constrained by lower consumption rates relative to downstream, which is supported by a high proportion of empty stomachs (see Appendix 1) and low relative weights at sites farther from Mobile Bay (Norris et al. 2010). In contrast to patterns for age-1 and older largemouth bass, incremental growth analysis showed that age-0 largemouth bass growth declined linearly with distance from Mobile Bay. Thus, age-0 largemouth bass appeared to benefit from the estuarine environment, consistent with previous findings (Peer et al. 2006). The relative costs and benefits of the estuarine environment not only change over the life of largemouth bass, but also change linearly with distance from the source of the marine influence.

Bioenergetics simulations suggested that high discharge would provide the best environment for growth both upstream and downstream due to lower salinity levels, reduced peak summer temperatures, and increased caloric intake through greater consumption of fish prey. However, incremental growth analyses indicated that the age-specific effects of discharge varied along the freshwater-estuarine gradient. Specifically,

discharge 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 discharge level were similar across sites. With decreasing levels of discharge, however, the growth advantage increased downstream relative to upstream. Although the bioenergetics simulations did not include the age-0 to age-1 cohort, lower summer and fall discharge 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 a quicker switch to and greater degree of piscivory downstream versus upstream due to the higher availability of small-bodied estuarine fish prey. Combined with my study, this suggests that discharge 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 are influenced by discharge.

By age-1, all largemouth bass were piscivorous to some degree and while largemouth bass consumed higher proportions of freshwater fish prey upstream than downstream, consumption of estuarine- and marine-derived fish was evident in both regions, particularly during low discharge. Thus, the higher availability of estuarine- and marine-derived fish prey at lower discharge during summer may outweigh the negative costs associated with abiotic factors in both regions between age-1 and age-2. The lower degree of piscivory observed downstream relative to upstream combined with increased metabolic cost of salinity, due not only to higher salinity levels but also increased

osmoregulatory expenditures with size, may have limited the net benefits of the estuarine environment downstream. This resulted in approximately equal growth rates among most sites within the Mobile Delta between age-1 and age-2. Discharge 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 summer temperatures could no longer be offset by influx of estuarine- and marine-derived fish prey or an ontogenetic shift in prey use. In fact, the amount of blue crabs consumed by largemouth bass increased with age (see Appendix 1) resulting in reduced rates of caloric consumption in both regions, yet to a greater degree downstream. These combined effects resulted in a switch in the relationship between growth rates and proximity to Mobile Bay, such that faster growth rates were observed at sites farther upstream of Mobile Bay between age-2 and age-3. Low summer and fall discharge resulted in reduced growth rates between age-3 and age-4 at all sites within the Mobile Delta. Taken together, the influence of discharge on growth appears to change through life of largemouth bass due to ontogenetic shifts in prey use such that young fish benefit from low discharge due to availability of high-quality prey whereas adults are negatively affected by low discharge due to the combined effects of poor prey quality, increased salinity, and high peak summer temperatures.

Previous studies suggest that this discharge-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 discharge and could, therefore, affect abundance of small-bodied fish prey available to upstream predators. In addition, several studies on estuarine systems have documented the contribution of marine-derived subsidies to freshwater predators, including blue catfish (MacAvoy et al. 2000) and largemouth bass (Yako et al. 2000). In fact, among four coastal river systems within North Carolina, the highest largemouth bass growth rates were observed in those with the highest salinity, which was attributed to a greater influx of marine-derived fish prey (Guier et al. 1978).

It appears that the relative costs and benefits of the estuarine environment change rapidly throughout the life of largemouth bass, becoming progressively poorer for growth of older largemouth bass. The change in the cost to benefit ratio is largely due to ontogenetic changes in salinity-related metabolic cost and shifts in prey use toward less energetically dense prey in older largemouth bass. The interaction of these factors with temperature ultimately dictates growth potential. Specifically, as mean caloric intake decreases with age, the critical temperature at which maintenance costs exceed consumed energy decreases (Figure 3.22a), thereby limiting the range of temperatures where positive growth can occur. Increasing metabolic costs of salinity during summer exacerbates this effect, particularly for large fish at peak metabolic costs of salinity (i.e., ~3 ppt; Figure 3.22b). In fact, a 2268 g largemouth bass consuming a diet consisting completely of blue crabs ($595 \text{ cal} \cdot \text{g}^{-1}$) with salinities from 0 to 8 ppt would not be able to maintain positive growth at any temperature. The reduced caloric intake per gram of prey with fish age observed in my study may therefore help explain why abiotic factors appeared to become more important with age.

It is important to note, however, that the response of maximum consumption rates of largemouth bass in relation to temperature is a critical element for determining the point at which weight loss would occur. I assumed that consumption rates for largemouth bass in the Mobile Delta respond similarly to temperature as those used to build the largemouth bass bioenergetics model, which were collected from Ontario (Niimi and Beamish 1974). The standard 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 I found strong differences in how largemouth bass responded to temperature in the Mobile Delta compared to the standard largemouth bass respiration function, which was also determined for fish collected from Ontario (Beamish 1970; Rice et al. 1983), the consumption function may differ as well. The latitude of source fish used in an evaluation of the bioenergetics model on age-0 largemouth bass has a large influence on the performance of the model predictions (Slaughter et al. 2004); therefore, this problem is not unique to this study. 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 (personal observation; Norris et al. 2010), presumably due to thermoregulatory behavior. Given that the bioenergetics simulations indicated that just a few degrees change in these extreme temperatures can have profound growth consequences, improving temperature-related parameters in the bioenergetics model is warranted.

The curvilinear respiration function in relation to salinity determined in my study was similar to previous findings for age-0 largemouth bass exposed to contrasting levels of salinity (Susanto and Peterson 1996). Specifically, Susanto and Peterson (1996) observed lowest respiration rates were at 0 ppt, but these rates did not differ from those observed at 8 ppt. Peak respiration occurred at 4 ppt but did not differ from 12 and 16 ppt (Susanto and Peterson 1996). When exposed to 8 ppt, adult coastal largemouth bass had nearly half the gill ATPase relative to inland freshwater largemouth bass despite a significantly higher plasma osmolality (Meador and Kelso 1990b). These results suggested that coastal largemouth bass conserved energy by reducing active ion transport near the isosmotic level (~9 ppt) and may represent an adapted mechanism to tolerate periods of high salinity. A possible explanation is that blood flow is diverted to gill filaments with greater resistance to ion exchange, not only limiting fluctuations in plasma osmolality and reducing water loss, but also reducing oxygen consumption (Peterson 1988). The higher gill ATPase of freshwater largemouth bass relative to coastal largemouth bass at 8 ppt also suggests that fish not adapted to salinity would have greater metabolic costs associated with salinity and would require either greater consumption or consumption of higher energy-dense prey to maintain positive growth. Combined with the finding that metabolism at freshwater was much lower at high temperatures compared to the standard largemouth bass metabolic function (Rice et al. 1983), it is likely that largemouth bass not adapted to cope with high salinity or to high peak summer temperatures would not be able to maintain positive growth in a wide range of temperatures. The lack of success achieved for 10 years of stocking Florida largemouth bass *M. s. floridanus* throughout the 1990s (Hallerman et al. 1986; Armstrong et al. 2000)

may therefore be due in part to their being maladapted to an estuarine environment. In addition, experiments evaluating growth differences of largemouth bass at varying salinities found that largemouth bass held at 12 ppt stopped feeding within 1 wk and did not survive the experiment (Meador and Kelso 1990a). In contrast, I did not observe any changes in feeding behavior or mortality during the 2-wk acclimation period at any salinity level up to 12 ppt for largemouth bass used in the respirometry experiment. This suggests that largemouth bass in the Mobile Delta may be better adapted for tolerating salinity than those found in Louisiana marshes.

Low discharge provided the poorest environment for growth in terms of increased consumption of invertebrates and high summer temperatures, yet bioenergetics simulations indicated the salinity during the average year reduced growth to a greater degree than during the low discharge year. This was counterintuitive given that salinity was higher during the low discharge year compared to the average discharge year. This counterintuitive result was due to the nonlinear effect of salinity on metabolism. Specifically, during the average discharge year largemouth bass were exposed to salinity levels that had the largest effect on metabolism (~3 ppt) for greater periods of time compared to the low discharge year.

Interestingly, bioenergetics simulations suggested that the cost of consuming energy-poor invertebrates reduced growth rates to a greater degree than salinity in both regions, but to a greater extent downstream. Specifically, in simulations where the effect of consuming blue crab was removed by increasing the caloric density of consumed prey, largemouth bass reached 2.3 kg sooner relative to simulations in which the salinity effect was removed by setting salinity to 0 ppt. Further, when the blue crab effect was

removed, the final mass achieved after 10 years was 58 to 302 times higher compared to when salinity was removed. 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. It is important to note that bioenergetics simulations among the varying levels of discharge predicted that the effects of diet were greater upstream and were largely age-specific. However, analyses of consumed energy indicated that caloric density of consumed prey declined at similar rates with age in both regions and discharge had similar effects between regions. Therefore, it would be reasonable to expect that the effect of diet was similar between regions with respect to discharge. This conflicting result was likely due to the small sample size of largemouth bass available for determining diet proportions for low and high discharge simulations particularly for fish \geq age-3. Therefore it is likely that diet had similar effects on growth between regions across varying levels of discharge, but the overall negative impact of diet was higher downstream due to the greater consumption of energy-poor invertebrates. Other studies in the 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; Mittelbach 1984).

Higher caloric density of prey consumed by largemouth bass upstream and the lower salinity levels in the upstream region appear to be favorable for the production of large largemouth bass, yet very few large fish were present during the 7 y of this study. Specifically, out of a total of 9,988 adult largemouth bass (\geq age-1) only 7 were \geq 2268 g, 6 of which were collected from the upstream region. Moreover, less than 2% of collected fish were \geq 1361 g (3 lb). The bioenergetics simulations indicated that age-specific consumption rates of largemouth bass ranged from 6 to 54% lower upstream relative to downstream and generally increased with age, which may have limited growth potential. 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 cypress trees upstream relative to downstream (Norris et al. 2005), 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; Bettoli et al. 1992; Sammons and Maceina 2006). 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 enhance the size structure of largemouth bass in the Mobile Delta, even under the best environmental conditions expected for this system (i.e., high discharge).

IV. Understanding the slow-growth, high-condition paradox of coastal largemouth bass using an optimal energy allocation model

Abstract

“Bigger is better” has been a pervasive phenomenon concerning the effect of body size on life history of fishes. Largemouth bass (*Micropterus salmoides*) in coastal systems often exhibit slow growth and small size, due largely to energetic constraints. Yet, their high condition factors suggest an alternate energy allocation strategy. In this study, I examined whether estuarine conditions select against larger fish and if high condition factors could be the results of an alternate energy allocation strategy. I quantified life history and energy allocation characteristics of largemouth bass across an estuarine-freshwater gradient in the Mobile-Tensaw River Delta, Alabama. An optimal annual routine (OAR) model was used to estimate lifetime optimal energy allocation among growth in length, reproduction, and energy reserves as a function of annual survival rate and ration for female largemouth bass in estuarine and freshwater environments. Field results suggested age-0 initial length decreased, asymptotic length increased, and condition decreased with distance from Mobile Bay. The probability of maturing at earlier ages was greater downstream compared to upstream for both sexes. Length-at-maturity was similar between regions for males, whereas females matured at slightly smaller sizes in the downstream region. Annual survival rates were similar between regions, suggesting that maturation differences were largely growth rate dependent.

Results from the OAR model suggested the expectation of salinity led to increased energy allocation toward energy reserves at the cost of length when compared with a freshwater strategy. High lipid reserves not only decreased starvation risk, but

also limited scope for growth, thereby limiting the duration and magnitude of energy deficits experienced. Lipid reserves also allowed females to switch allocation toward ovary development prior to spawning to ensure reproductive output in the face of poor energy availability. Fish exhibiting an estuarine strategy performed well in a freshwater environment in terms of growth, condition, and reproductive output; the freshwater strategy, however, was incompatible with an estuarine environment. These results suggest slow growth and high condition factors observed in coastal systems are the result of an adapted energy allocation strategy, and also suggest that smaller, and more precisely, fatter is better for fish in brackish systems.

Introduction

The amount of energy allocated among somatic tissue, reproduction, and energy reserves throughout the life of an organism affects key life history characteristics such as growth, age- and size-at-maturity, frequency of reproduction, and survival (Roff 1992; Stearns 1992). Allocation of energy among these pathways ultimately affects body size of an organism at any one time and, therefore, has strong ecological implications (Peters 1983; Werner and Gilliam 1984). In fishes, large body size often confers enhanced survival and individual fitness. For example, relative to small individuals, larger individuals often are less vulnerable to predators (Miller et al. 1988; Hambright et al. 1991; Fuiman and Magurran 1994), are more efficient foragers (Mittelbach 1981), and are less constrained by gape limitation (Lawrence 1958; Hambright et al. 1991; DeVries et al. 1998; Slaughter and Jacobson 2008), thereby having a greater breadth of available prey sizes (Werner 1974; DeAngelis and Gross 1992; Wright et al. 1993; DeVries et al. 1998). Large individuals also possess a higher capacity for storage of energy reserves (Oliver et al. 1979; Toney and Coble 1979; Post and Evans 1989; Garvey et al. 1998) and require less energy per unit mass for maintenance than small individuals (Edwards et al. 1971; Niimi and Beamish 1974; Brett and Groves 1979; Peters 1983); permitting large individuals to withstand periods of low food availability and/or high energy demand. Large body size also has positive effects on fecundity (Bagenal 1966; Bagenal 1978; Shine 1988). As such, the allocation of energy toward either reproduction or energy reserves can increase fitness through higher reproductive output or enhanced survival. However, both reproduction and lipid reserves are energetically expensive and detract

from energy available for somatic growth and body size, thereby potentially limiting future fitness (Bell 1980; Roff 1982; Stearns 1992; Shertzer and Ellner 2002).

Uncertainty of future feeding conditions (King and Roughgarden 1982; Shertzer and Ellner 2002; Bunnell and Marschall 2003), length of growing season (Hom 1987; Kozlowski and Teriokhin 1999; Garvey and Marschall 2003), and adult mortality (Kozlowski and Uchmanski 1987; Pugliese 1987; Engen and Saether 1994; Kozlowski and Teriokhin 1999) have been predicted to influence energy allocation among somatic tissue, reproduction, and energy reserves. The extent to which these factors influence energy allocation can have profound consequences on the ecology and management of fish species. For example, coastal populations of largemouth bass occur in low salinity environments along the U.S. coasts of the Atlantic Ocean and Gulf of Mexico (Meador and Kelso 1990a). The life history of largemouth bass is well understood throughout its freshwater range, but coastal populations possess substantially different population characteristics compared to their freshwater counterparts. Relative to inland populations, largemouth bass in coastal systems have slower growth, higher body condition, and reduced annual survival (Colle et al. 1976; Guier et al. 1978; Meador and Kelso 1990a; Norris et al. 2010). Coastal largemouth bass are faced with several stresses in an estuarine environment, including fluctuations in salinity, high risk of predation (e.g., from large predators such as alligator gar *Atractosteus spatula*, red drum *Sciaenops ocellatus*, and other marine and estuarine predators), and catastrophic events such as hurricanes (Meador and Kelso 1989; Peterson and Meador 1994; Norris et al. 2010). Despite these stresses, coastal largemouth bass populations are successful, based on their high abundance, often supporting valuable sport fisheries (Nack et al. 1993; Richardson-Heft

et al. 2000; Krause 2002). Therefore, determining if and how estuarine stressors have shaped the life history and growth patterns of coastal largemouth bass is important from both an ecological and management perspective.

The relative benefits and costs of the estuarine environment appear to change throughout the life of largemouth bass in the Mobile-Tensaw River Delta, Alabama (hereafter called the Mobile Delta). Specifically, growth rate at both age-0 and age-1 was fastest downstream and declined linearly with distance from Mobile Bay (Peer et al. 2006; Norris et al. 2010; Chapter III). Peer et al. (2006) attributed the downstream growth advantage to high availability of small, energy-rich fish prey, which allowed both a faster shift to, and a higher degree of, piscivory. The relationship between age-specific growth and proximity to Mobile Bay quickly reversed, however, such that relatively slower growth was observed downstream after age-2 and increased linearly with distance from Mobile Bay (Chapter III). Bioenergetics modeling revealed that growth of largemouth bass older than age-0 in the Mobile Delta was negatively influenced by salinity, consumption of energy-poor macroinvertebrates (i.e., blue crabs *Callinectes sapidus*), and high peak summer temperatures (Chapter III). Moreover, the metabolic costs of salinity increased with size and the proportion of diet made up of crabs increased with age, such that mean caloric intake declined with age, severely limiting growth potential of older individuals. In addition, coastal largemouth bass experience high annual mortality rates (Lorio et al. 1982; Krause 2002; Norris et al. 2010; Chapter III). Decreased chances of living to old ages combined with poor adult growth rates may reduce the reproductive value (sensu Fisher 1930) of older largemouth bass and select for earlier age-at-maturity at the cost of reduced somatic growth. Size-selective exploitation

of larger individuals has resulted in earlier age-at-maturity and decreased growth rates in sport fishes (Diana 1983; Drake et al. 1997) and many commercially fished species (e.g., Ricker 1981; Rijnsdorp 1993; Olsen et al. 2005). Further, high predation rates resulted in earlier age-at-maturity, smaller size-at-maturity, greater reproductive investment and fecundity, and reduced growth rates of guppies *Poecilia reticulata*; these changes in life-history traits occurred as early as within 7 generations (reviewed by Reznick and Ghalambor 2005). Coastal largemouth bass exhibit slower growth rates than freshwater populations (reviewed by Meador and Kelso 1990a), but no information on age-at-maturity exists to determine if differences in growth are due to differences in reproductive schedules or effort.

Despite the apparent negative energetic consequences of the estuarine environment, condition of largemouth bass is typically high in coastal systems (Colle et al. 1976; Guier et al. 1978; Meador and Kelso 1990a; Norris et al. 2010). Based on the standard weight equation developed for largemouth bass throughout North America (Wege and Anderson 1978), average relative weights in the Mobile Delta ranged from 83 to 105 (Norris et al. 2010) and from 83 to 152 in a Louisiana marsh (Meador and Kelso 1990a). The high body condition of coastal largemouth bass is counterintuitive given the fact that slow growth is often coupled with low condition (Wege and Anderson 1978; Gablehouse 1991; Willis et al. 1991). Further, morphometric analyses revealed that coastal largemouth bass in Louisiana had a significantly stockier body form compared to a nearby freshwater population (Meador and Kelso 1990a). These differences in morphology suggest that estuarine largemouth bass may possess a different energy allocation pattern than freshwater populations. I hypothesize that coastal largemouth bass

devote energy toward reserves as an adaptive response to the expectation of increased metabolic demands induced by salinity. Given that energy reserves are normally positively related to body condition (McComish et al. 1974; Brown and Murphy 1991; Neumann and Murphy 1992), this allocation strategy would explain the high condition factors of coastal largemouth bass despite slow growth. Energy reserves are important for many organisms during stress (Tessier et al. 1983; Olsson 1997; Kooijman 2000) and during low food availability to enhance their survival (e.g., Oliver et al. 1979; Thompson et al. 1991; Ludsin and DeVries 1997). Energy reserves also play an important role in reproductive development and behavior (Diana and Mackay 1979; Stearns 1992). Despite increased chances of survival, there is a tradeoff between allocation of energy to reserves and future fecundity due to reduced growth rates and body size (Silby and Calow 1986; Bulmer 1994; Shertzer and Ellner 2002; Garvey and Marschall 2003).

In this study, I assessed if observed slow growth and high condition indices of coastal largemouth bass were the result of an adaptive energy allocation strategy. I quantified several life-history characteristics of largemouth bass (age- and size-at-maturity, reproductive investment, energy reserves, somatic growth, survival) in habitats that vary in their abiotic (e.g., salinity) and biotic conditions (e.g., prey quantity/quality, potential competitors, and predators) along an estuarine-freshwater gradient in the Mobile Delta. An optimal annual routine (OAR) model (Fero et al. 2008), also known as state-dependent dynamic programming (Mangel and Clark 1988), was used to determine optimal energy allocation strategies among growth in length (i.e., somatic tissue), reproduction (i.e., gonads), and energy reserves (i.e., lipid stores) that maximized expected lifetime fitness while being influenced by an annual salinity regime, variable

feeding conditions, and differing probability of survival. Observed life-history characteristics were then compared with model predictions to determine if growth and condition factors of largemouth bass in estuarine systems could be the result of an adaptive energy allocation strategy.

Materials and methods

Fish collection and laboratory processing of largemouth bass

This study was conducted in the Mobile Delta (see Chapter III for a description of the study site). Largemouth bass were collected monthly (2002-2008) from 8 sites using a combination of boat and prod-pole electrofishing (Smith-Root DC electrofisher, 7.5 GPP, 7500 W) for a total of 1 h per site. All sampled age-0 largemouth bass were returned to the laboratory where they were weighed (nearest 0.01 g) and measured (nearest mm; TL). Every 3 mo from 2005 to 2008 (Jan, Apr, July, and Oct), up to 10 adult largemouth bass (\geq age-1) per site were chosen across a size range at \sim 25-mm intervals and returned to the laboratory to estimate energy within the somatic, gonad, and mesenteric fat tissues. Similar size ranges of fish were returned to the laboratory throughout the spawning period (Feb – Jun) to estimate age-at-maturity. In fall of each year (Oct, Nov, or both), all sampled largemouth bass were returned to the laboratory for age-and-growth estimates. Largemouth bass that were of intermediate size between age-0 and age-1 were returned to the laboratory for age verification. Largemouth bass not returned to the laboratory were measured (nearest mm; TL), weighed (nearest g), and released at the collection site.

Age-1 and older largemouth bass that were returned to the laboratory were measured (nearest mm; TL) and weighed (nearest g) and their saggital otoliths were

removed and stored dry for age-and-growth measurement. Gonads were removed, weighed (nearest 0.01 g), and during non-spawning months were frozen whole for later caloric determination. During spawning months, one randomly chosen lobe from each gonad was used for caloric analyses and the other was preserved in Bouin's fixative for maturity staging (below). Mesenteric fat, used as an index of available energy reserves (Brown and Murphy 2004), was removed from the viscera and along the swim bladder and dried immediately for caloric determination. After processing was complete, the whole fish (minus gonads) was frozen for later somatic caloric determination.

Energetic density of somatic tissue (i.e., whole-body minus gonads and fat), gonads, and mesenteric fat was determined using a semimicro bomb calorimeter (Parr Instrument Co., Model 1425 and Model 6725). For somatic tissue, an autoclave procedure was used to aid in obtaining a 40- to 60-g subsample prior to oven drying (Glover et al. 2010), whereas standard techniques were used to determine energetic density of gonads and fat (Rand et al. 1994). See Chapter III for additional details concerning laboratory processing of largemouth bass.

Observed growth

An extended von Bertalanffy growth curve was used to examine the effect of sex and the effect of distance upstream from Mobile Bay on growth rate parameters (Kimura 2008). I used largemouth bass collected during the fall from 2005-2008 to evaluate these effects because sex-specific information was not recorded prior to this. The general form

of the von Bertalanffy growth curve (TL) was:

$$TL = L_{\infty}(1 - \exp(-K(t - t_0)))$$

where L_{∞} is the asymptotic length, K is the growth coefficient, t is age (years), and t_0 is the theoretical age at which TL is equal to zero. TL was extended to include the linear effect of distance from Mobile Bay (d):

$$\begin{pmatrix} L_{\infty} \\ K \\ t_0 \end{pmatrix} = \begin{pmatrix} \beta_{0L} + d \cdot \beta_{1L} \\ \beta_{0K} + d \cdot \beta_{1K} \\ \beta_{0t} + d \cdot \beta_{1t} \end{pmatrix}$$

where β_{0L} , β_{0K} , and β_{0t} correspond to estimated TL growth parameters at $d = 0$, and β_{1L} , β_{1K} , and β_{1t} correspond to the effect of distance from Mobile Bay on TL . 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 (km). Sex-specific parameters were estimated simultaneously and allowed for site-specific comparisons of parameter estimates between sexes. Initial parameter estimates were specified using a grid search method to reduce the potential of converging on a local minimum within the sum of squares surface (SAS Institute 2008). Parameters were estimated using the Newton-Raphson optimization (PROC NLMIXED; SAS Institute 2008), and $\alpha = 0.05$.

Observed condition

Relative weight (W_r) was used to estimate the condition of largemouth bass (≥ 150 mm TL) by

$$W_r = 100 \cdot \frac{M}{M_s}$$

where M is the observed mass, and M_s is the standard mass for a given length. Standard

mass (M_s) was determined by

$$W_s = 2.96 \cdot 10^{-6} \cdot TL^{3.273}$$

where W_s is the standard-weight equation developed using the regression-line-percentile technique (Henson 1991).

Repeated-measures analysis of variance (RMANOVA) was used to assess the spatial and temporal trends in fish condition (PROC MIXED; SAS Institute 2008). Relative weight was first pooled across fish by determining the mean relative weight for each site, month, and year combination. RMANOVA was then used to determine if 1) relative weight was influenced by proximity to Mobile Bay, and 2) whether month influenced the slope or elevation of this relationship. A first-order autoregressive covariance structure was used to account for correlations among observations within fixed sites (SAS Institute 2008). However, several other covariance structures were evaluated (i.e., unstructured, compound symmetry, and Toeplitz covariance structures) using Akaike's Information Criterion (AIC; Akaike 1973; Burnham and Anderson 2002), all of which reduced the model fit ($\Delta AIC \geq 29.6$). Although year effects were ignored to examine general spatial and temporal trends, I assumed that error structures were heterogeneous among years and thus estimated covariance structures for each year separately. Least-squares means was used to examine where differences existed when differences were detected by the RMANOVA.

Observed annual survival rate

Age-specific abundance of all fall-collected largemouth bass was pooled across years to estimate general patterns of annual survival rate using weighted catch-curve analysis (Maceina 1997). ANCOVA was used to determine whether survival rates

differed between regions (PROC GLM; SAS Institute 2008). I also used sex-specific information from 2005 to 2008 to determine if survival rates differed between sexes or if there was an interaction between sex and region using ANCOVA.

Observed age- and size-at-maturity

Gonads that were removed from largemouth bass throughout the spawning period (Feb - Jun) were immediately preserved in Bouin's fixative for 24 h, rinsed with 70% EtOH, and then stored in a fresh solution of 70% EtOH. Preserved gonads were trimmed, dehydrated, cleared, and infiltrated with paraffin wax using Tissue Tek® automatic processor following standard histological techniques (Hinton 1990). Gonads were sectioned at 5 µm with a microtome, placed on glass slides, and stained with hematoxylin and eosin (Hinton 1990). Maturity stage was determined by histological appearance of the gonad under a compound microscope at 40x for females and 200x for males and was based on the latest stage present (James 1946; Kelley 1962; Gran 1995). Female ovaries were assigned into 6 maturation stages (i.e., primary growth, early secondary growth, vitellogenesis, final oocyte maturation, atresia, and spent), whereas male testes were assigned into 3 maturity stages (i.e., immature, mature, and spent) following Gran (1995). Although both immature and spent stages typically contain spermatogonial cells (i.e., the earliest stage of spermatogenesis indicative of immature testes), spent testes typically still contain mature sperm (James 1946). Therefore, I differentiated between immature and spent stages based on the presence of sperm.

Females in the vitellogenic or later stages (i.e., vitellogenesis, final oocyte maturation, and spent) were categorized as mature and all other stages were categorized as immature (i.e., primary growth, and early secondary growth) for analysis. Only two

female largemouth bass were categorized as undergoing atresia and were omitted from the analyses. Males in the mature or spent stage were categorized as mature and those lacking the presence of sperm were categorized as immature. Logistic regression was used to determine the effect of size and age on the odds of maturation and whether there were differences in maturation schedules between regions (PROC LOGISTIC; SAS Institute 2008). Separate analyses were performed for male and female largemouth bass.

Optimal annual routine model

I used an optimal annual routine model (OAR) to determine the energy allocation strategy that maximized expected future lifetime fitness, $F(L, r, f, t, y)$, of a female largemouth bass with length L ($L = 15, 25, \dots, 625$ mm TL), having r proportion of its maximum ovarian tissue ($r = 0, 0.15, 0.3, 0.45, 0.6, 0.65, 0.7, 0.85, 0.9, 0.95, 1$) and f proportion of its maximum energy reserves ($f = 0, 0.05, 0.1, 0.15, 0.2, 0.25, 0.4, 0.55, 0.7, 0.85, 1$) for each week ($t = 1, 2, \dots, 52$) of each year ($y = 1, 2, \dots, 10$). Optimal allocation decisions were determined for a completely freshwater environment and one in which fish experienced an average salinity regime as found in the Mobile Delta throughout their lives at different levels of annual survival rates (0.3, 0.5, and 0.7) and maximum consumption rates (0.5 and 0.6). I was primarily interested in allocation “decisions” through age-5 because largemouth bass rarely live past this age in the Mobile Delta (Norris et al. 2010). However, simulations were carried out for 10 years to reduce the potential for allocation decisions to be influenced by an artificially imposed life span (Mangel and Clark 1988).

The optimal allocation strategy was determined using backward iteration for all possible state combinations (i.e., L, r, f, t, y) to define a strategy for fish to follow using

forward iteration. For each week, an individual fish compared its expected future fitness from each possible allocation strategy ϕ [$\phi = (\phi_L, \phi_r, \phi_f)$], where ϕ_L , ϕ_r , and ϕ_f is the proportion of energy allocated to length L , ovaries r , and energy reserves f , respectively, such that $\phi_L + \phi_r + \phi_f = 1$. Weekly changes in L , r , and f were the result of net energy available (NE) after paying metabolic costs of maintenance, the proportion of energy allocated to each, and tissue-specific caloric density. The NE for allocation on any given week was determined using a bioenergetics model incorporating the metabolic cost of salinity (see Chapter III), which was a function of total mass, consumption rate, temperature, salinity, and caloric density of consumed prey ($1000 \text{ cal}\cdot\text{g}^{-1}$ in all models). Temperature and salinity conditions used in the model were average weekly values from all available data (2002-2008) within the downstream region of the Mobile Delta (Figure 4.1). Length at week $t + 1$ [$L'(\phi)$], given length L at week t was determined by

$$L'(\phi) = \begin{cases} 5.1274(0.0058L^{3.15} + NE \cdot \phi_L)^{0.3175} & \text{for } NE > 0 \\ L & \text{for } NE \leq 0 \end{cases}$$

where the 0.0058 coefficient and 3.15 exponent convert length L at week t to total calories based on relationships determined between total length and total lean body mass calories from proximate analysis data provided in Barziza and Gatlin (2000), assuming a caloric density of $5,637 \text{ cal}\cdot\text{g}^{-1}$ for protein (Brett and Groves 1979) and a negligible caloric contribution from ash and water content. The 5.1274 coefficient and 0.3175 exponent is the inverse relationship between total length and calories, which determines the new length at week $t + 1$. The proportion of maximum ovary mass at week $t + 1$ [$r'(\phi)$],

given proportion of ovary mass r and length L at week t was

$$r'(\phi) = \begin{cases} \frac{r \cdot R_{\max}(L) + \frac{NE \cdot \phi_r}{694.70 \cdot R_{\max}[L'(\phi)]^{0.2441}}}{R_{\max}[L'(\phi)]} & \text{for } NE > 0 \\ \frac{r \cdot R_{\max}(L)}{R_{\max}[L'(\phi)]} & \text{for } NE \leq 0 \end{cases}$$

where R_{\max} is the length-specific [i.e., L at week t or $L'(\phi)$ at week $t + 1$ given ϕ] maximum ovary size determined using quantile regression (PROC QUANTREG; SAS Institute 2008) based on the upper 95th percentile of ovary mass from female largemouth bass collected during the spawning period (March-May) from 2005-2008 ($R_{\max} = 0.39L - 79.81$; Figure 4.2a), and the coefficient 694.70 and exponent 0.2441 are based on the relationship between ovarian caloric density and ovary mass (Figure 4.2b). Because the R_{\max} function would produce negative maximum ovary mass for lengths less than 203 mm, I assumed that allocation decisions below this size were only between length and energy reserves (i.e., $\phi_r = 0$) and that ovary mass $R = 0$. The proportion of maximum energy reserve mass at week $t+1$ [$f'(\phi)$], given f proportion of maximum energy reserves and L length at week t was

$$f'(\phi) = \begin{cases} \frac{f \cdot F_{\max}(L) + \frac{NE \cdot \phi_f}{8,694}}{F_{\max}[L'(\phi)]} & \text{for } NE > 0 \\ \frac{f \cdot F_{\max}(L) + \frac{NE}{8,694}}{F_{\max}[L'(\phi)]} & \text{for } NE \leq 0 \end{cases}$$

where F_{\max} is the length-specific [i.e., L at week t or $L'(\phi)$ at week $t + 1$ given ϕ] maximum energy reserve mass determined using quantile regression based on the upper 95th percentile of lipid mass as a function of TL based on proximate composition data

provided in Barziza and Gatlin (2000) ($F_{\max} = 1.523 \cdot 10^{-8} L^{3.82}$; Figure 4.3), and 8,694 is the caloric density of lipids (Brett 1995). Thus, when net energy is < 0 , energy reserves are used to meet metabolic demands, whereas length and ovaries remain constant. Because some energy reserves are necessary for survival, simulated fish died if energy reserves were depleted to $f'(\phi) = 0$. Length was constrained to 625 mm, which was the maximum length determined for largemouth bass in Alabama (Beamesderfer and North 1995).

The OAR model determined the allocation strategy ϕ that maximized expected future fitness from any given week t to week $t + 1$ for each environment separately. For non-spawning weeks ($t = 1$ to 51) expected future fitness, $F(L, r, f, t, y)$, was maximized using

$$F(L, r, f, t, y) = \beta \max_{\phi} F(L'(\phi), r'(\phi), f'(\phi), t + 1, y)$$

where β is the probability of surviving from the current week t to week $t + 1$ ($\beta = \text{annual survival}^{(1/52)}$). For the spawning week of each year ($t = 52$), expected future fitness was maximized using

$$F(L, r, f, 52, y) = Q[r \cdot R_{\max}(L)] + \beta \max_{\phi} F(L'(\phi), r'(\phi), f'(\phi), 1, y + 1)$$

where Q is the number of eggs produced in a given year by a female of length L and proportion of maximum ovary reserves r , determined from fecundity data provided by Kelley (1962) as

$$Q(R) = 988.21R - 2558.1$$

where R is the ovary mass (g), which was determined as $R = r \cdot R_{\max}(L)$ in the model. This relationship explained 90% of the variation in fecundity ($F_{1,18} = 161.78$; $P < 0.001$; Figure 4.4). Because this relationship would result in negative fecundity values for fish $<$

210 mm TL based on the maximum ovary size that a fish of this size could have, females were only allowed to spawn if they were ≥ 210 mm. Further, for females to spawn, ovary mass had to be maximized for a given length (i.e., $r = 1$) and energy reserves had to be positive ($f > 0$). If these conditions were not met, females that were alive (i.e., $f > 0$) postponed spawning and transferred any gonad mass accumulated to the following year. Because gonad mass does not return to zero after spawning, I used gonads collected after spawning (June-August) from 2005-2008 to determine residual gonad mass by estimating the lower 95th percentile of gonad mass (PROC QUANTREG; SAS Institute 2008) as a function of female total length ($R = 0.0094TL - 1.8859$; Figure 4.2a). The optimal energy allocation decision that maximized expected future fitness for any given combination of L , r , and f was solved using backward iteration by searching through all possible allocation strategies at 10% increments (Mangel and Clark 1988; Feró et al. 2008). Expected future fitness for non-indexed state variables was determined using trilinear interpolation (Press et al. 1992).

When net energy available for allocation was negative, any given allocation strategy produced the same expected fitness. For these situations or any others that produced equal fitness, I forced the maximization procedure to choose to allocate all energy toward length despite the fact that only energy from energy reserves would be used to meet metabolic demands. This allocation strategy did not make a difference until fish were simulated using this allocation strategy in a different environment (see below) and net energy was then available for allocation. Although this biased the results toward growth in length, it is a conservative approach to the question of whether fish grow more slowly in a suboptimal habitat due to increased allocation toward fat.

Performance of suboptimal strategies

I used a theoretical reciprocal transplant experiment approach (Garvey and Marschall 2003) to examine the performance of fish in their suboptimal habitats relative to the optimal strategy using forward iteration. Specifically, female largemouth bass that were optimized for either a completely freshwater environment or an estuarine environment were placed in both a completely freshwater environment for one set of simulations and one in which they experienced an average annual salinity regime for their entire life in another set of simulations. The performance of fish with a given strategy was evaluated in terms of growth in length, relative weight, and expected lifetime reproductive output. Initial length was set at 23 mm, which was the mean TL of age-0 largemouth bass in April across all sites within the Mobile Delta from 2002-2008 (N = 1914). I assumed ovary mass was negligible at this length, thus set $r = 0$. I also assumed that initial energy reserves were at 10% of their maximum ($f = 0.1$), but found that overall patterns of model predictions were insensitive to initial energy reserves. Annual survival rates and ration for the forward iteration simulations were set at the level where fish were previously optimized (i.e., annual survival rate = 0.3, 0.5, or 0.7, and proportion of maximum consumption = 0.5 or 0.6). Energy allocation decisions for non-indexed states were determined using trilinear interpolation (Press et al. 1992).

Results

Observed Growth

Female asymptotic length (L_{∞}) increased with distance from Mobile Bay at a rate of $1.6 \text{ mm} \cdot \text{km}^{-1}$ ($t_{773} = 3.03$; $P = 0.003$; Figure 4.5a), whereas male L_{∞} was similar throughout the Mobile Delta ($t_{773} = 0.83$; $P = 0.41$). L_{∞} was similar between sexes at all

sites throughout the Mobile Delta, however ($t_{773} \leq 1.57$; $P \geq 0.12$). The growth coefficient (K) did not differ across distance from Mobile Bay for either sex ($t_{773} \leq 0.61$; $P = 0.54$), and was similar between sexes at all sites ($t_{773} \leq 0.37$; $P \geq 0.71$; Figure 4.5b). The theoretical age at which length was zero (t_0) increased with distance from Mobile Bay for both sexes ($t_{773} \geq 3.26$; $P \leq 0.001$) at a similar rate ($t_{773} = 0.50$; $P = 0.62$), and estimates were similar between sexes across all sampling sites ($t_{773} \leq 1.85$; $P \geq 0.07$; Figure 4.5c). This indicates that initial sizes (i.e., TL intercept at age = 0) tended to decrease with distance from Mobile Bay in a similar fashion between sexes.

Observed Condition

The relationship between relative weight and distance from Mobile Bay did not differ across months ($F_{11, 464} = 1.51$; $P = 0.13$); therefore, the interaction term was omitted from the model. The reduced RMANOVA model indicated that relative weight was influenced by distance from Mobile Bay ($F_{1, 6} = 36.26$; $P < 0.001$; Figure 4.6) and that differences in elevation existed in this relationship among months ($F_{11, 77} = 11.22$; $P < 0.001$; Figure 4.7). It was evident that the relationship between relative weight and proximity to Mobile Bay was not linear, however, and a quadratic term greatly improved the fit of the model ($\Delta AIC = 21.5$; Figure 4.6). The linear ($F_{1, 5} = 69.06$; $P < 0.001$), quadratic ($F_{1, 5} = 48.21$; $P = 0.001$), and month effects ($F_{1, 77} = 11.22$; $P < 0.001$) were all significant in the quadratic model. Relative weights adjusted for distance from Mobile Bay were highest in Oct ($t_{77} \geq 3.03$; $P \leq 0.003$), and lowest during Jan, Aug, Sep, and Dec ($t_{77} \geq 2.13$; $P \leq 0.04$; Figure 4.7). Condition was similar among Jan, Aug, Sep, and Dec ($t_{77} \leq 0.79$; $P \geq 0.43$) as well as among Feb, Mar, Apr, May, Jun, Jul, and Nov ($t_{77} \leq 1.28$; $P \geq 0.20$).

Observed annual survival rate

Annual survival rates for the upstream and downstream region were 0.54 and 0.49, respectively, and these values were not statistically different ($F_{1,14} = 1.02$; $P = 0.12$). Annual survival rate was not affected by sex ($F_{1,29} = 0.20$; $P = 0.66$) and sex-specific estimates of survival were similar between regions ($F_{1,29} = 0.25$; $P = 0.78$). Pooling age-specific abundance information across years, regions, and sexes yielded an annual survival rate estimate of 0.51 (95% C.I. = 0.47 to 0.55).

Observed age- and size-at-maturity

I assessed 465 females and 339 males for maturity stage from 2005 to 2008. Logistic regression indicated that regional differences in maturation of females did not change with size ($\chi_1^2 = 0.41$; $P = 0.52$) or age ($\chi_1^2 = 0.54$; $P = 0.46$); therefore, these interactions were removed from the model. The reduced models indicated that relative to upstream, downstream females were 8.5 times more likely to be mature at any particular age (95% C.I. = 3.5 to 20.0 times; $\chi_1^2 = 24.18$; $P < 0.001$; Figure 4.8b) and were 3.2 times more likely to be mature at any particular size (95% C.I. = 1.4 to 7.1 times; $\chi_1^2 = 8.27$; $P = 0.004$; Figure 4.8a). The predicted length at which females had a 50% chance of being mature was 233 and 216 mm TL in the upstream and downstream region, respectively.

The relationship between length or age and probability of maturity for males was not statistically different between regions ($\chi_1^2 \leq 0.91$; $P \geq 0.34$); thus, these interaction effects were omitted from the models. Downstream males were 3.14 times more likely to be mature at any given age relative to upstream (95% C.I. = 1.2 to 8.2 times; $\chi_1^2 = 5.41$; $P = 0.02$; Figure 4.8d). Length-at-maturity probabilities were similar between regions for males ($\chi_1^2 = 0.00$; $P = 0.99$; Figure 4.8c), suggesting that regional differences in age-at-

maturity was influenced mostly by growth rates. The model including only the effect of length predicted that males had a 50% chance of being mature at 201 mm TL.

Observed allocation of energy

Both the ovarian gonadosomatic index (GSI) and total ovarian energy peaked in April (Figures 4.9a and b) followed by a sharp decline after spawning. Females began rebuilding ovaries by October. There were no strong differences between regions with respect to GSI after age-1. Similar trends were seen in males (Figures 4.10a and 4.10b), however, regional differences in testicular GSI were not apparent at age-1 and gonadal investment was at least an order of magnitude lower than females.

Quarterly assessments of tissue-specific energy indicated that peaks in ovarian energy occurred simultaneously with declines in mesenteric fat energy during spring (Figure 4.11a). Reductions in somatic tissue energy also occurred concurrently with declines in mesenteric fat energy for females age-4 and older. This suggests that somatic tissue was also catabolized to meet the energetic demands of reproduction. Simultaneous changes in mesenteric fat and somatic tissue energy was also seen for males (Figure 4.11b), yet their energetic investment toward gonads was much less than females.

Optimal energy allocation

The optimal allocation of energy within the simulated freshwater and estuarine environment through life appeared to be dictated by seasonal changes in the expectation of net energy available. Specifically, a surplus of available energy occurred during spring and fall, whereas less energy was available during peak temperatures in late summer, and an energy deficit occurred during winter (Figure 4.12). The summer decline in energy and the winter deficit increased in duration and magnitude with age and size in

both environments. However, these periods were longer in duration and higher in magnitude within the estuarine environment than in the freshwater environment due to the increased metabolic expenditures related to osmoregulation. Not only were salinity levels near the peak osmoregulatory costs (~3 ppt; see Chapter 2) during these periods, but the metabolic cost of salinity also increased with size and age.

Allocation of energy for the freshwater and estuarine strategies was similar within the first year of life and was focused primarily towards growth in length (Figure 4.12). Allocation toward fat reserves and ovaries at this point depended on whether fish could reach the minimum size required to reproduce in the model (i.e., 210 mm). Using an initial length of 23 mm, ovary mass of 0 g, and energy reserves at 10% of their maximum, females reproduced within their first year of life at a 60% ration and in their second year of life at a 50% ration regardless of survival rate and environment (Figures 4.13, 4.14, and 4.15). Thus, age at first reproduction was largely growth rate dependent. Fish unable to reach the minimum size required for spawning within their first year of life diverted energy into energy reserves rather than gonads.

Within a freshwater environment, females age-1 and older at a 50% ration allocated energy toward length primarily during periods of excess energy (i.e., spring and fall; Figures 4.12, 4.13, 4.14, and 4.15). Allocation toward fat reserves occurred primarily during fall prior to the winter deficit (Figures 4.12, 4.13, 4.14, and 4.15). Most allocation toward ovary development occurred during summer and late fall, and gonad development was finalized just prior to spawning (Figures 4.12, 4.13, 4.14, and 4.15). Allocation toward ovaries occurred earlier in the year with age due to the expectation of an increased duration in winter energy deficit with size and age. The increased

availability of energy at a 60% ration allowed females to approach their asymptotic length of 625 mm TL by ~age-3 and energy was then diverted more toward energy reserves and ovary development (Figures 4.13, 4.14, and 4.15). These patterns were similar across all survival rates for the freshwater strategy.

Growth in length by the estuarine strategy was primarily focused from spring to early summer, prior to the strong reduction in available energy during late summer (Figure 4.12). Similar to the freshwater strategy, females in the estuarine environment allocated energy toward fat reserves primarily during fall to prepare for the winter energy deficit (Figures 4.12, 4.13, 4.14 and 4.15). However, the proportion of energy allocated toward fat reserves by the estuarine strategy was much higher compared to the freshwater strategy, particularly at a 50% ration. At a 60% ration energy reserves were maintained at lower levels relative to the 50% ration. Most energy for gonadal development was allocated almost immediately after spawning (Figures 4.12, 4.13, 4.14, and 4.15). As fish grew and maximum ovary size increased, energy was allocated as needed to keep ovaries near their maximum size. By spring, only a small amount of energy was required to maximize ovary mass for spawning.

Unlike the freshwater strategy, annual survival rate did affect the optimal energy allocation strategy in the estuarine environment. Specifically, as the annual survival rate increased so too did the amount of energy allocated toward energy reserves (Figures 4.13, 4.14, and 4.15). The increased allocation of energy toward fat reserves came at the cost of growth in length, but differences in growth trajectories among survival rates were inconspicuous. Although differences in growth were minimal, this strategy of decreased allocation toward growth in length increased fecundity later in life at the cost of fecundity

in the first few reproductive events given the higher probability of living to older ages. Conversely, allocation of energy toward fat reserves increased with annual survival rates because of the greater reliance upon reproductive output at older ages and enhanced the chances of surviving to the next reproductive event based on the reduced chance of depleting energy reserves. These differences were most evident at the 50% ration level.

Performance of suboptimal strategies

The expectation of experiencing an annual salinity regime increased allocation of energy toward fat reserves by female largemouth bass at the cost of growth in length relative to those optimized for a freshwater environment. Females with a freshwater strategy grew faster in length than salinity-adapted fish across all annual survival rates and ration levels when placed in either a freshwater or an estuarine environment (Figure 4.16). Salinity-adapted fish generally maintained higher age-specific relative weights than freshwater fish (Figure 4.17), due to the higher amount of energy reserves (Figure 4.18), at the cost of growth in length. The exception to this trend was at higher ration level in which freshwater fish reached the maximum length of 625 mm earlier than salinity-optimized fish (Figure 4.13, 4.14, and 4.15). Thus, freshwater fish were able to divert all available energy into either energy reserves or reproduction, increasing their relative weight, which was an artifact of the model constraints on length. It is important to note that females with the estuarine strategy were smaller in length at any particular age compared to those with a freshwater strategy, as such, length-specific differences in relative weights were even greater than depicted using age-specific differences.

Expected lifetime fitness of females possessing an estuarine strategy was 6.4 to 9.6% lower than that of a freshwater strategy when placed in a freshwater environment at

a 60% ration (Figure 4.19). These differences increased at a 50% ration and ranged from 16.7 to 19.7% lower. The larger differences were due to increased allocation of energy toward fat reserves at the cost of growth in length and fecundity by fish with the estuarine strategy. When placed in an estuarine environment, freshwater fish had at least a 60% reduction in expected lifetime fitness relative to fish optimized to an estuarine environment. Moreover, freshwater fish did not reproduce at either 30% or 50% survival rates with a 50% ration (Figure 4.19)

Missed reproductive opportunities by females possessing a freshwater allocation strategy were due to the expectation of higher and longer periods of energy availability immediately prior to spawning. Specifically, prior to spawning females in the freshwater environment typically had 4 weeks of surplus energy to finalize ovary development following the winter energy deficit. In the estuarine environment however, females only had 3 weeks prior to spawning to finalize ovary development by age-3. Therefore, fish with a freshwater strategy were unable to complete their ovary development in time to reproduce in an energy-poor estuarine environment (Figure 4.20). The surplus of energy within a freshwater environment did not pose a problem for females with an estuarine strategy as they did not miss a reproductive opportunity (Figure 4.20).

Comparison of model predictions with observed length-at-age and relative weight

Using predictions of growth trajectories from the 50% annual survival rate, a freshwater energy allocation strategy over-predicted observed female largemouth bass length-at-age when placed in either a freshwater or an estuarine environment (Figure 4.21). Likewise, the estuarine strategy over-predicted length-at-age estimates when placed in a freshwater environment at either a 50% or 60% ration, as well as in an

estuarine environment at a 60% ration. At a 50% ration, the estuarine strategy within an estuarine environment provided an excellent fit to observed female length-at-age (Figure 4.21).

Observed female largemouth bass relative weights were also best predicted by strategies in an estuarine environment at a 50% annual survival rate and 50% ration (Figure 4.22). Relative weights of females collected upstream were best depicted by a freshwater strategy, suggesting that females within the upstream region may possess an energy allocation strategy that is intermediate between a freshwater and estuarine strategy. Observed relative weights from fish collected downstream were underpredicted by the estuarine strategy (Figure 4.22), suggesting that these fish allocate even higher amounts of energy towards lipids than predicted by the optimal energy allocation models.

Using mesenteric fat as an index of the total amount of lipids, the proportion of maximum energy reserve did help explain differences in relative weights from fish collected during quarterly energy assessments (Figure 4.23). Observed relative weight increased with proportion of maximum energy reserves ($F_{1,367} = 47.16$; $P < 0.001$) at a similar rate between regions ($F_{1,367} = 0.32$; $P = 0.57$). However, downstream fish had higher relative weights for any given proportion of maximum energy reserves than upstream fish ($F_{1,367} = 58.18$; $P < 0.001$). The addition of sex or its interaction with the other variables did not help explain more of the variance in this relationship ($P > 0.05$).

Discussion

The results of my study provide important insights into the ecology of largemouth bass within coastal systems that are contrary to the “bigger is better” paradigm. From an energetics perspective, large individuals are often less susceptible to starvation because of

lower metabolic costs per unit mass (Kleiber 1932; Peters 1983) and greater capacity for energy reserves (Oliver et al. 1979; Toney and Coble 1979; Post and Evans 1989; Garvey et al. 1998) than small individuals. However, large size can actually be selected against in environments with variable or limited prey resources, because absolute energetic requirements are greater for these individuals (Wikelski et al. 1997; Blanckenhorn 2000). The results from the optimal energy allocation model suggest that there may be selective pressure against large size for largemouth bass in the Mobile Delta. Specifically, salinity-related metabolic costs increase with mass (Chapter III) and energy deficits increase in magnitude and duration with body size, due to greater absolute energetic demands with an increase in size. Allocating energy toward fat reserves not only has the benefit of being able to meet metabolic demands during periods of energy deficits, but also limits body size, which limits salinity-related metabolic expenditures. High fat reserves also provide females with extra resources to build ovaries when net energy availability is poor prior to spawning. In essence, smaller and, more precisely, fatter, is better for adult largemouth bass in brackish environments.

Reducing annual survival rates decreased allocation of energy toward fat reserves within the estuarine environment. This strategy maximized fecundity within the first few years of life through faster growth rates via higher allocation toward lean body mass, but put them at a greater risk of starvation later in life. At higher survival rates, older ages had greater influence on optimal allocation strategies, and energy reserves became more important to decrease the chance of starvation at the cost of fecundity within their first few years of life. This general finding is similar to other theoretical investigations involving unavoidable or background mortality rates. For example, defensive substances

in plants that protect against herbivory, which come at the cost of growth and reproductive output, are more likely to be produced when herbivory is high and “external” mortality is low (Janczur 2009). These general findings, although from a different perspective, are also similar to reduced rates of cellular repair with age that decrease the rate of ageing as a function of extrinsic mortality (i.e., disposable soma theory; Kirkwood 1981). Given that annual survival rate of age-1 and older largemouth bass was similar between regions in the Mobile Delta, it is unlikely that survival affected observed differences in growth rates, maximum size, and body condition from upstream to downstream.

It is important to note that I used a salinity regime averaged from 2002-2008 in the dynamic programming model to determine optimal energy allocation, which does not capture the dynamic nature of salinity from year to year. Salinity is negatively related to upstream freshwater discharge, as is peak summer water temperature and mean caloric density of consumed prey (Chapter III); thus, energetic demands are highly influenced by annual river discharge. Dynamic environments such as the Mobile Delta are predicted to select for intermediate strategies because individuals possessing strategies in either extreme direction may not fare as well over the long term (Shertzer and Ellner 2002). Yet, when simulated fish with the estuarine strategy were placed in a completely freshwater environment, expected lifetime fitness was only reduced by 6 to 20% depending on ration, whereas lifetime fitness of the freshwater strategy was reduced by 60 to 100% when placed in an estuarine environment. We would expect, therefore, that there should be stronger selection against a completely freshwater strategy than a

completely estuarine strategy even in a dynamic estuarine environment, particularly in the downstream regions of the Mobile Delta.

The extended von Bertalanffy growth curve indicated that asymptotic length increased with distance from Mobile Bay, whereas relative weights decreased with distance. Although it is difficult, if not impossible, to separate the environmental and genotypic effects with these data it is likely that the expectation of experiencing the negative energetic consequences of an estuarine environment decreases with distance from Mobile Bay. Thus, there could be a continuum of strategies along the estuarine-freshwater gradient of the Mobile Delta. The high site fidelity (Norris et al. 2005; Farmer 2008; Lowe et al. 2009) and parental care aspects of largemouth bass (Heidinger 1975) increase the likelihood of spatial segregation and could help promote such a gradient of adaptation.

Greater allocation toward lean body mass by largemouth bass with a freshwater strategy allowed them to grow faster in length and mass than those with an estuarine strategy, regardless of the environment to which they were subjected. Previous experiments found that instantaneous growth rates of largemouth bass collected from a Louisiana marsh grew significantly less in mass than those collected from a nearby freshwater system at 0 ppt (Meador and Kelso 1990a). This indicated that the fish from the brackish environment converted consumed energy less efficiently, possibly due to higher allocation toward energy-dense lipids. Coastal largemouth bass within this same experiment, however, grew faster at 8 ppt than the freshwater largemouth bass. Although contrary to my modeling results, this finding may be due to a physiological adaptation to reduce osmoregulatory expenditures at higher salinity levels by coastal largemouth bass

(Meador and Kelso 1990b; Susanto and Peterson 1996), which was not addressed with my simulations.

A strategy toward greater energy reserves may help to explain their stockier body form as has been revealed by meristics (Meador and Kelso 1990a) and the pervasive high body condition exhibited by coastal largemouth bass (Colle et al. 1976; Guier et al. 1978; Meador and Kelso 1990a; Norris et al. 2010). Underpredicted relative weights for downstream fish in the Mobile Delta by the optimal energy allocation model may be due to differences in morphometry between largemouth bass residing in freshwater and coastal systems. Specifically, the relationship between lean body mass and total length used in my optimal energy allocation model was derived from largemouth bass collected from freshwater systems in Texas (Barziza and Gatlin 2000). Differences between predicted and observed condition may have also been due to an underestimate of effects of salinity on consumption rates, given that this effect was not included in my bioenergetics model (Chapter III). Niklitschek and Secor (2009) found that consumption rates of Atlantic sturgeon (*Acipenser oxyrinchus*), albeit a euryhaline fish, were strongly depressed at salinity levels outside of their isoosmotic level. Further, I assumed a prey caloric density of $1,000 \text{ cal} \cdot \text{g}^{-1}$ for simplicity and to reduce potential circularity between model predictions and observations. Mean caloric density of consumed prey declined with age due to increased consumption of blue crabs at older ages, particularly downstream (Chapter III). Therefore, effects of the estuarine environment on net energy availability were not completely captured in my simulations and the predicted energy allocation toward fat reserves likely represents a conservative estimate.

I allowed the optimal energy allocation model to determine whether it was optimal for fish to allocate energy toward reproduction early and reproduce in their first year of life or to delay reproduction and allocate all energy to some combination of length and energy reserves. Despite differences in energy allocation with the expectation of salinity and among differing annual survival rates, females consistently reproduced at age-1 at the 60% ration level and delayed reproduction until age-2 at the 50% ration level. If females could reach 210 mm within their first year of life, which was the minimum TL required to have a positive fecundity, the simulated fish chose to receive a fitness payoff. From a theoretical standpoint, the lack of an effect due to survival was surprising given the fact that most literature documents the importance of survival rates on age-at-maturity (e.g., Grime 1977; Southwood 1988; Charnov and Berrigan 1991). My model may have underestimated the consequences of early maturation for young fish because of behavioral-related increases in metabolism related to spawning, potentially reduced viability of offspring, and a survival cost due to spawning was not included in the model. Therefore the tradeoff between age-at-maturity and growth was not strong enough to force fish to delay maturation in my simulations. Nevertheless, field observations of age-at-maturity showed a greater likelihood of earlier maturation downstream in both sexes compared to upstream fish. Given that survival rates were similar between regions, it is unlikely that survival would account for differences in age-at-maturity. Simulation results suggest that differences in age-at-maturity between regions should be mostly influenced by growth, which is supported by the observation of faster growth of young largemouth bass closer to Mobile Bay (Chapter III; Peer et al.

2006; Norris et al. 2010) and increased proportions of individuals earlier maturing individuals.

Theoretical reciprocal transplants suggested that larger, leaner fish possessing a freshwater growth strategy were unable to complete their ovary development in time for reproduction when placed in an estuarine environment due to the lack of energy availability immediately prior to spawning. Despite the growth disadvantage by simultaneously allocating energy toward growth and reproduction earlier, the estuarine strategy ensured reproductive output in the expectation of poor energetic conditions prior to spawning, similar to previous findings for white crappie (*Pomoxis annularis*) ovary development in Ohio reservoirs (Bunnell and Marschall 2003). As has been the case in previous studies (Garvey and Marschall 2003), I constrained reproduction to occur only if ovaries were maximized for a given length (i.e., $r = 1$). Yet, it is certainly possible that fish would not forego this reproductive opportunity and either spawn at that time with a presumably lower fecundity or spawn later after ovaries were completely developed. No such data exist on the necessary amount of gonad development for largemouth bass to spawn or the level at which they will forego reproduction. Moreover, it is unknown whether offspring produced from a less developed ovary would have the same viability as those from a fully developed ovary. Largemouth bass that wait to spawn until ovary development is complete may jeopardized the viability of their offspring given that earlier hatched offspring tend to have enhanced survival compared to later-hatched offspring (Miranda and Muncy 1987; Miranda and Hubbard 1994; Ludsin and DeVries 1997). Nevertheless, my results indicate that largemouth bass adapted to experiencing an average annual salinity regime can perform well in a freshwater environment, whereas

the converse does not appear to be true. The fact that numerous stockings of Florida largemouth bass *M. s. floridanus* over a 10-year period in the 1990s did not contribute to the population (Hallerman et al. 1986; Armstrong et al. 2000) supports the notion that a freshwater-adapted fish may not allocate sufficient energy toward reserves to allow it to survive periods of increased salinity and/or it may not allocate energy toward reproduction early enough to successfully reproduce. Further, Monroe County Lake, a state-managed public fishing lake in Monroe County, AL, was renovated and restocked with largemouth bass collected from the Mobile Delta in 1999. Length-at-age estimates were statistically larger for this population compared to those in the Mobile Delta at all ages (Norris et al. 2010) and largemouth bass within Monroe County Lake continue to have excellent growth rates as the population has stabilized after the initial stocking (D. Armstrong, personal communication). This is consistent with my model predictions that largemouth bass adapted to an estuarine environment can perform quite well in a completely freshwater environment.

I presented sex-specific life-history information for largemouth bass in the Mobile Delta, but was not able to determine the optimal energy allocation strategy for males due to the difficulties associated with estimating their fitness. The optimal allocation of energy among growth, reproduction, and fat reserves is likely to differ between sexes due to differences in energy requirements for gonad production (Bateman 1948; Love 1970; Shul'man 1978) and the mechanisms determining fitness and often leads to sexual size dimorphism (Blanckenhorn 2005). For example, female fecundity can be used as a surrogate measure of their fitness (Mangel and Clark 1988), yet male fitness is more difficult to quantify because of their dependency on females. For some fish species,

including many centrarchids, males provide parental care with larger males tending to be more tenacious nest guards, which can enhance offspring survival (Gross and MacMillan 1981; Wiegmann et al. 1992; Wiegmann and Baylis 1995). Larger, more fecund females typically deposit eggs into nests of larger males (Downhower et al. 1983; Goto 1987; Magnhagen and Kvarnemo 1989; Wiegmann and Baylis 1995; Wiegmann et al. 1997) and mate selection is thought to govern male body size (Blanckenhorn 2000). Thus, larger body size in terms of length and/or mass should be favored in males, similar to that of females. Although sperm is energetically less costly to produce than eggs (Bateman 1948; Love 1970; Shul'man 1978), energy costs associated with nest construction and parental care by males are exacerbated by the cessation of feeding at the onset of reproductive activity (Beeman 1924; Coble 1975; Heidinger 1975; Hinch and Collins 1991). During this time, males may abandon nests prematurely if energy reserves become depleted (Hinch and Collins 1991), jeopardizing offspring survival. I argue that energy allocation in males is likely governed by a similar trade-off among growth, fecundity (measured as number of surviving offspring deposited in a nest), and survival. If true, then we would expect higher allocation toward fat reserves by male largemouth bass adapted to brackish environments compared to those adapted to freshwater environments as seen in females.

Garvey and Marschall (2003) used a state-dynamic programming approach to explore optimal energy allocation of largemouth bass along a latitudinal gradient to help explain patterns of body size that are counter to expectations based on Bergmann's rule. Results from theoretical reciprocal transplants of modeled fish in my study were similar to those of Garvey and Marschall (2003). Together, these results offer some general

insights into the importance of locally adapted energy allocation strategies. In general, fish optimized to a cooler northern climate tended to allocate higher proportions of energy towards energy reserves at the cost of growth in length when compared with those possessing a strategy for a warmer southern climate in which net energy intake was higher due to temperature-related consumption, albeit at a greater metabolic cost (Garvey and Marschall 2003). Fish possessing the northern strategy also allocated energy toward reproduction earlier in the year than the southern largemouth bass. Although fish from the northern climate were able to perform well in a southern climate, southern fish performed poorly in terms of expected lifetime reproductive output in an energy-poor northern climate. Therefore, when net energy is limited or variable, either through decreased resource acquisition (temperature- or prey-dependent) or increased metabolic demands (e.g., salinity-related metabolism), a higher allocation of resources toward energy reserves to meet future metabolic demands and for reproduction should be expected. Findings by Adams et al. (1982) mirror these predictions in which age-2 largemouth bass allocated energy toward energy reserves primarily during summer and fall periods of high consumption, which allowed them to maintain good condition throughout the year despite a seasonally fluctuating prey base. Although individuals that possess an energy allocation strategy favoring high energy reserves may have a growth disadvantage in length or overall mass compared to those allocating greater amounts of energy toward lean body mass, they should be able to perform well in terms of growth and reproductive output in environments that have a stable surplus of resources. However, individuals that do not allocate enough energy to storage are at risk of starvation, may even forego reproductive opportunities, and their offspring viability may

be jeopardized (e.g., by spawning at a less than fully-developed ovary or due to nest abandonment) when placed in environments of variable or less than expected energy.

Recently, much attention has been given to the potential effects of stocking locally adapted black bass outside of their native range (Kassler et al. 2002; Leitner et al. 2002; Philipp et al. 2002). The results of this study and those from Garvey and Marschall (2003) suggest that local adaptations in environments with abundant prey resources or low energetic demands are incompatible with environments that have low prey resources or high energetic demands. Therefore, largemouth bass adapted to environments with poor prey resources or high energetic demands may pose more of a conservation threat if considered for stocking in areas with other locally adapted largemouth bass through outbreeding depression (Philipp et al. 2002).

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Table 2.1 Piecewise regression model selection results displaying the number of knots, sample size (N), number of parameters (k), degrees of freedom (df), sum of squared errors (SSE), and Bayesian Information Criterion (BIC) for each model tested.

Model	Number of knots	N	k	df	SSE	BIC
#1	0	45	2	43	1715498.66	10.72
#2	1	45	4	41	932871.72	10.28
#3	2	45	6	39	816646.72	10.31
#4	3	45	8	37	781087.50	10.44

Table 3.1 Region-specific start and end mass (g) for each cohort used in bioenergetics simulations and estimated proportion of maximum consumption (C_{\max}) for the three different simulation scenarios. The upstream region included Tensaw Lake, McReynold's Lake, Dennis Lake, and Gravine Island, whereas the downstream region included Big Bayou Canot, Crab Creek, Bay Minette, and D'Olive Bay (Figure 3.1).

Region	Cohort	Start mass (g)	End mass (g)	Estimated proportion of C_{\max}		
				Low discharge	Average discharge	High discharge
Upstream	Age-1	91	222	0.455739	0.426273	0.438293
	Age-2	222	385	0.471454	0.451034	0.423815
	Age-3	385	560	0.525982	0.485565	0.430338
	Age-4	560	730	0.431238	0.439978	0.457592
	Age-5	730	885	0.433403	0.447981	0.455346
Downstream	Age-1	174	283	0.533151	0.524057	0.465972
	Age-2	283	417	0.556426	0.571298	0.530327
	Age-3	417	573	0.625044	0.602087	0.560420
	Age-4	573	746	0.646347	0.649218	0.565784
	Age-5	746	933	0.666688	0.652868	0.554538

Table 3.2. 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 for energetic values.

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

Table 3.3 Model selection results for the respirometry experiment to test for the effect of salinity on specific respiration rates, with the description of the effect of salinity on respiration, number of parameters (k) including the estimate of σ^2 , Akaike's information criterion corrected for small sample size (AIC_c), the difference in AIC_c values from the best model (Δ_i), likelihood of the model (l_i), Akaike weight of the model (w_i), and the evidence ratio for each model. Models are sorted from best to worst as indicated by AIC_c . See text for definitions of equation symbols.

Function	Effect of salinity	k	AIC_c	Δ_i	l_i	w_i	Evidence ratio
$RA \cdot M^{RB} \cdot e^{RS(\text{salinity} \cdot (\text{salinity} \cdot X)^2)} \cdot e^{RQ \cdot \text{temp}}$	Cubic effect, mass-dependent	6	442.00	0.00	1.00	0.43	1.00
$RA \cdot M^{RB} \cdot e^{RQ \cdot \text{temp} + RS(\text{salinity} \cdot (\text{salinity} \cdot X)^2)}$	Cubic effect, additive to temperature	6	442.80	0.80	0.67	0.29	1.49
$RA \cdot M^{RB} \cdot e^{RQ \cdot \text{temp}}$	No effect	4	445.30	3.30	0.19	0.08	5.21
$RA \cdot M^{RB} \cdot e^{RQ \cdot \text{temp} + RS \cdot \text{salinity} + RST \cdot \text{salinity} \cdot \text{temp}} \cdot e^{RQ \cdot \text{temp}}$	Mass- and temperature-dependent	6	445.80	3.80	0.15	0.06	6.69
$RA \cdot M^{RB} \cdot e^{RQ \cdot \text{temp} + RS \cdot \text{salinity}}$	Additive to temperature	5	446.30	4.30	0.12	0.05	8.58
$RA \cdot M^{RB} \cdot e^{RQ \cdot \text{temp} + RS \cdot \text{salinity}} \cdot e^{RQ \cdot \text{temp}}$	Mass-dependent	5	446.30	4.30	0.12	0.05	8.58
$RA \cdot M^{RB} \cdot e^{RQ \cdot \text{temp} + RS \cdot \text{salinity} + RST \cdot \text{salinity} \cdot \text{temp}}$	Temperature-dependent	6	447.00	5.00	0.08	0.04	12.18

Table 3.4. Parameter estimates from the best model (model 7, Table 3.2) describing the effects of salinity on specific respiration rates ($\text{mg O}_2 \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) for largemouth bass, along with SE of the estimate, df, the t -value, and probability of having a higher absolute t -value (P) given the df. See text for definitions of parameter symbols.

Parameter	Estimate	SE	df	t	P
RA	3.774	1.079	120	3.50	<0.001
RB	-0.239	0.046	120	-5.24	<0.001
RQ	0.038	0.008	120	4.86	<0.001
RS	-0.002	0.001	120	-2.40	0.018
X	9.300	0.414	120	22.49	<0.001

Table 3.5. Results of the projected growth under three different simulated scenarios showing the time required to reach 2.3 kg, the estimated annual survival rate from the weighted catch-curve analysis, number (N) per 1,000 fish that is expected to reach this size within the required time based on annual survival rates (S), and the mass (kg) attained at the end of age-9. A dash indicates that the simulated largemouth bass did not reach 2.3 kg.

Region	Discharge	Time to 2.3 kg (yrs)	S	N per 1,000	Mass after 10 y (kg)
Observed conditions					
Upstream	Low	-	0.54	-	1.36
	Average	-	0.54	-	1.37
	High	-	0.54	-	1.41
Downstream	Low	-	0.48	-	1.41
	Average	-	0.48	-	1.41
	High	-	0.48	-	1.50
Salinity removed					
Upstream	Low	8.33	0.54	6	2.21
	Average	8.57	0.54	5	2.14
	High	-	0.54	-	1.41
Downstream	Low	5.15	0.48	23	5.70
	Average	4.59	0.48	35	6.65
	High	6.57	0.48	8	3.26
Blue crabs removed (switched to fish)					
Upstream	Low	5.23	0.54	40	3.49
	Average	5.46	0.54	35	4.12
	High	5.24	0.54	40	7.39
Downstream	Low	4.14	0.48	48	11.74
	Average	4.12	0.48	48	13.03
	High	3.50	0.48	77	13.13

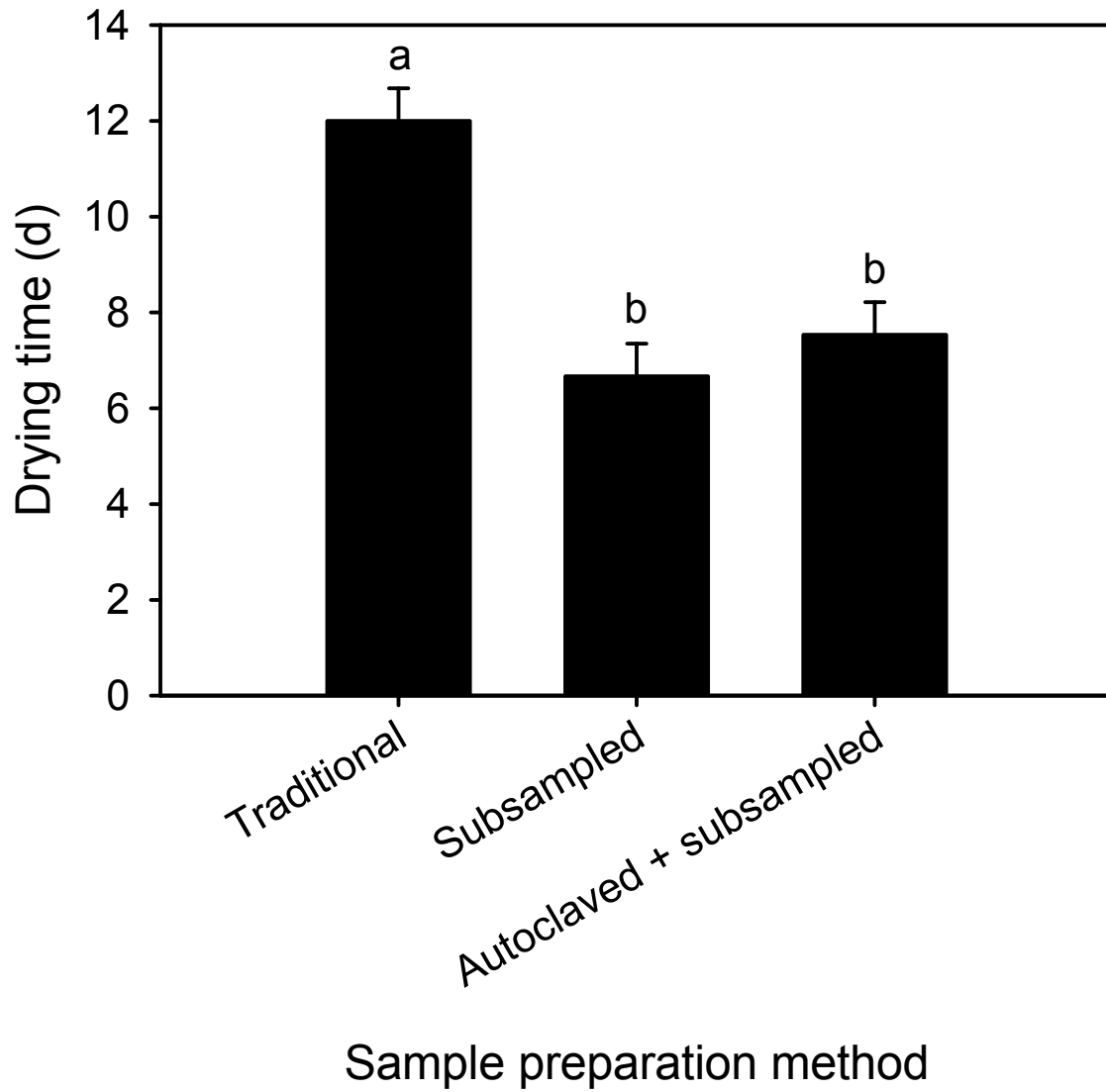


Figure 2.1

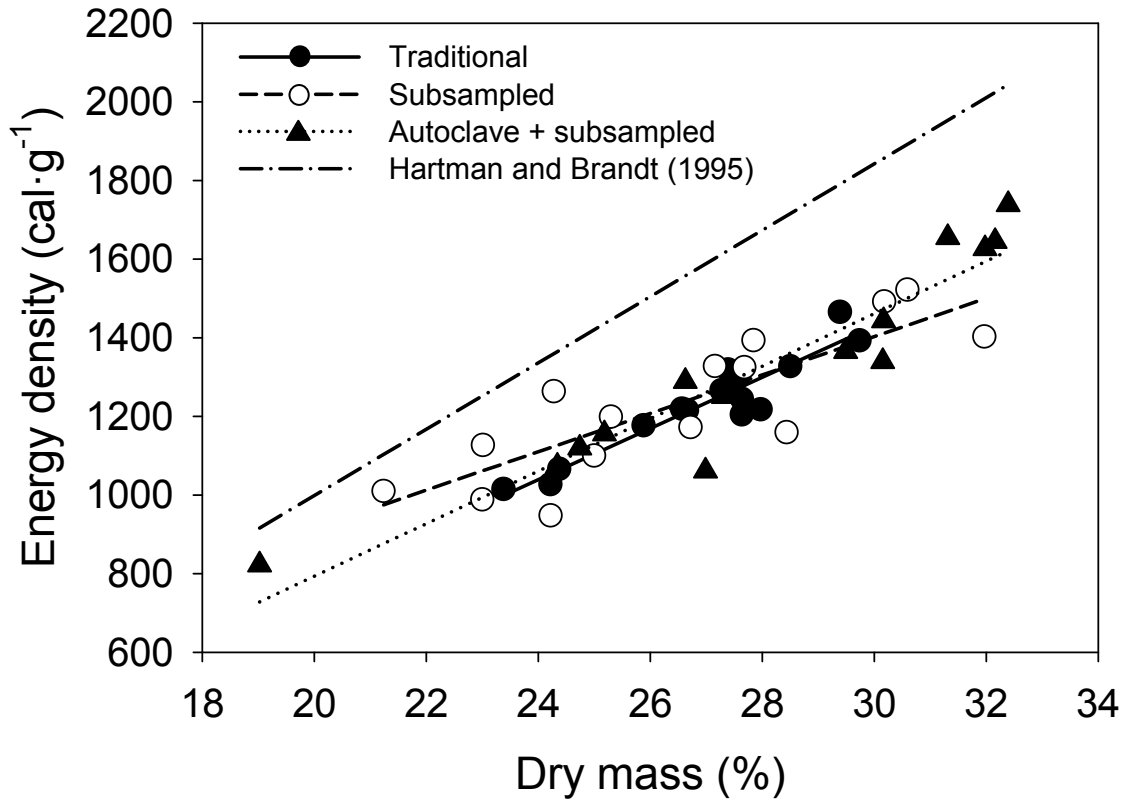


Figure 2.2

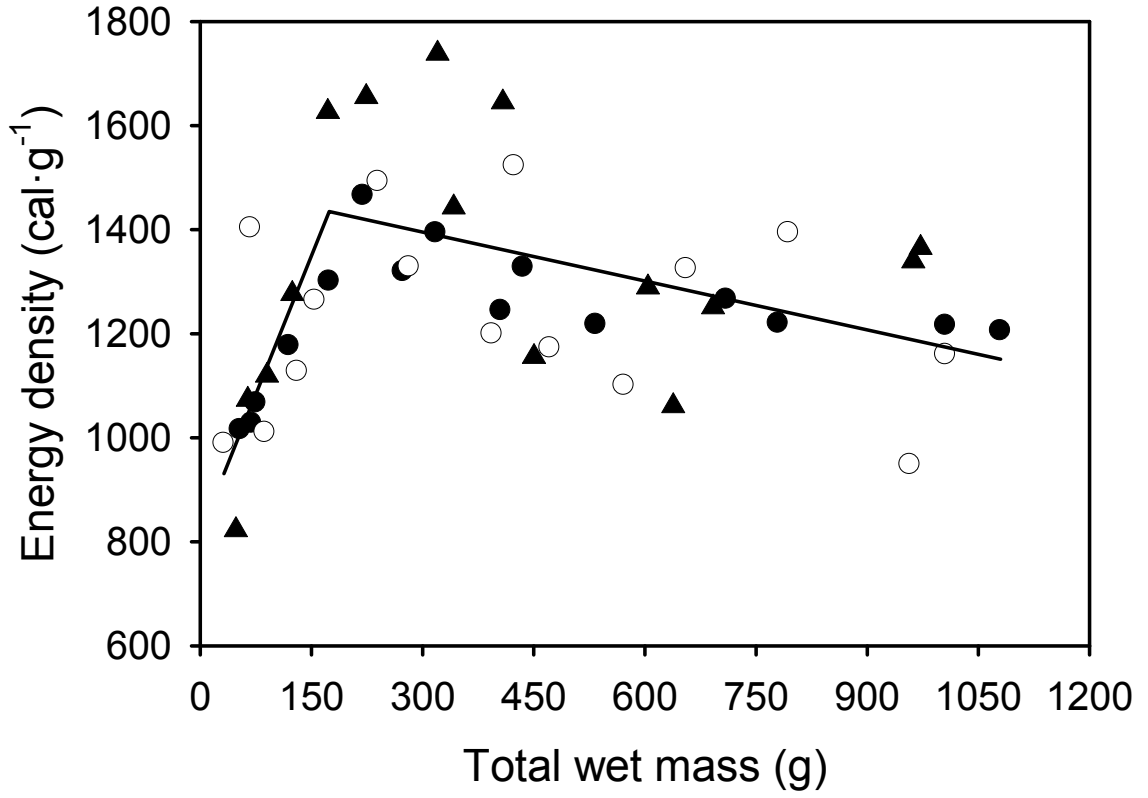


Figure 2.3

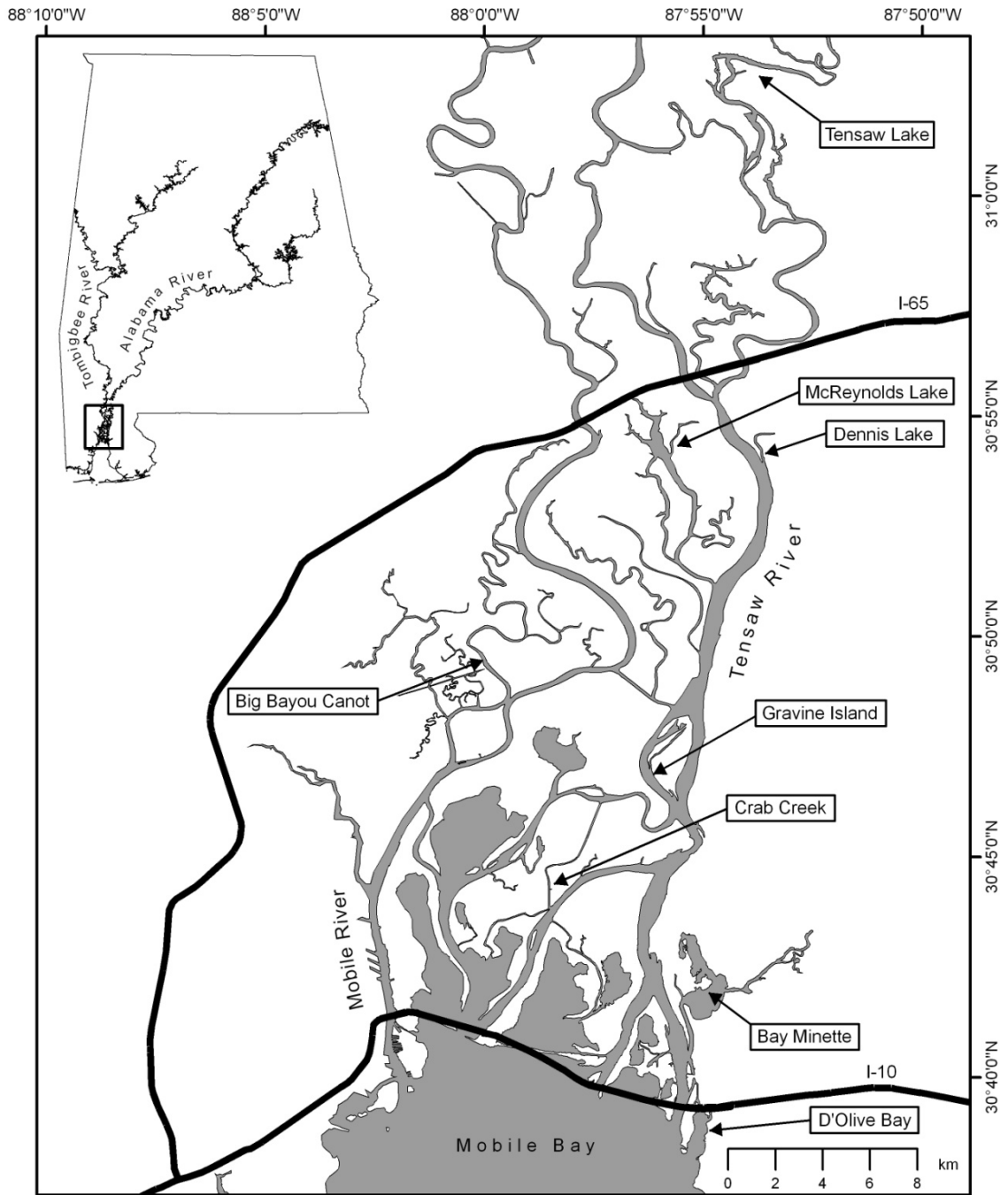


Figure 3.1

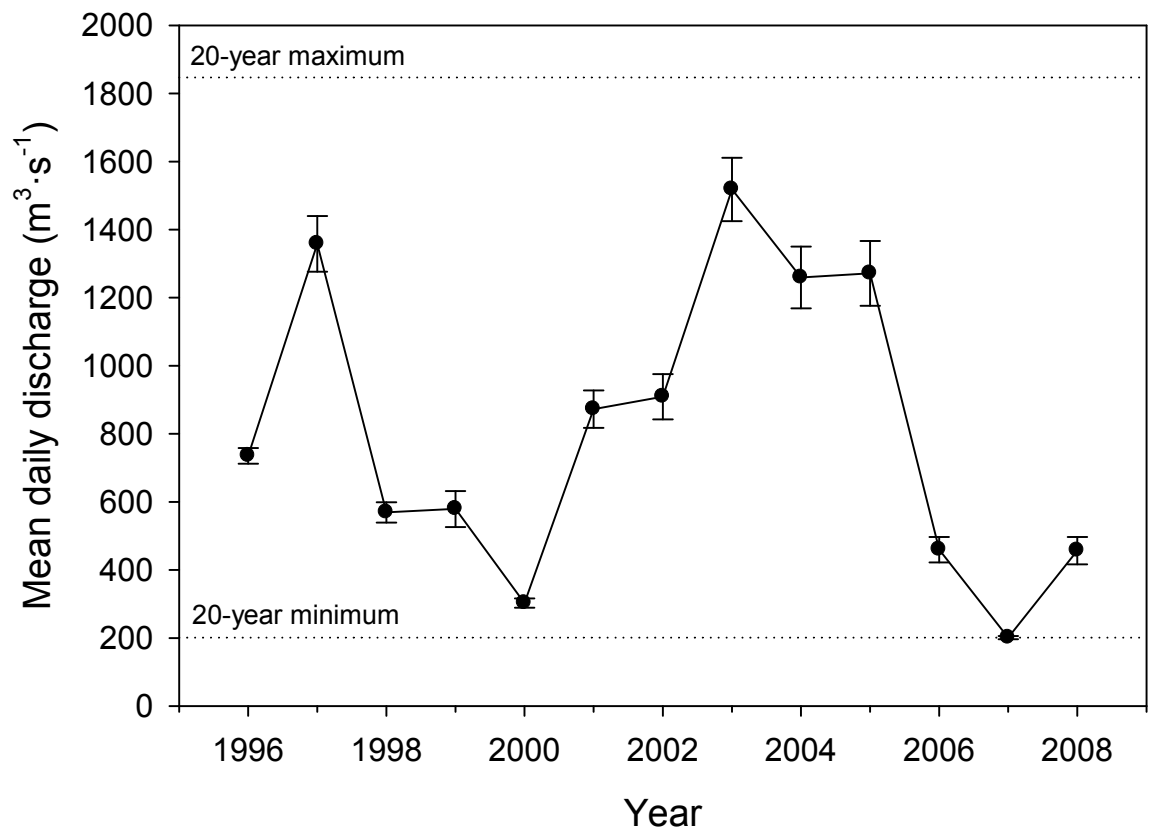


Figure 3.2

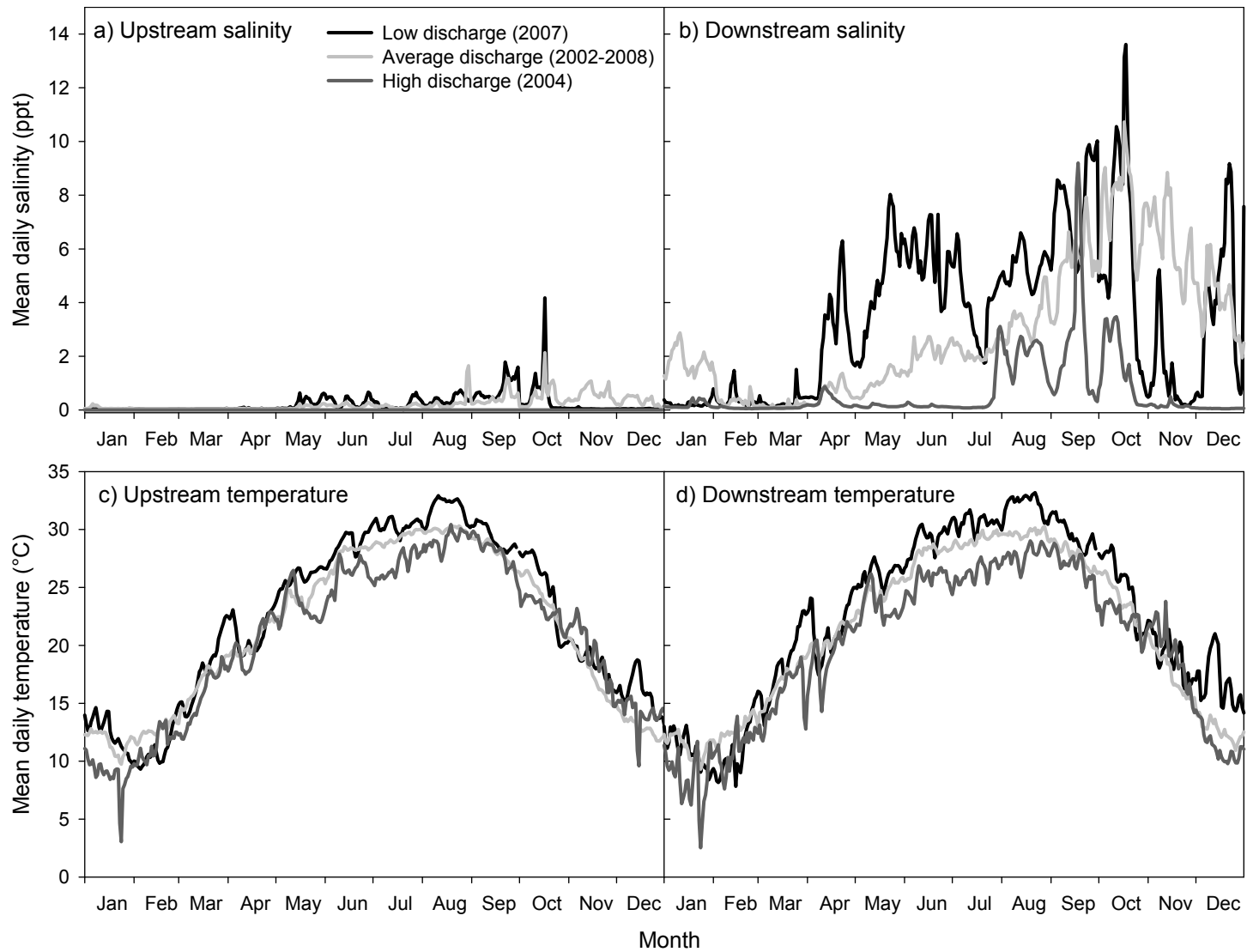


Figure 3.3

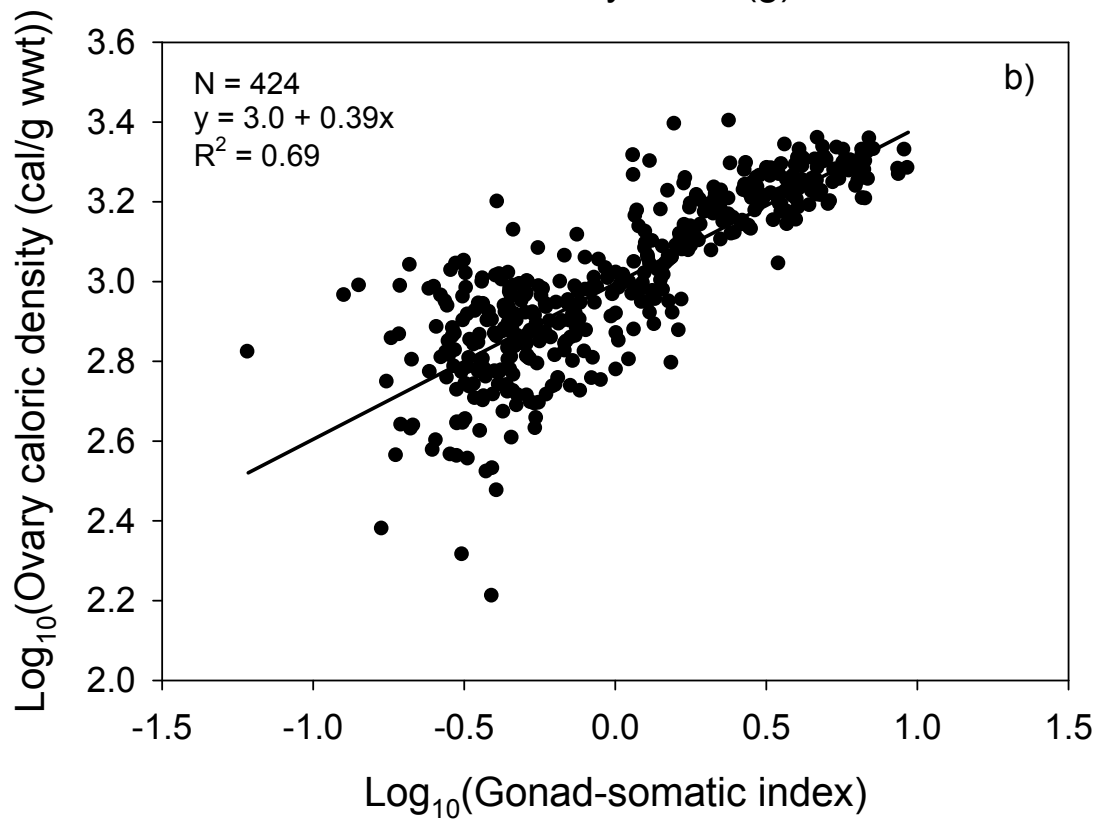
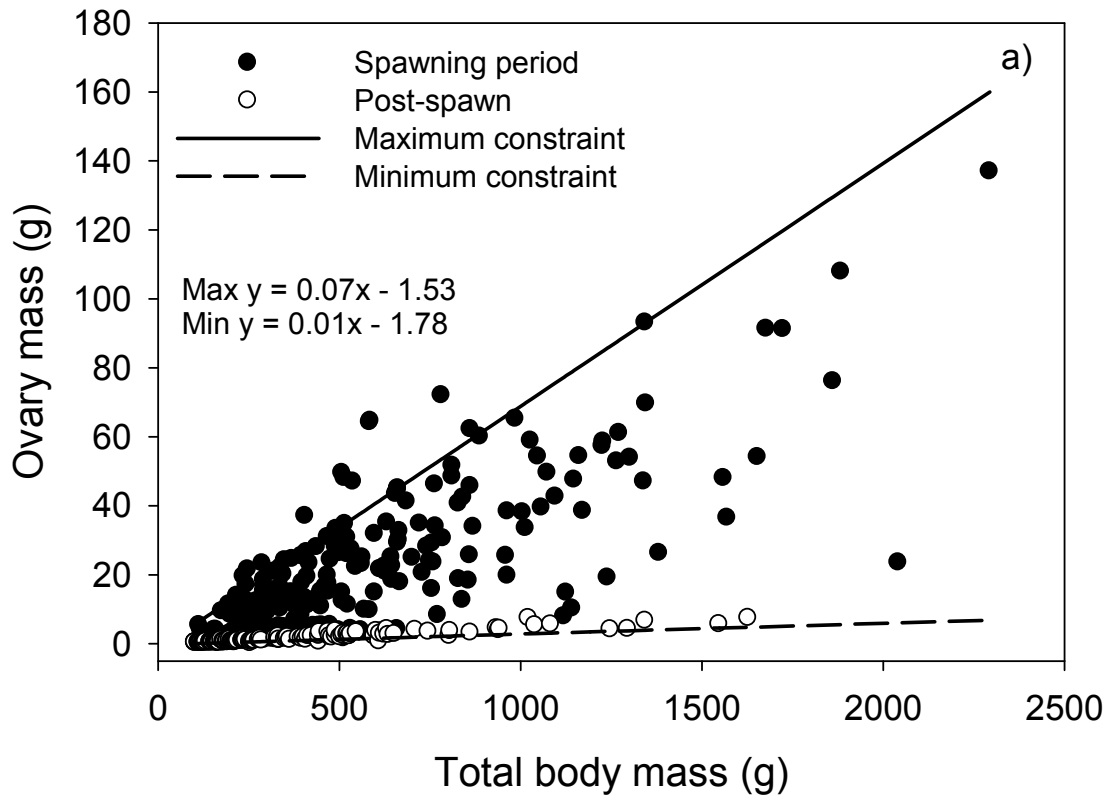


Figure 3.4

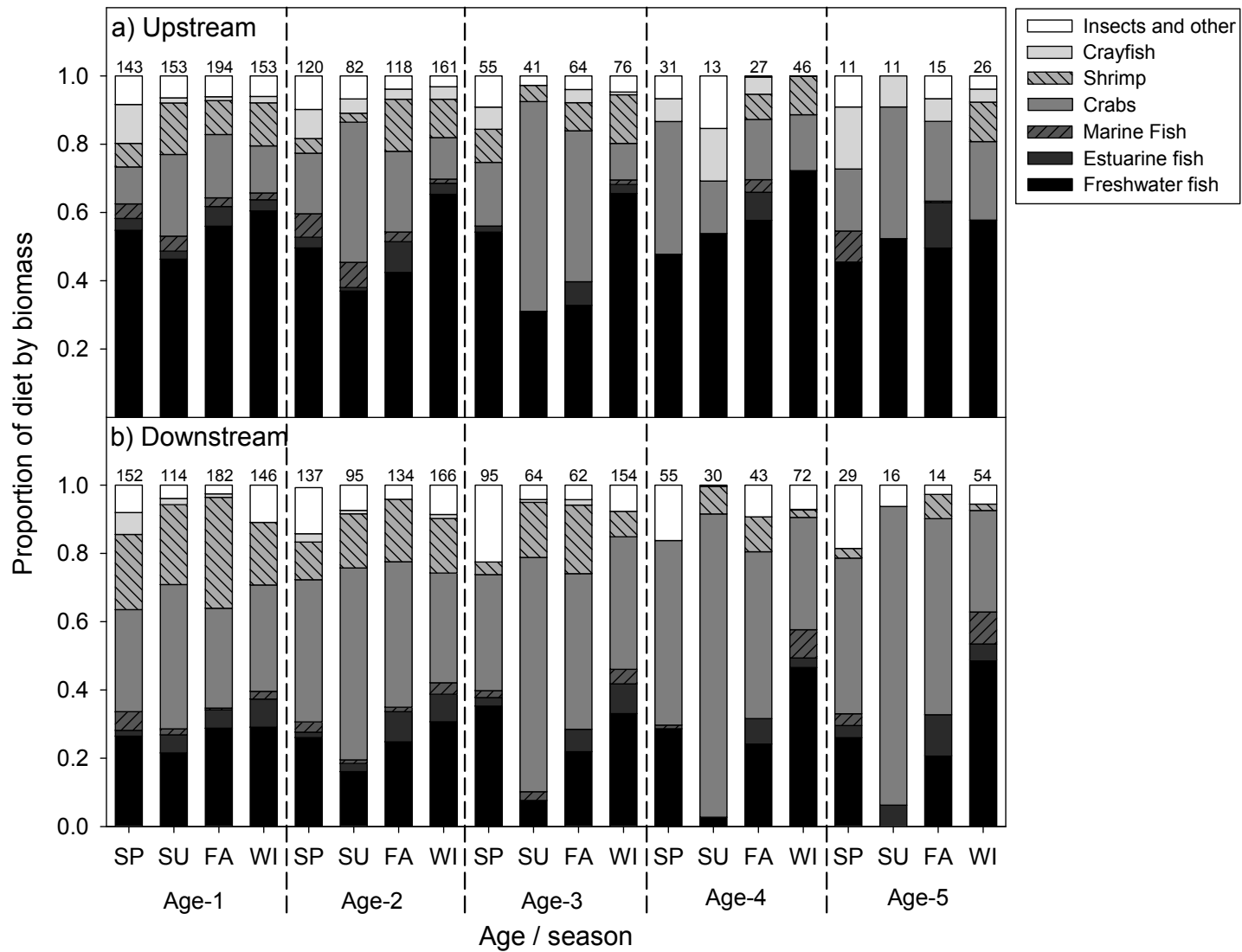


Figure 3.5

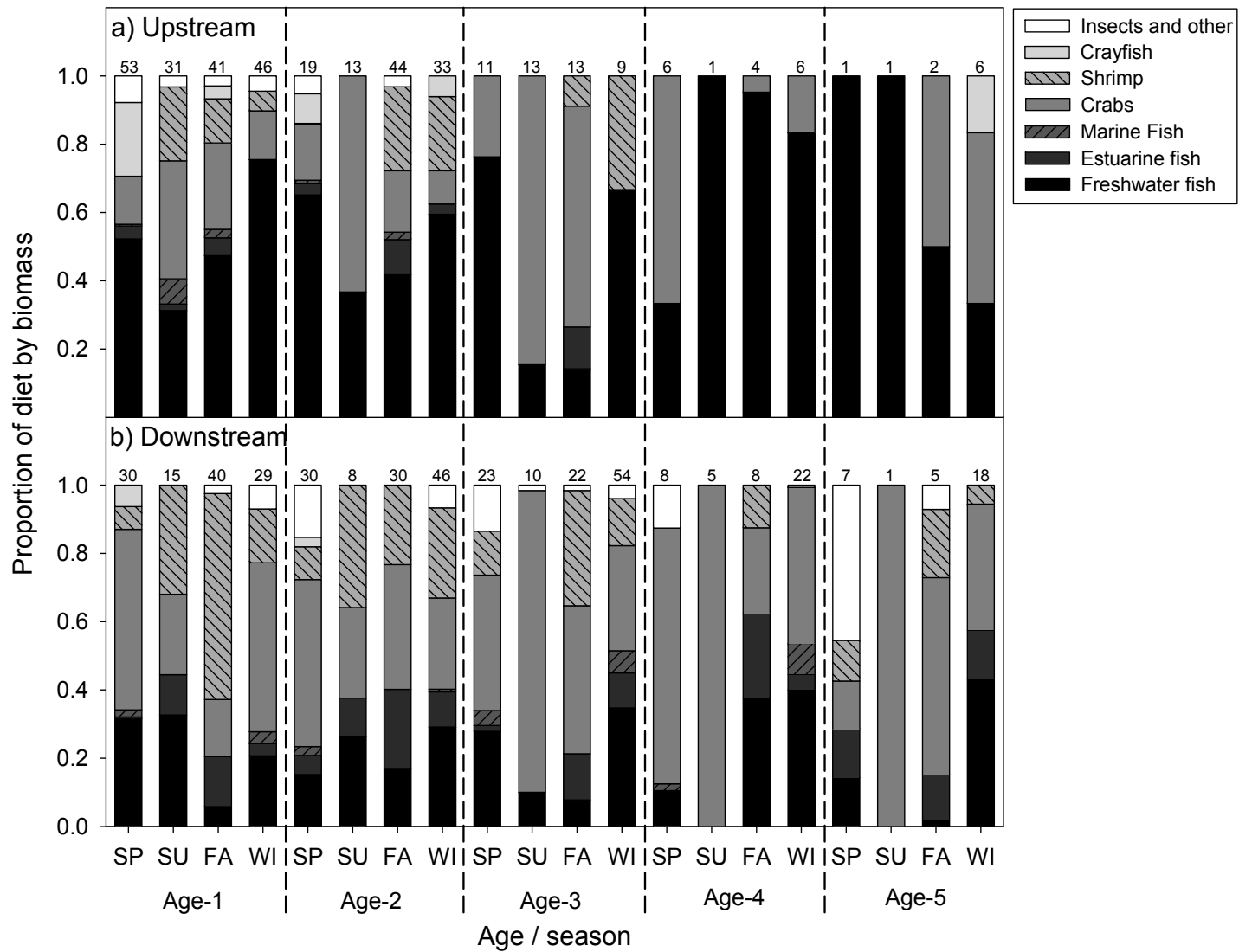


Figure 3.6

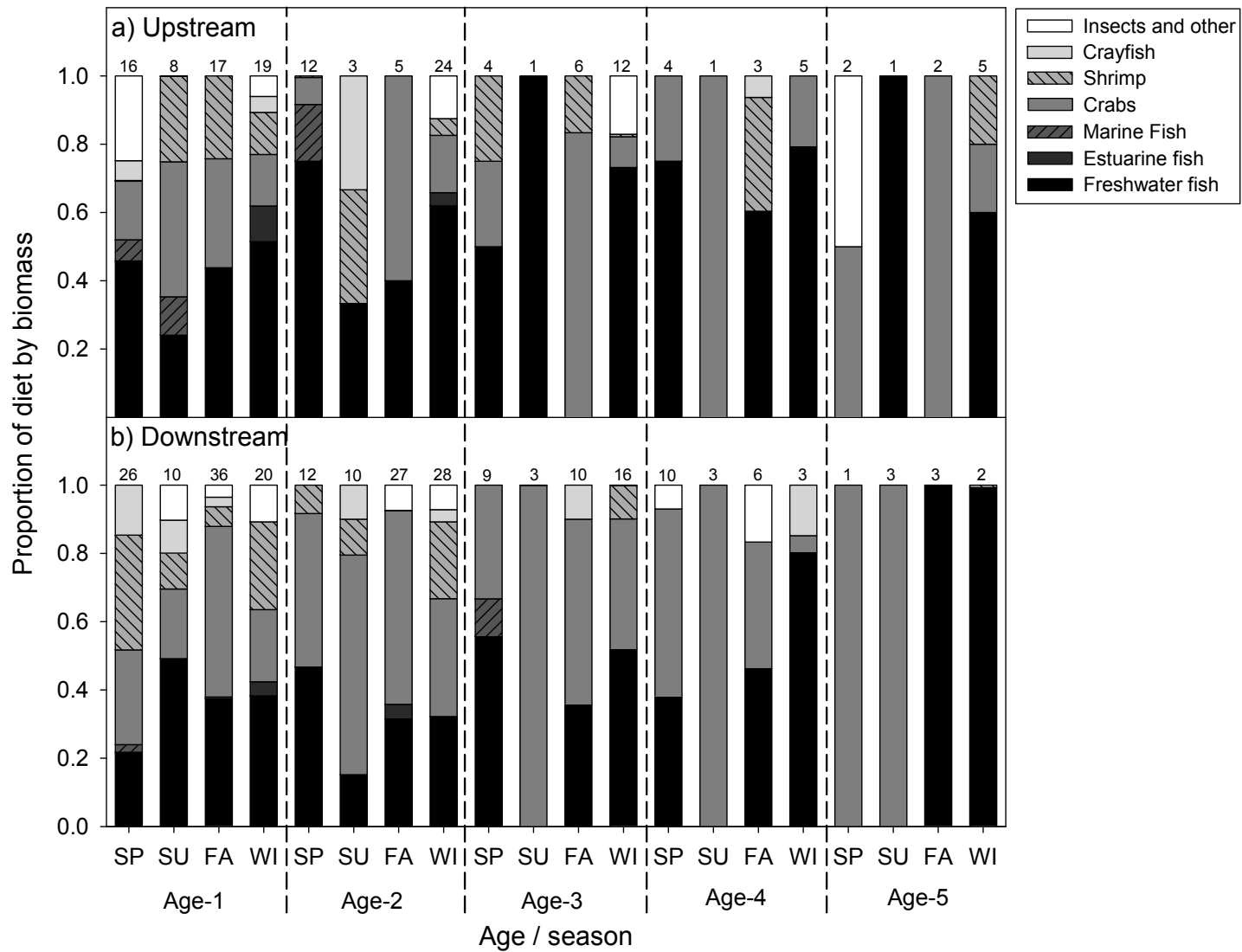


Figure 3.7

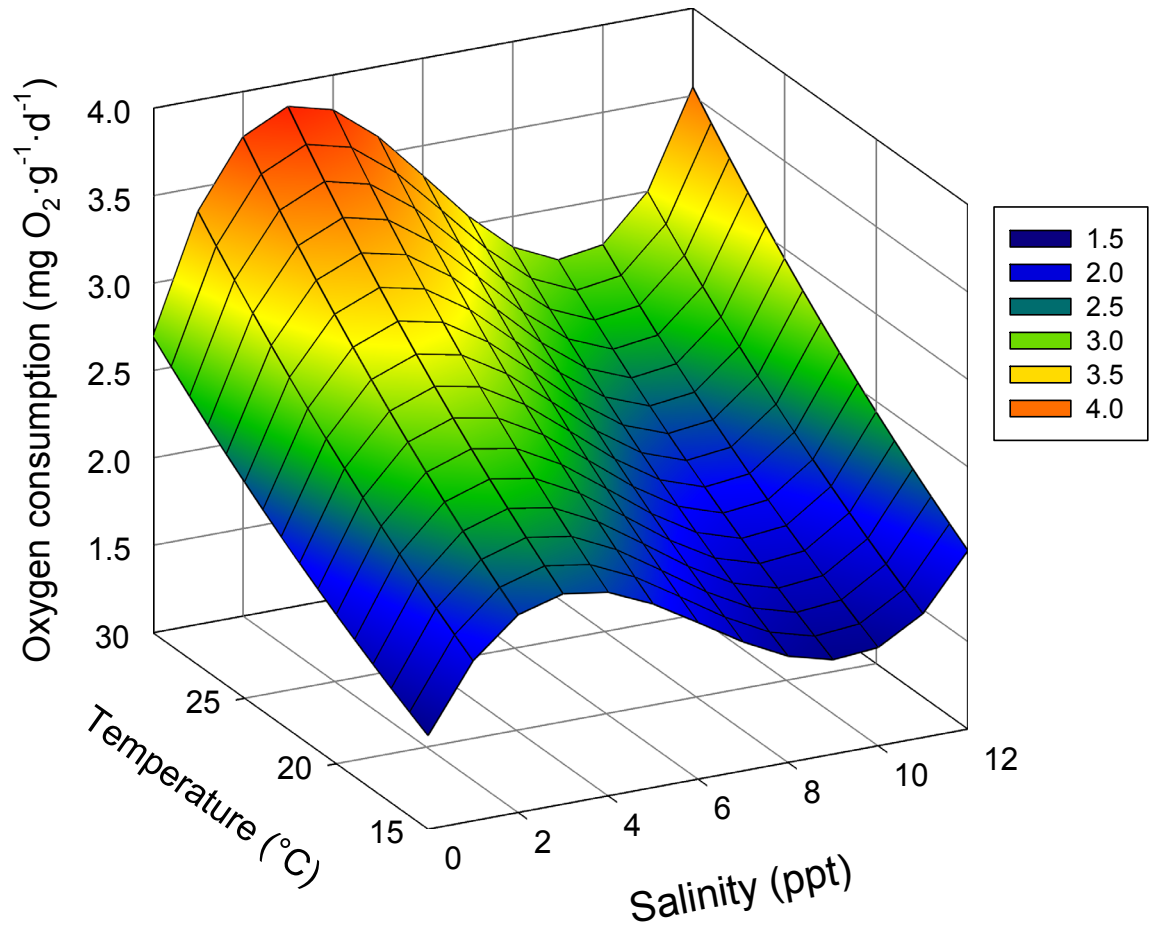


Figure 3.8

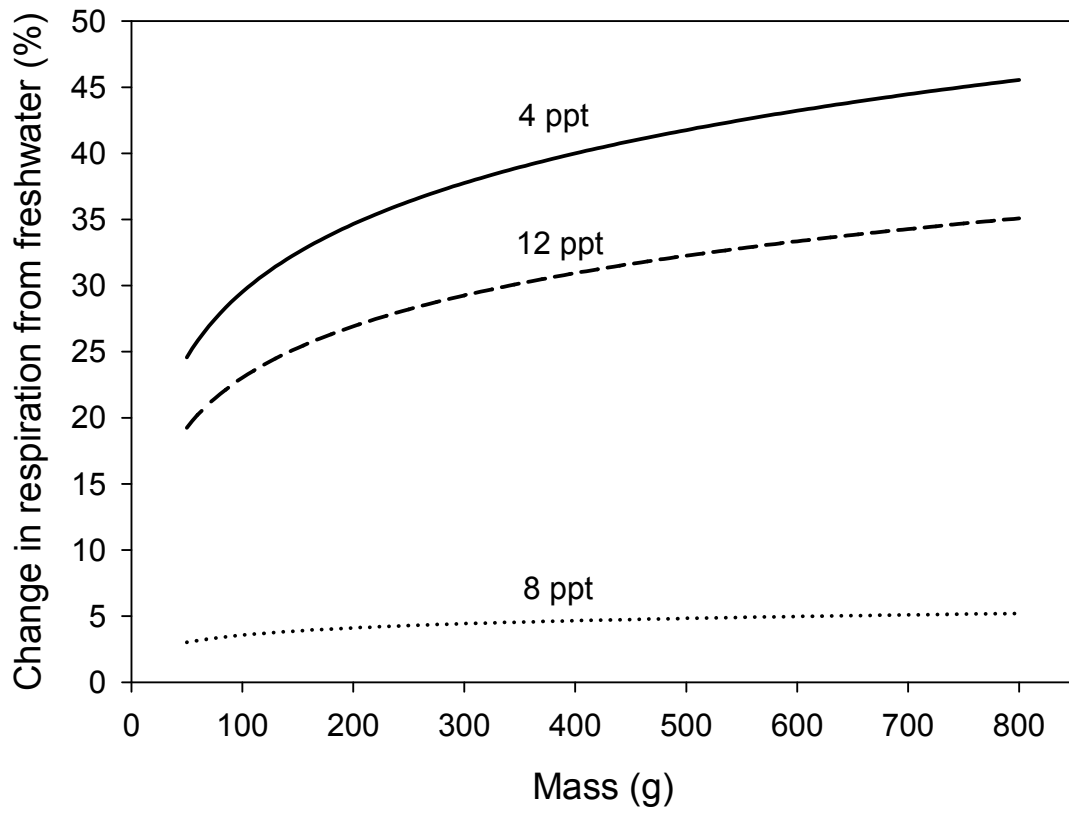


Figure 3.9

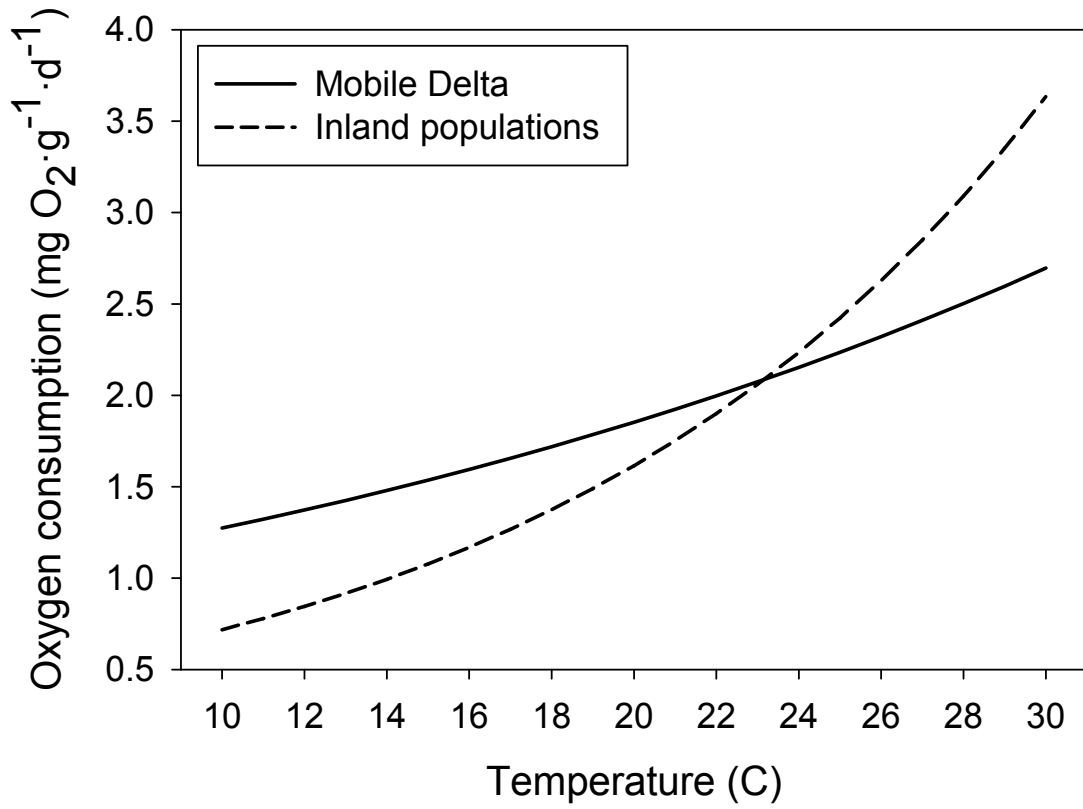


Figure 3.10

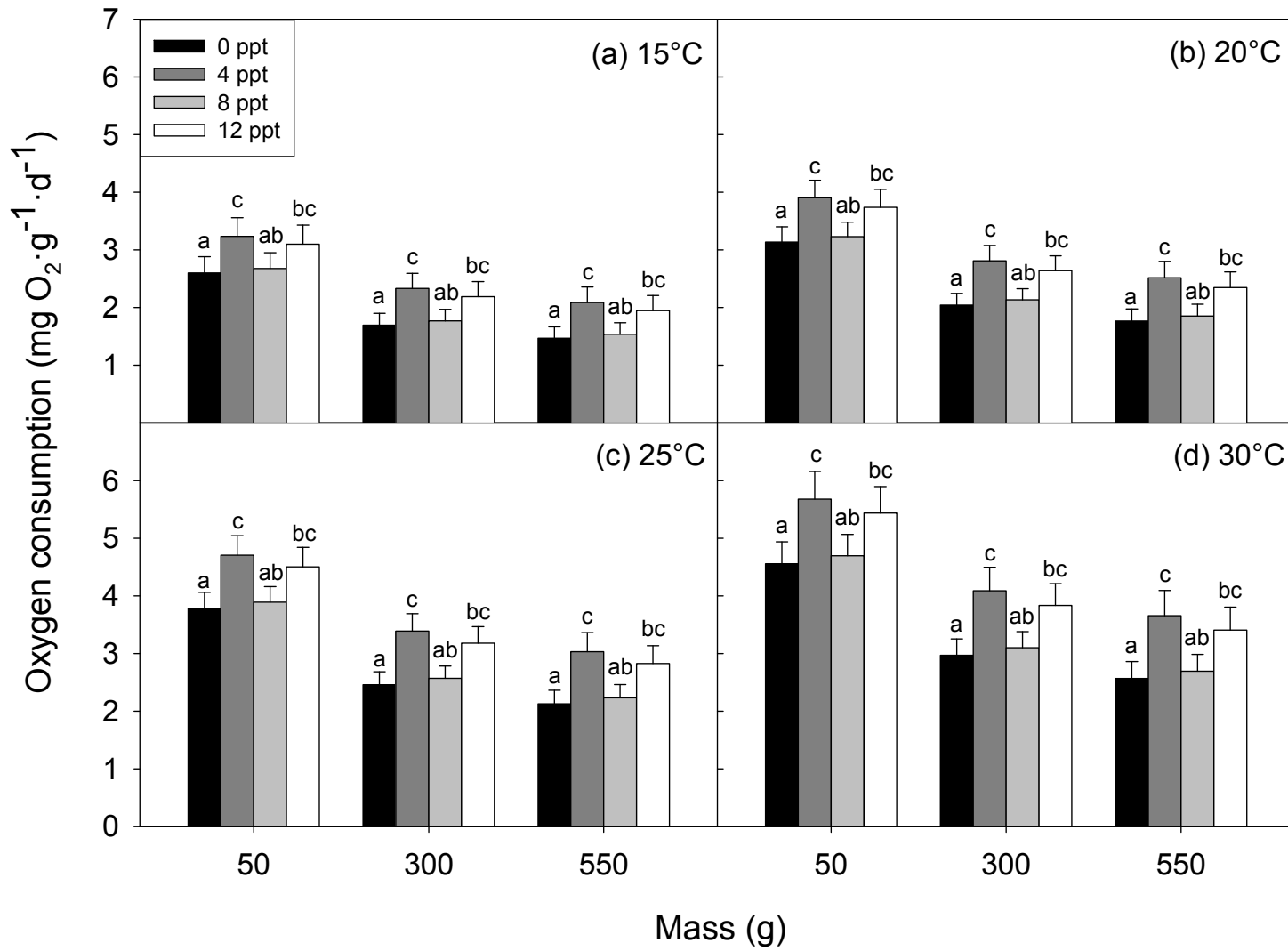


Figure 3.11

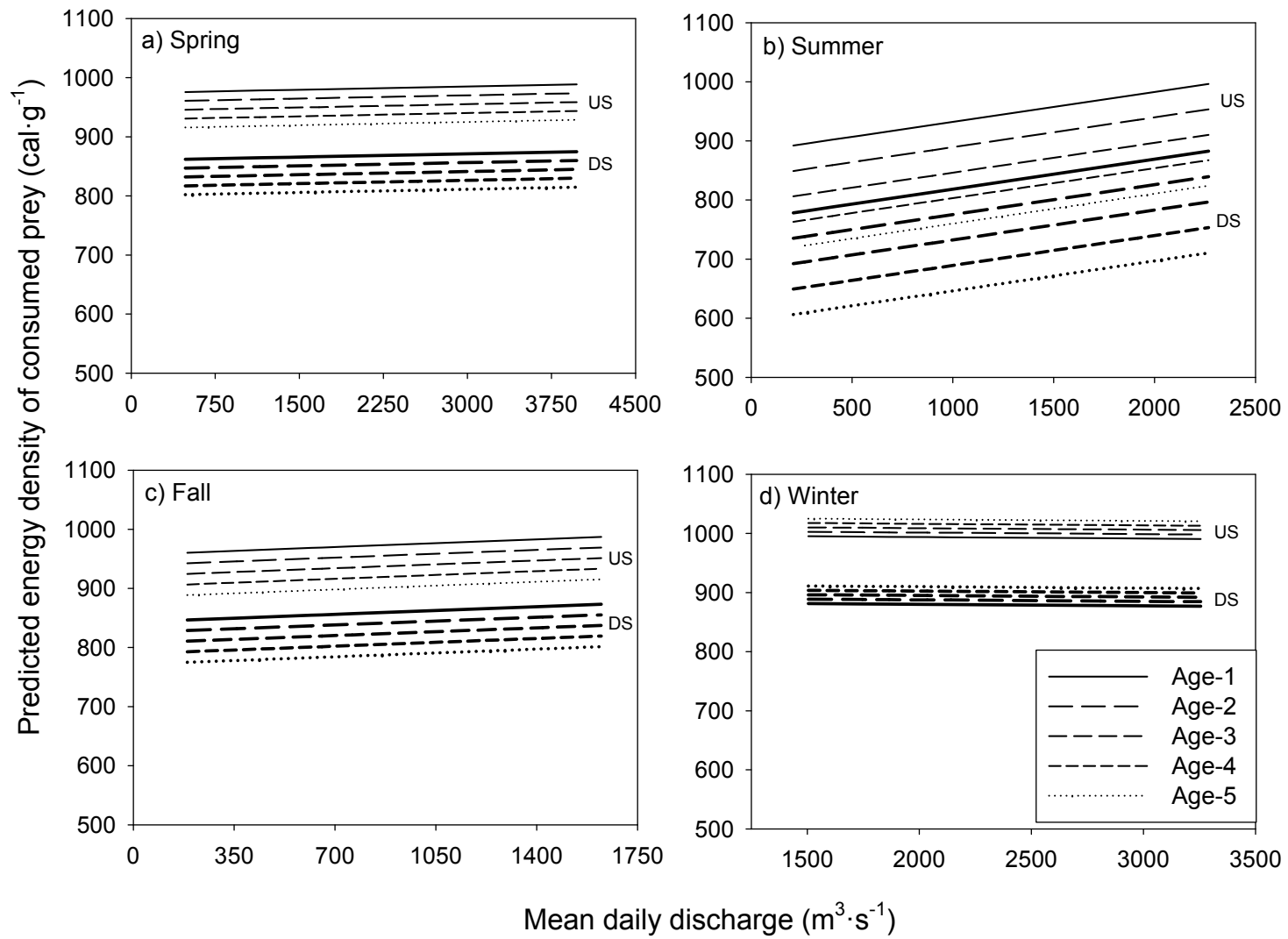


Figure 3.12

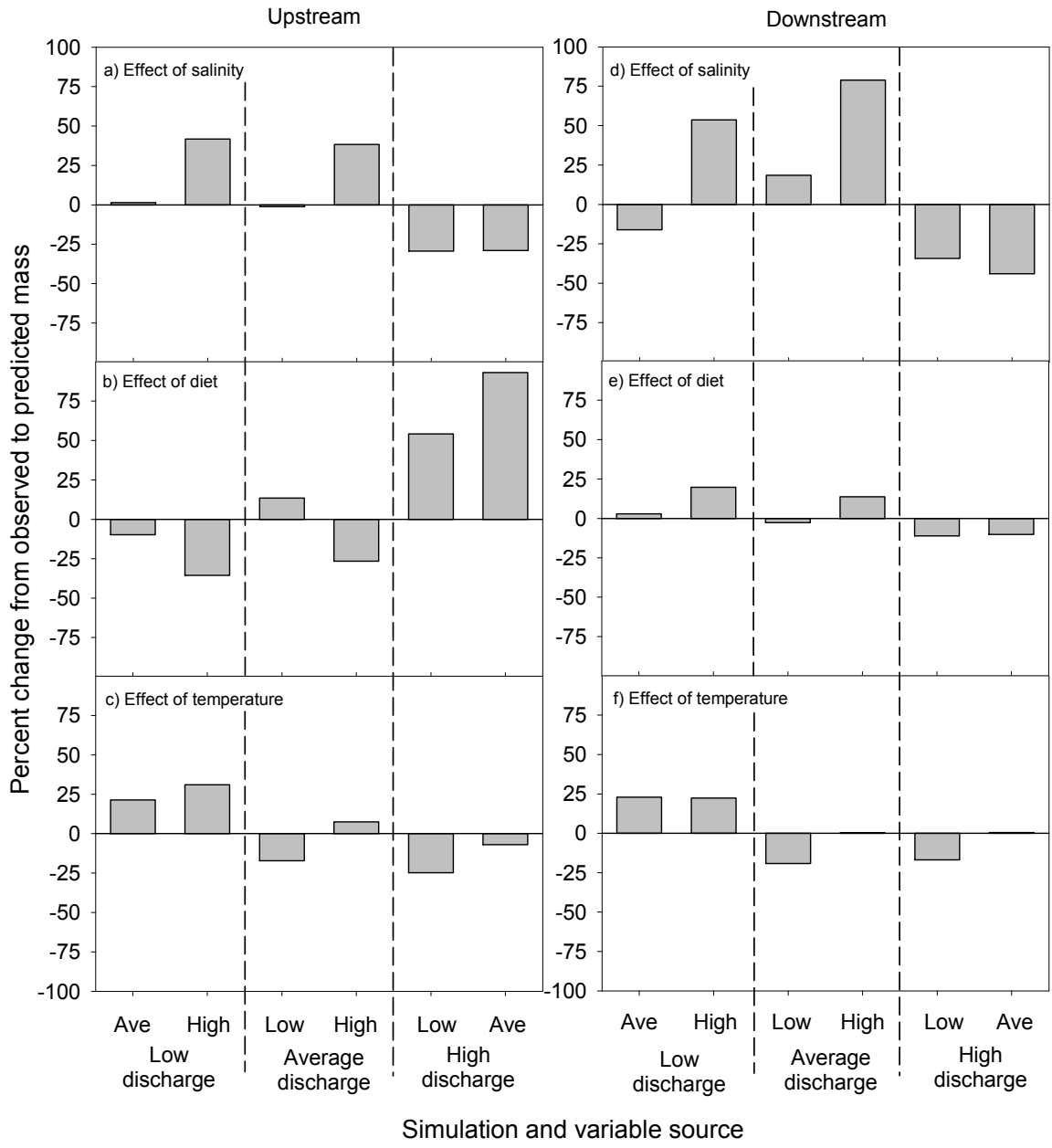


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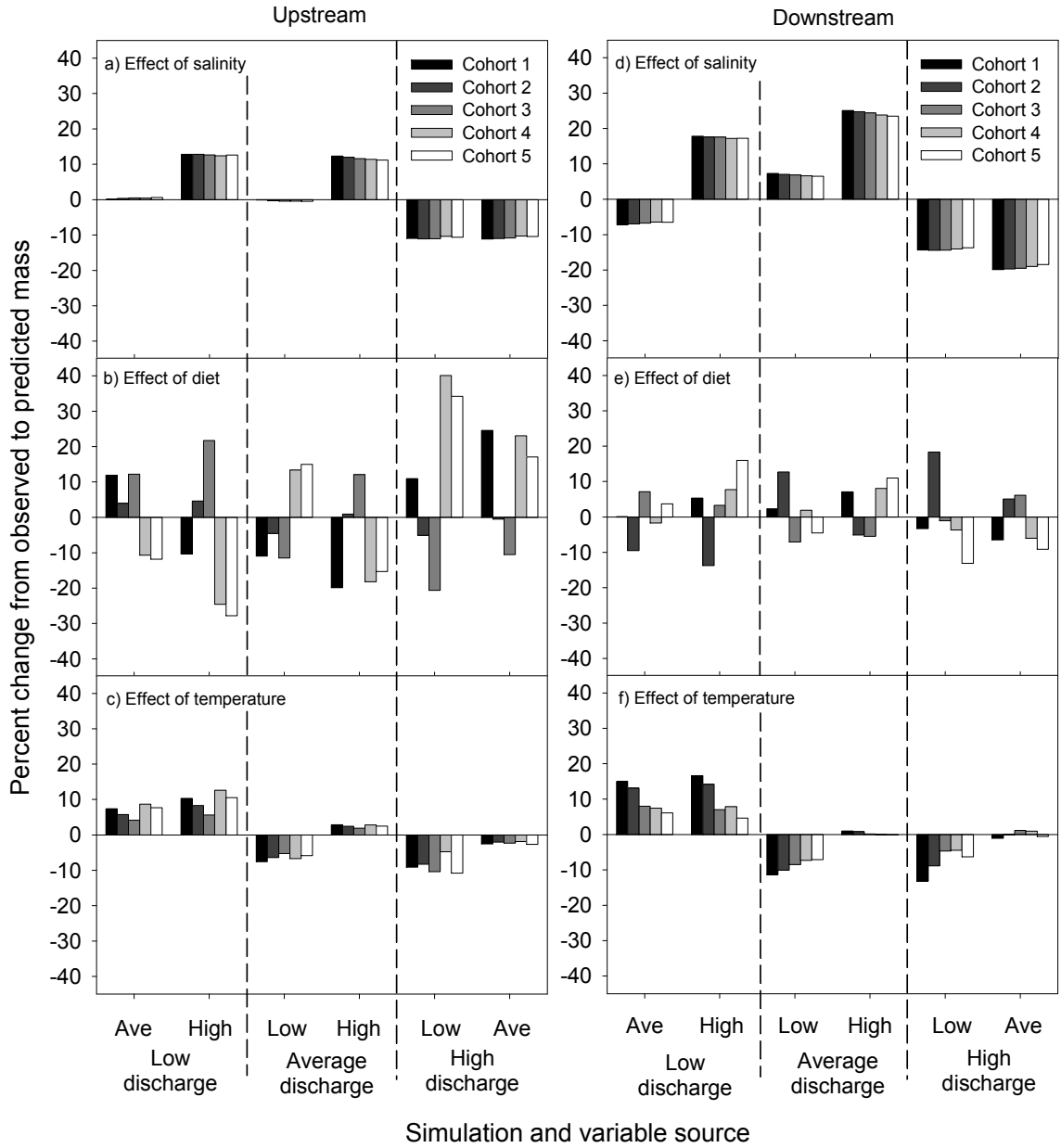


Figure 3.14

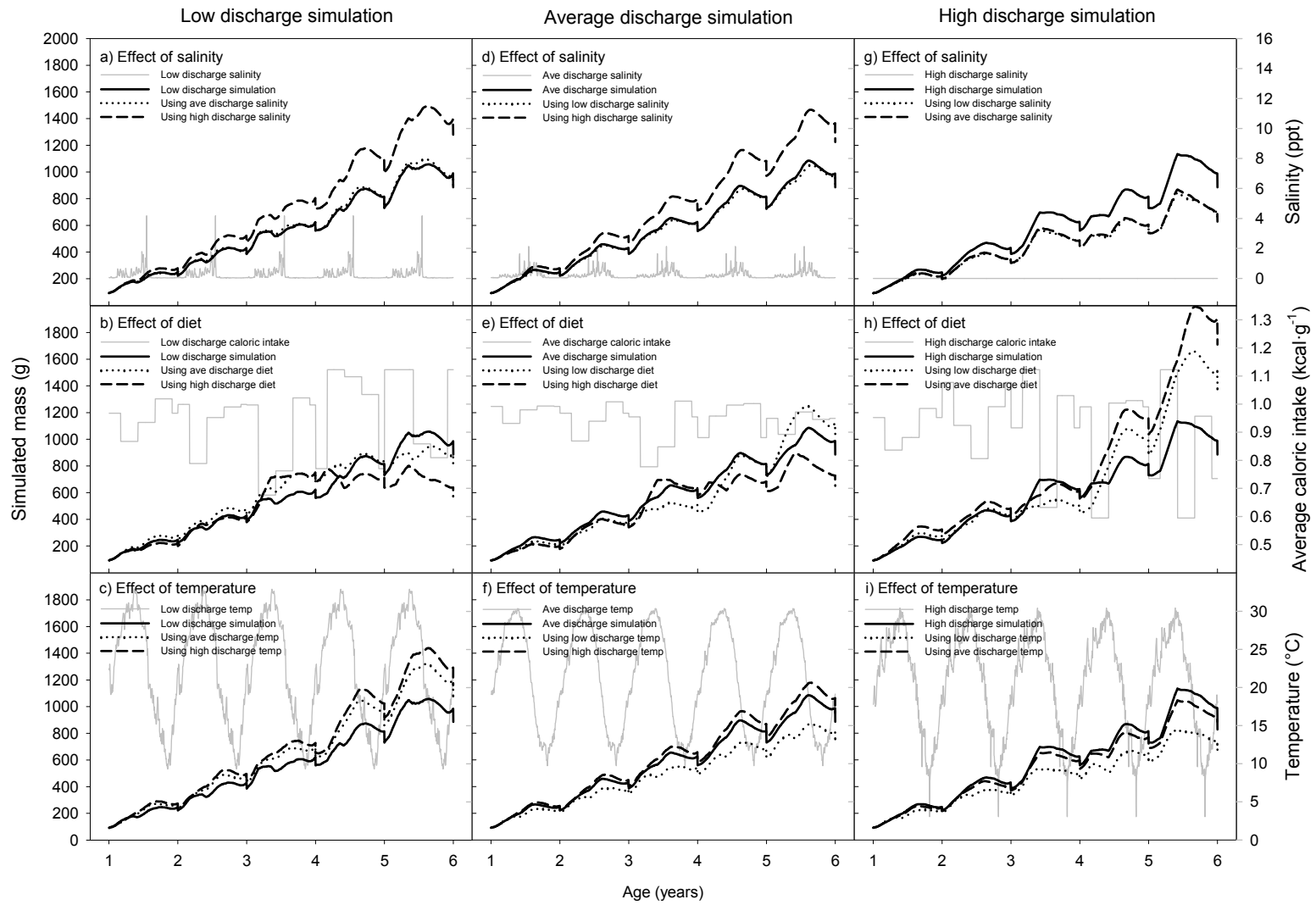


Figure 3.15

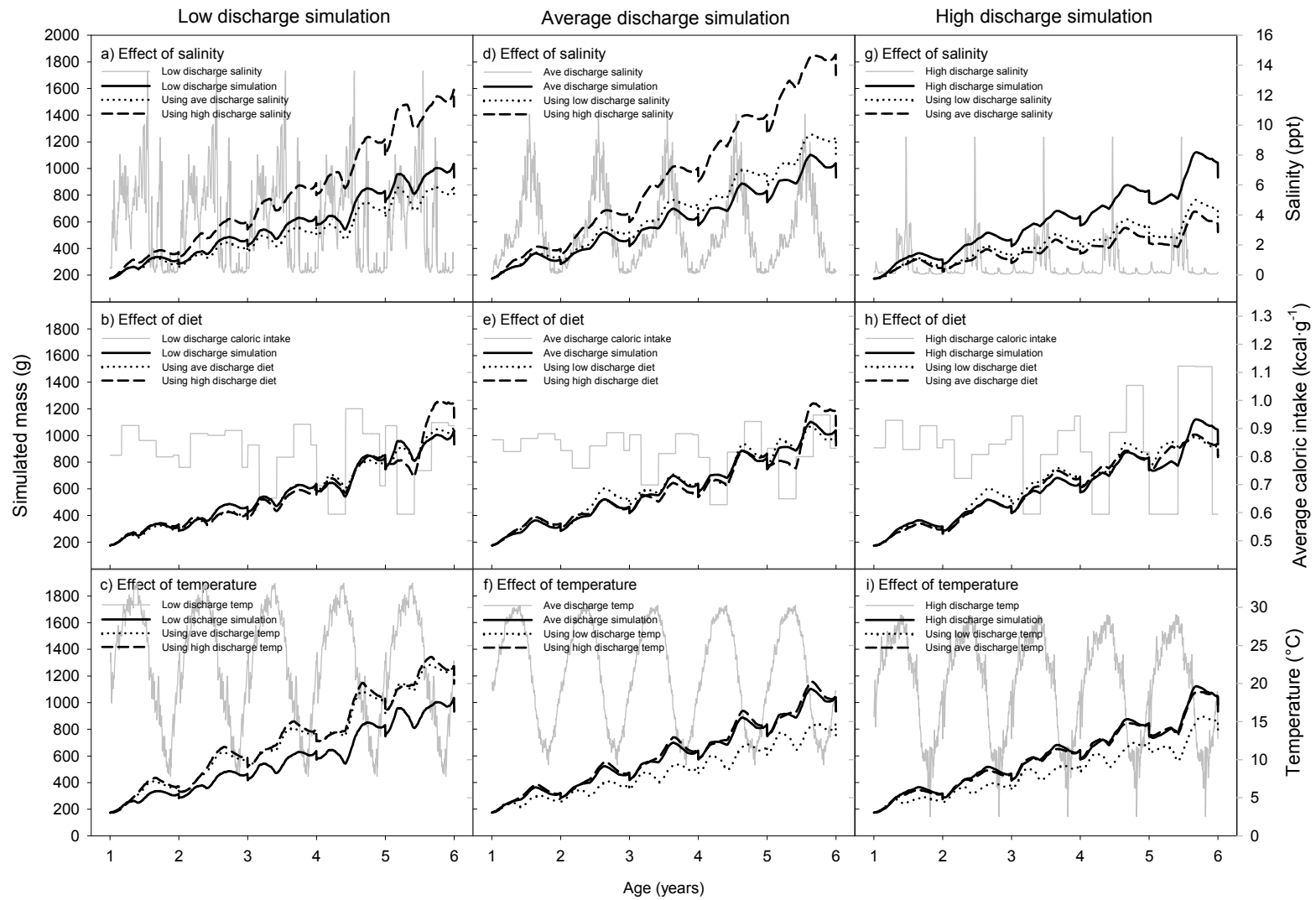


Figure 3.16

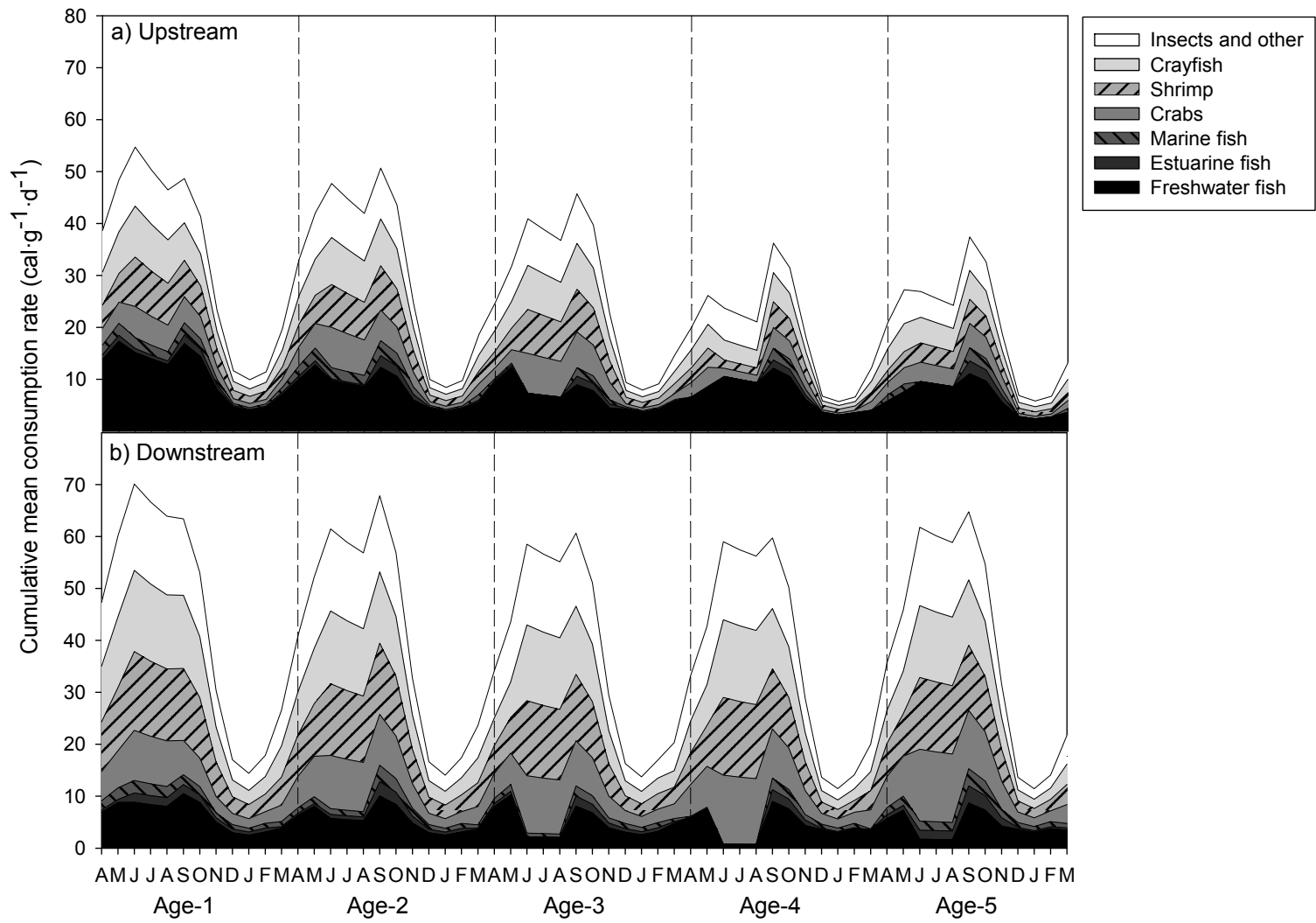


Figure 3.17

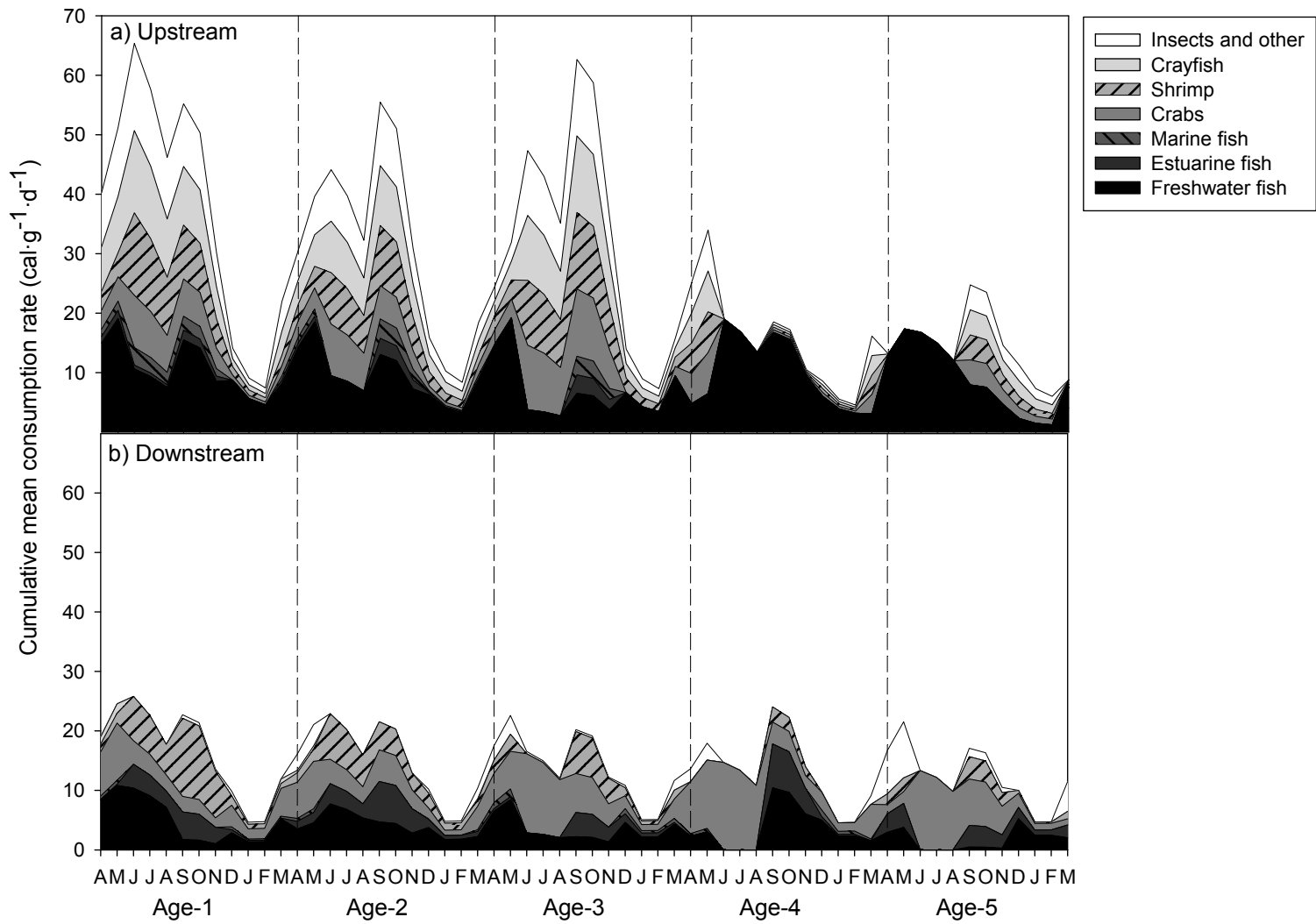


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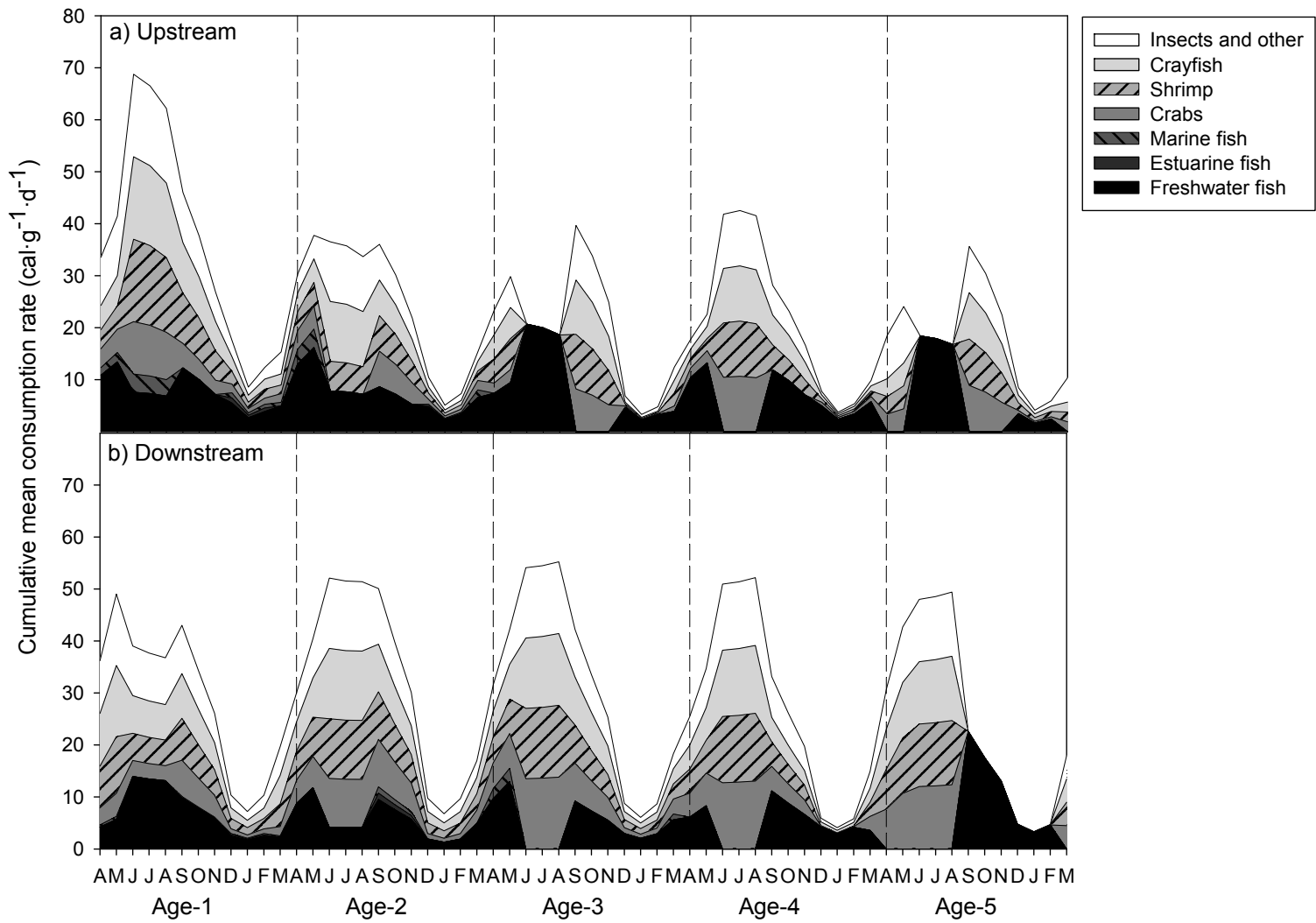


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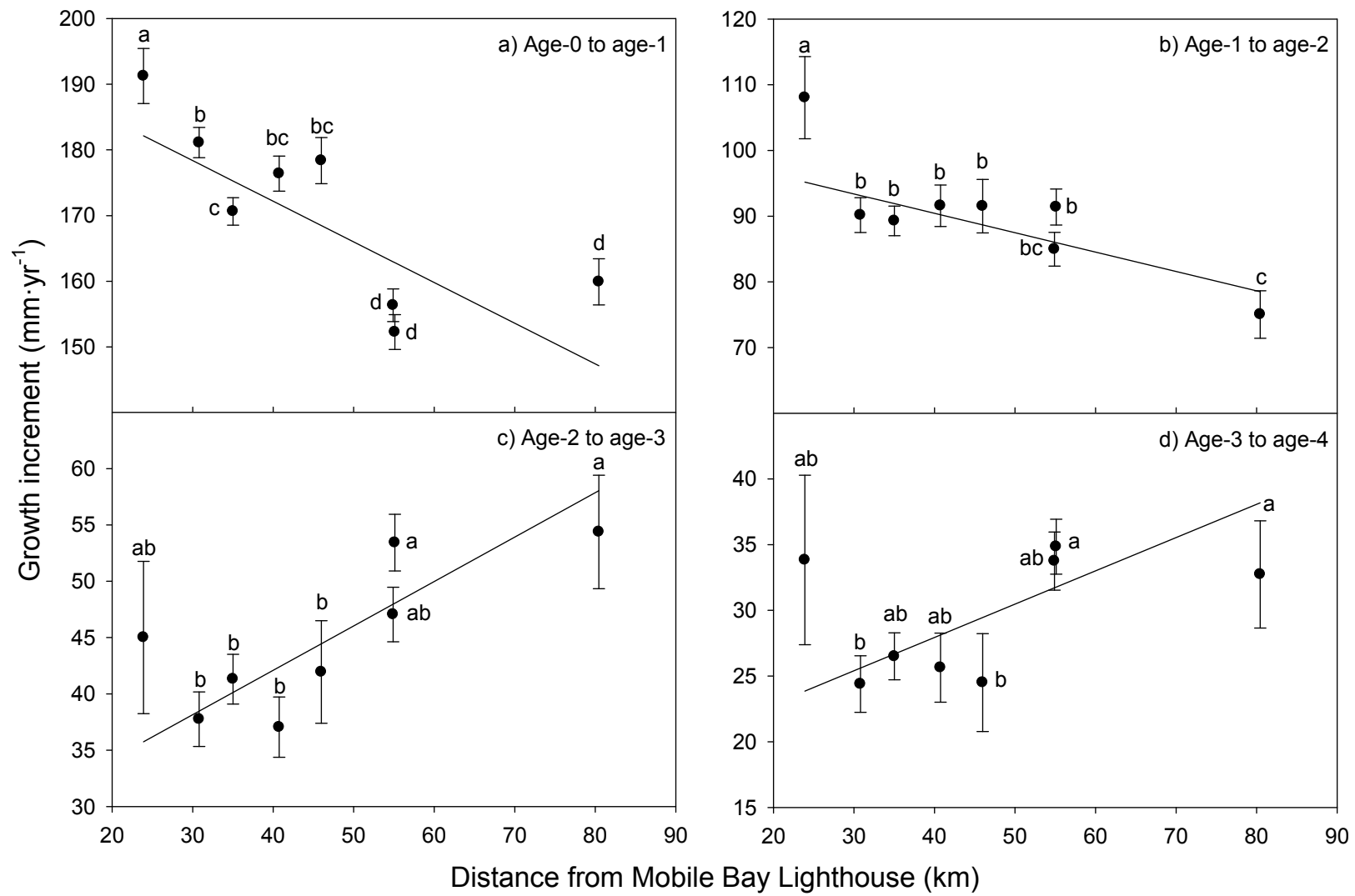


Figure 3.20

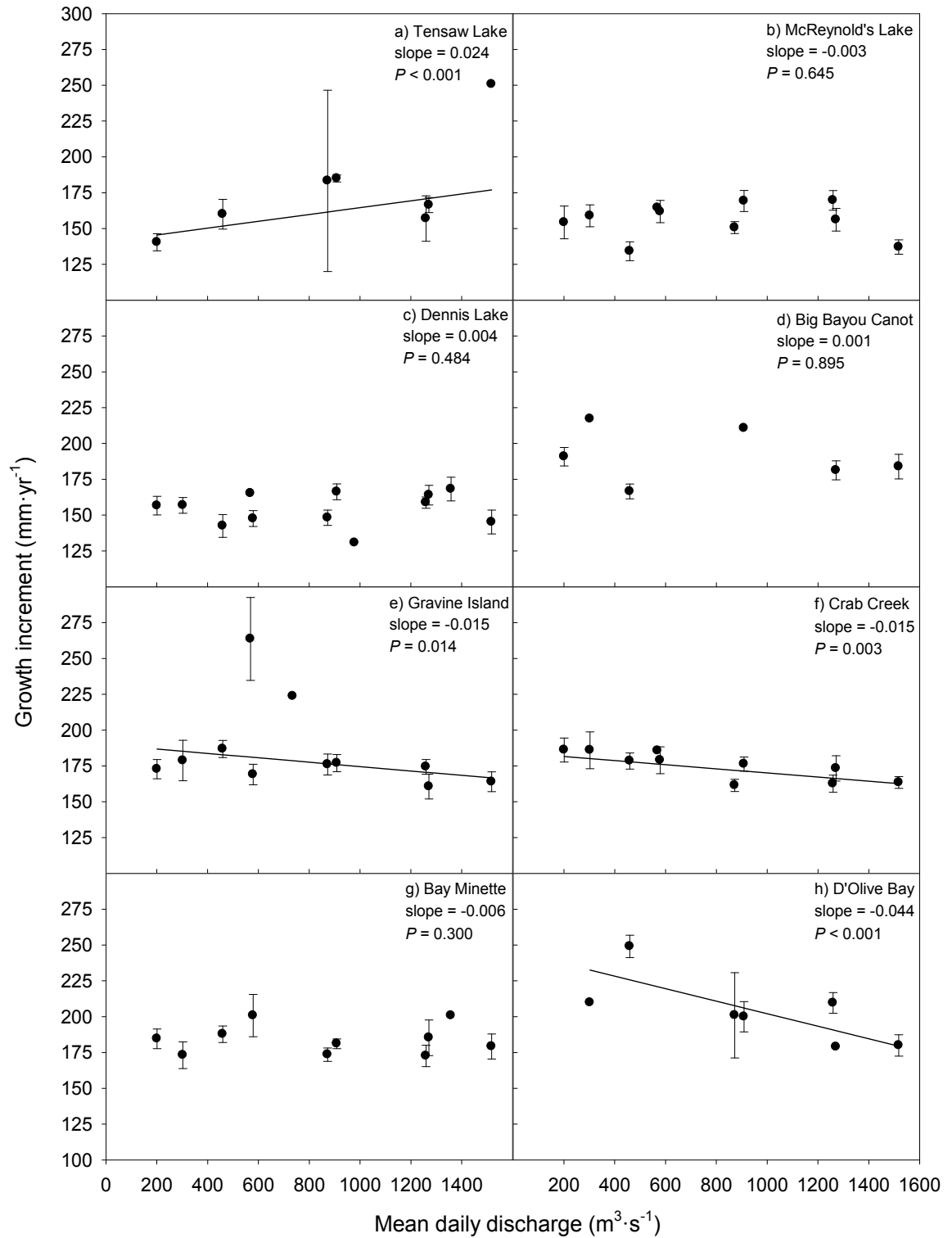


Figure 3.21

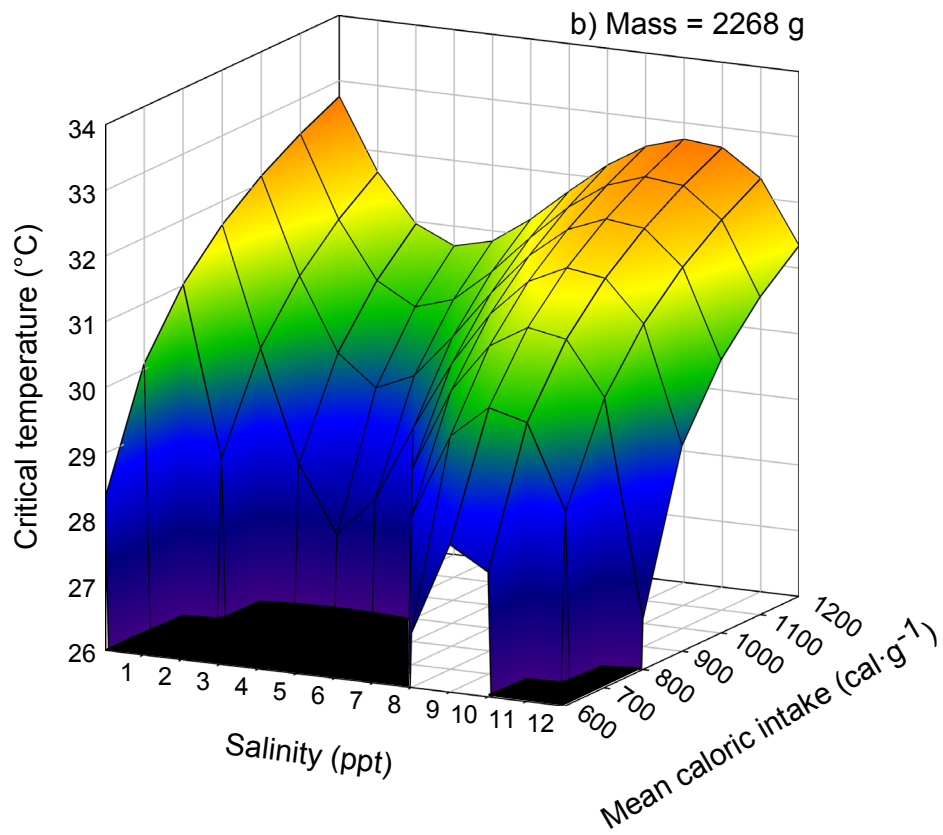
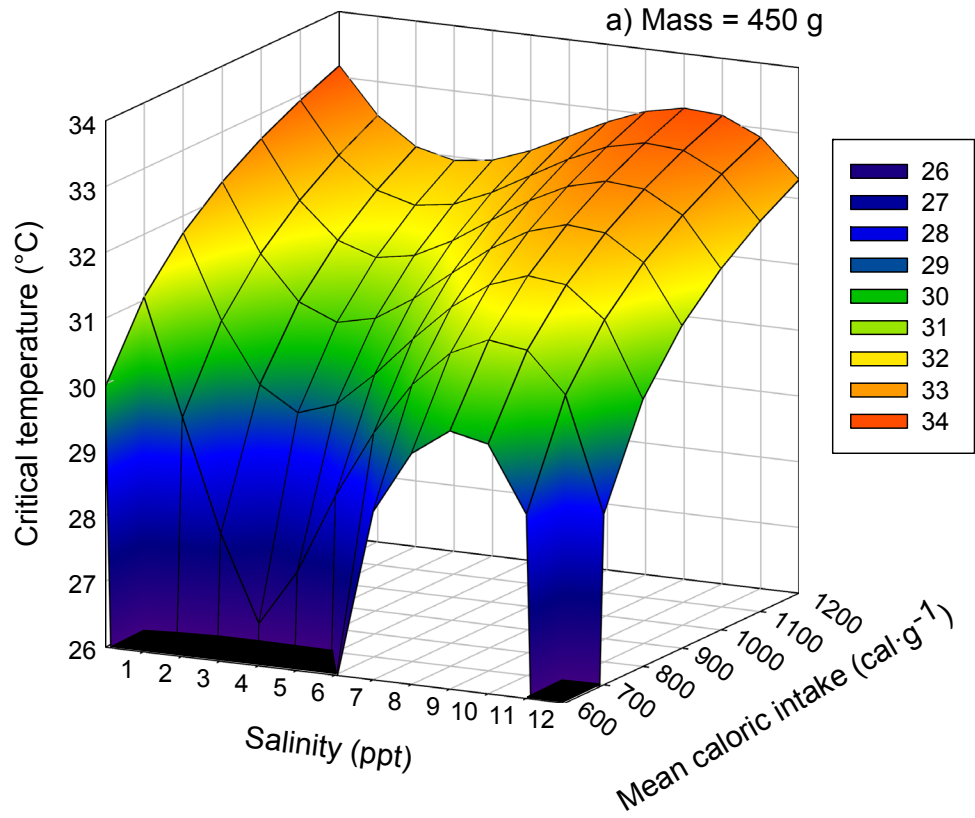


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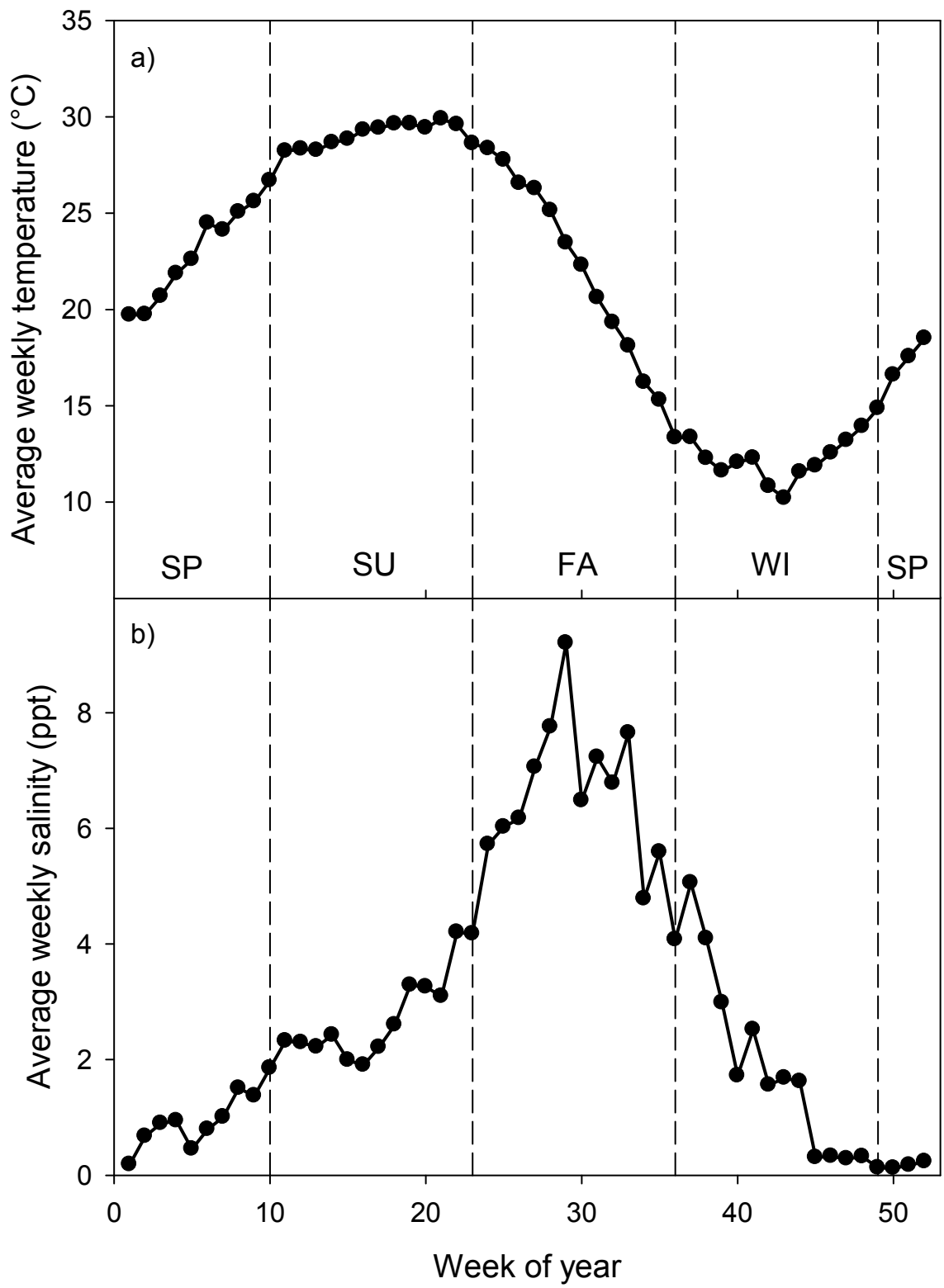


Figure 4.1

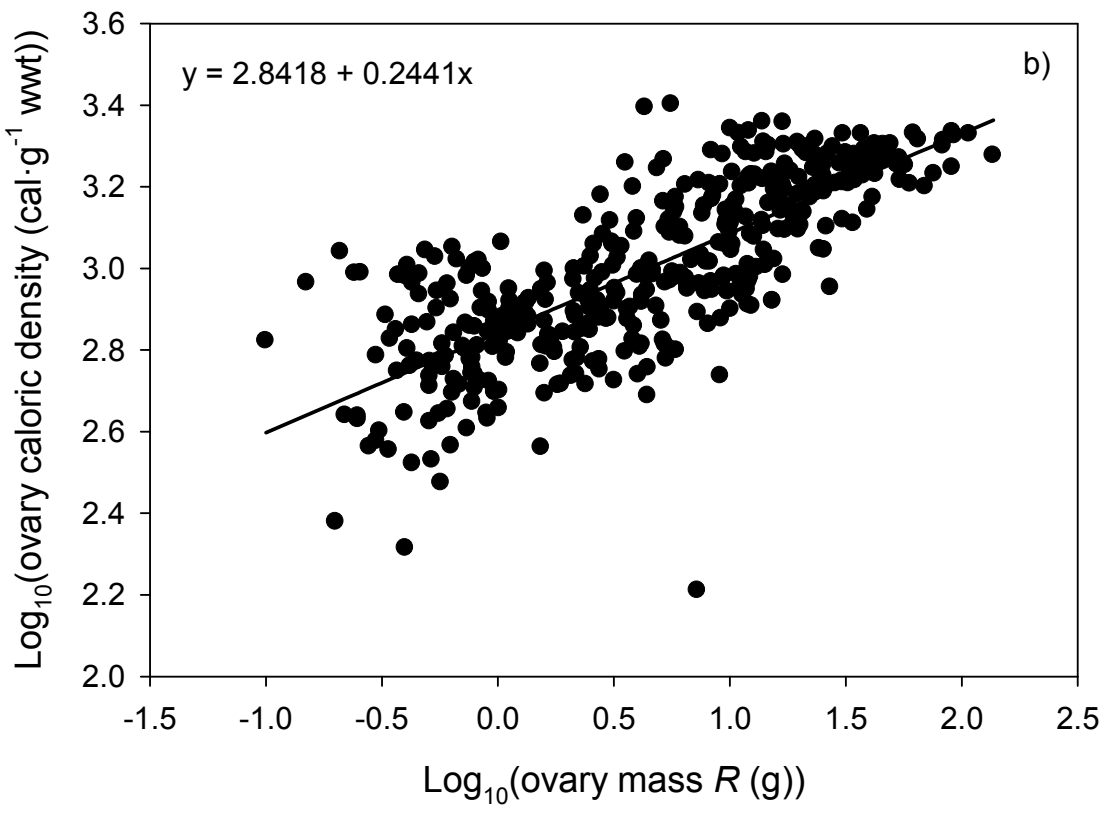
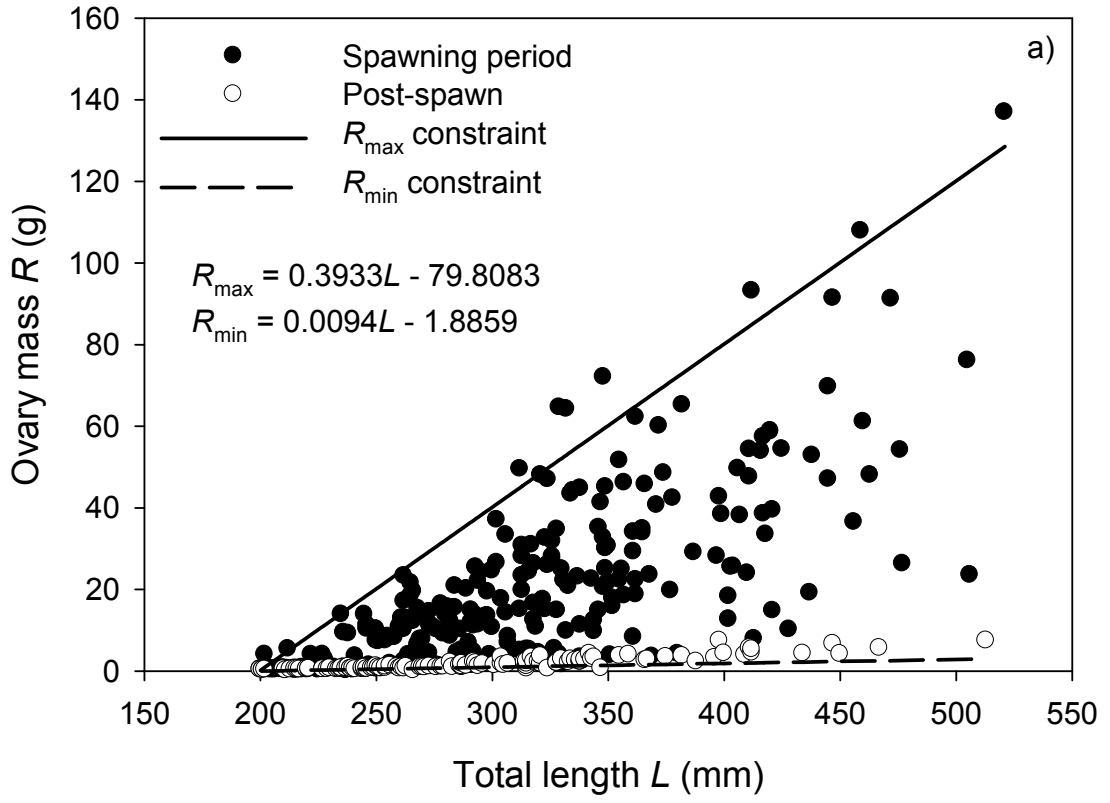


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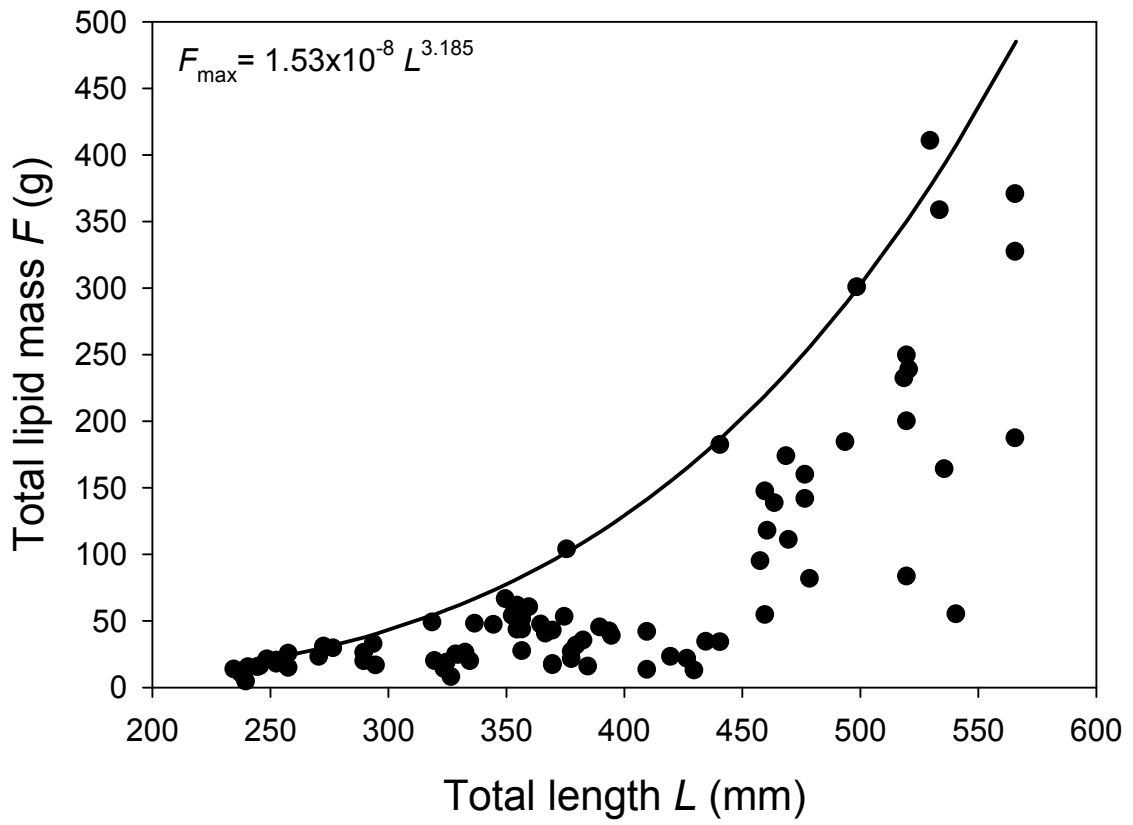


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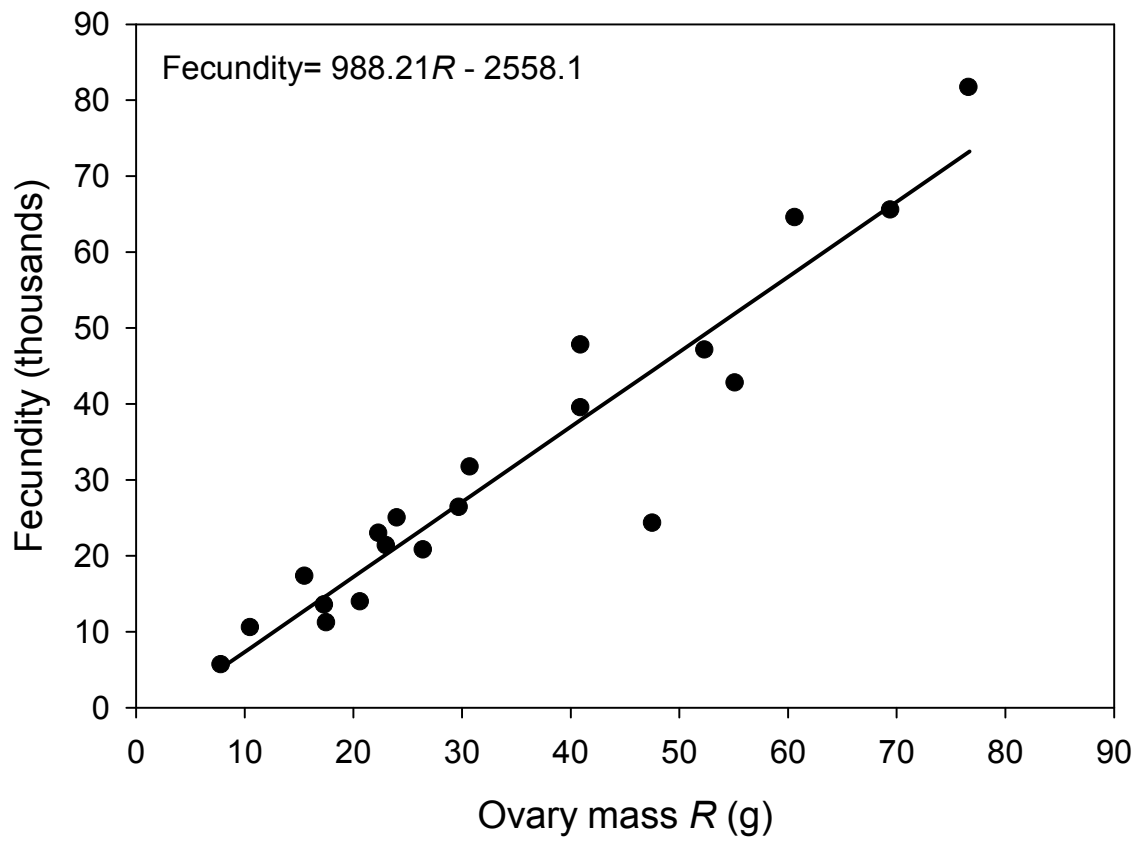


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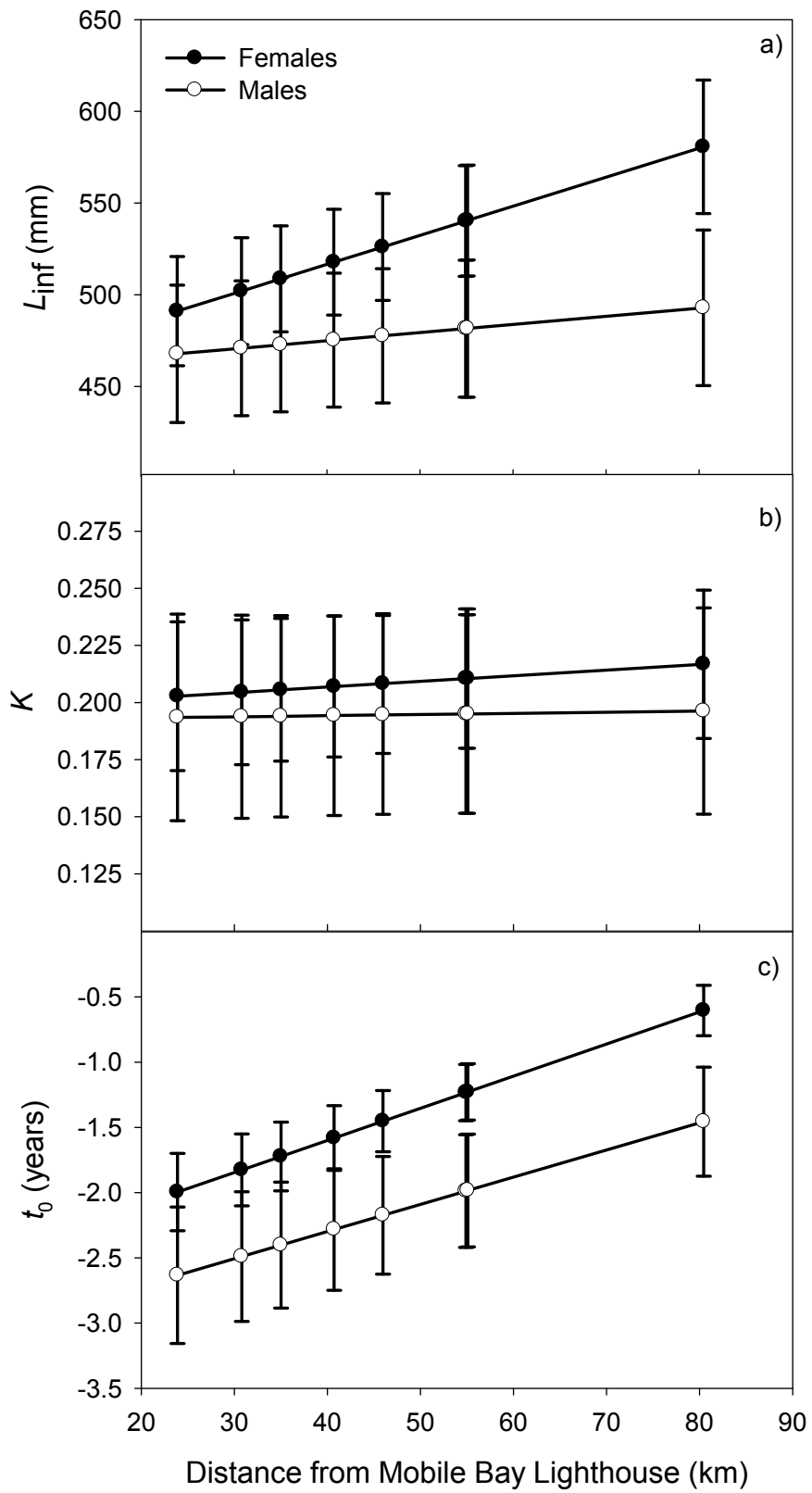


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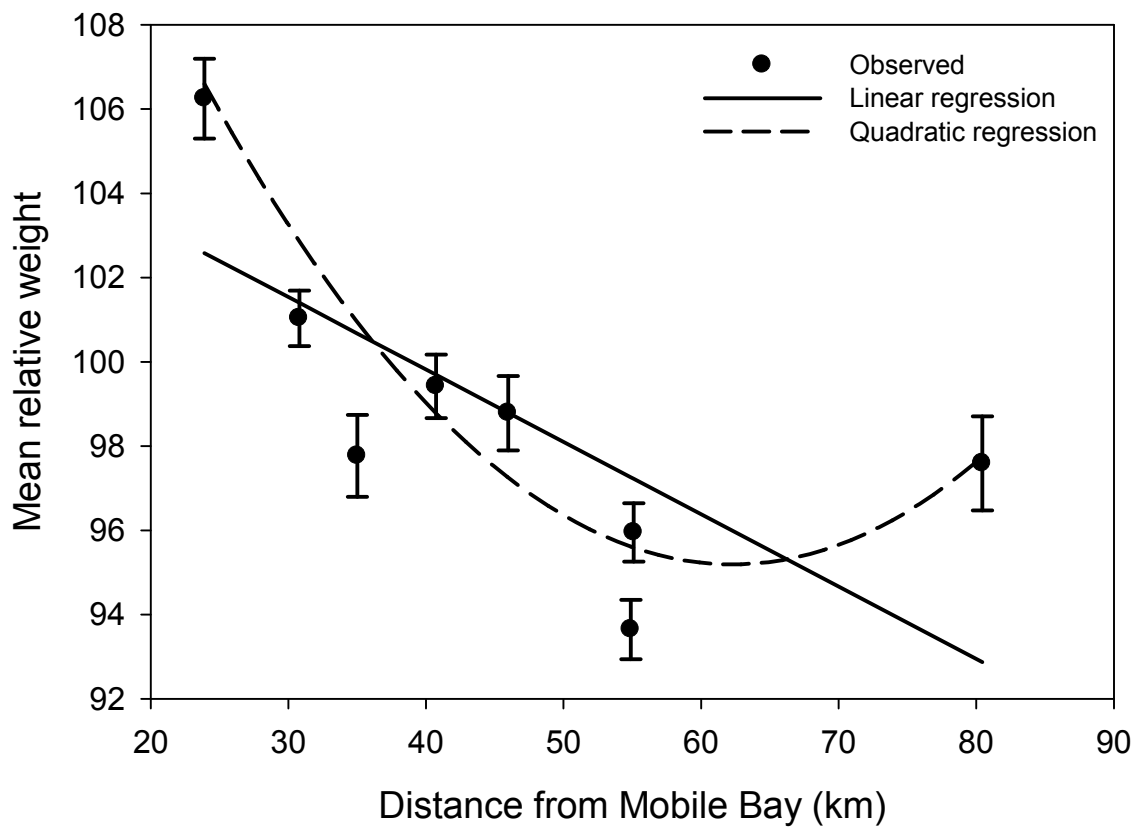


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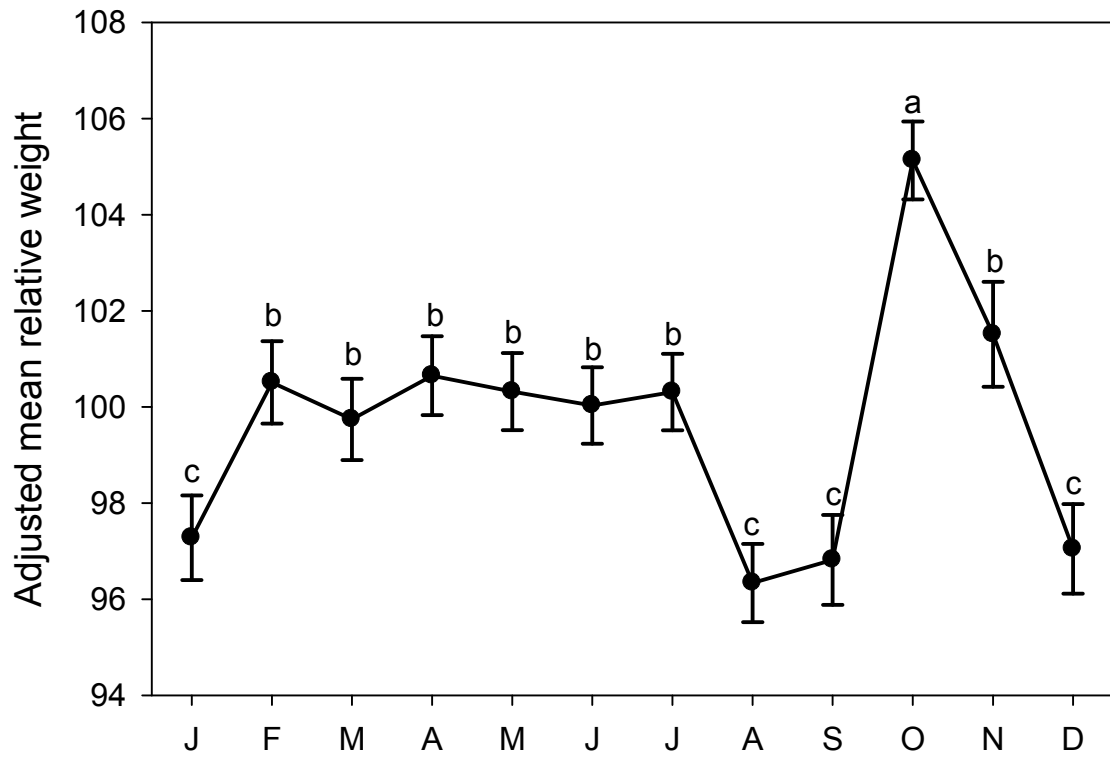


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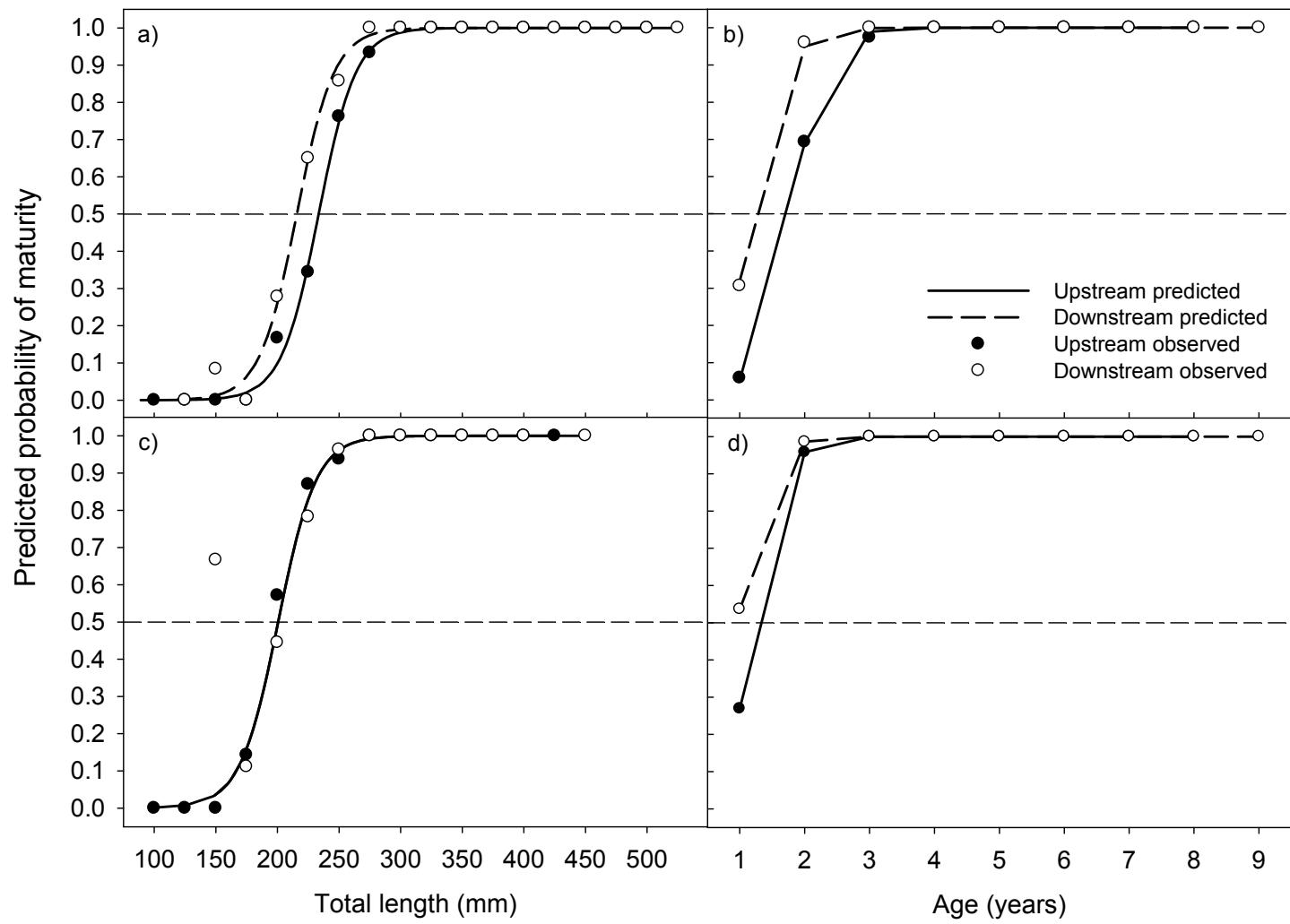


Figure 4.8

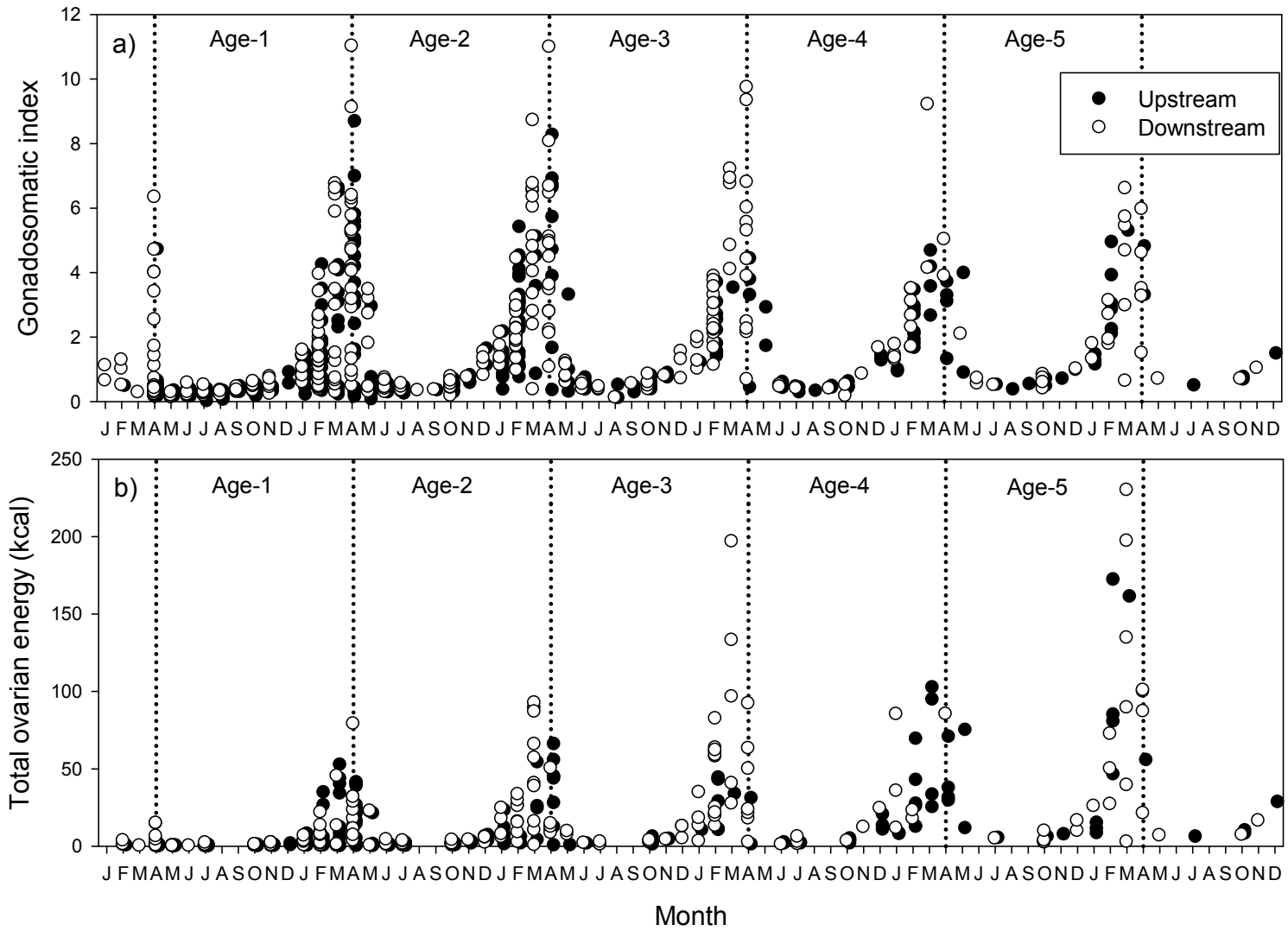


Figure 4.9

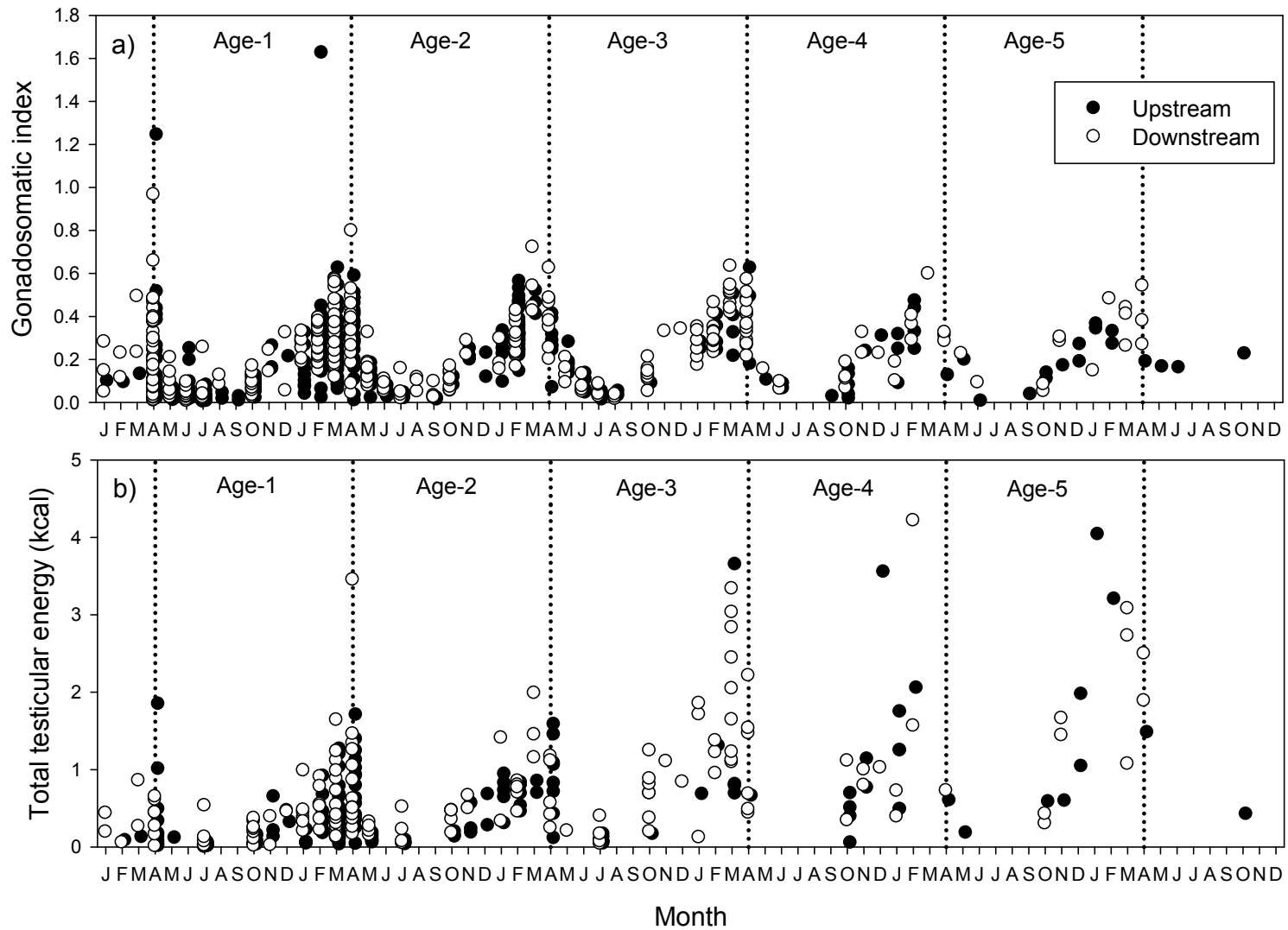


Figure 4.10

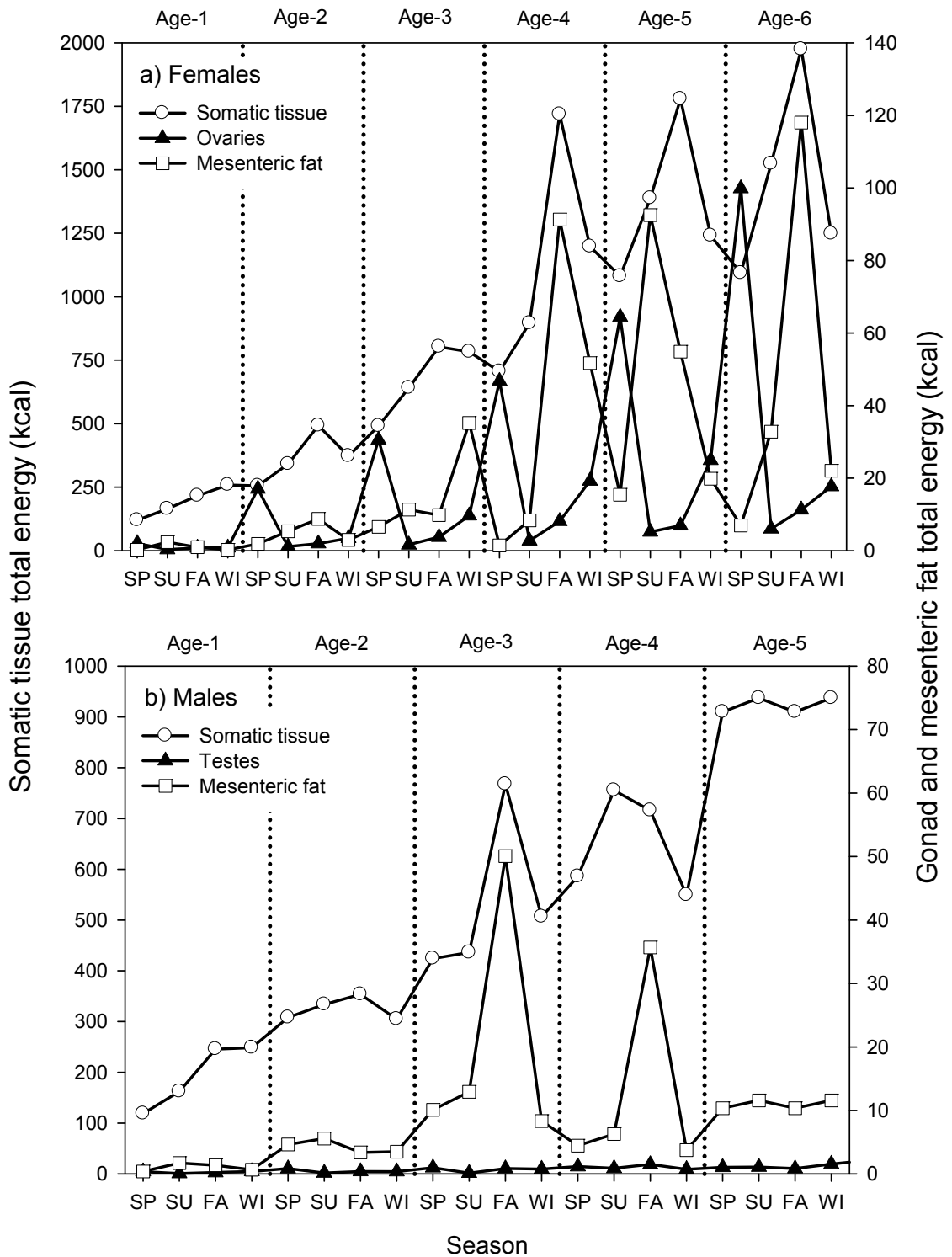


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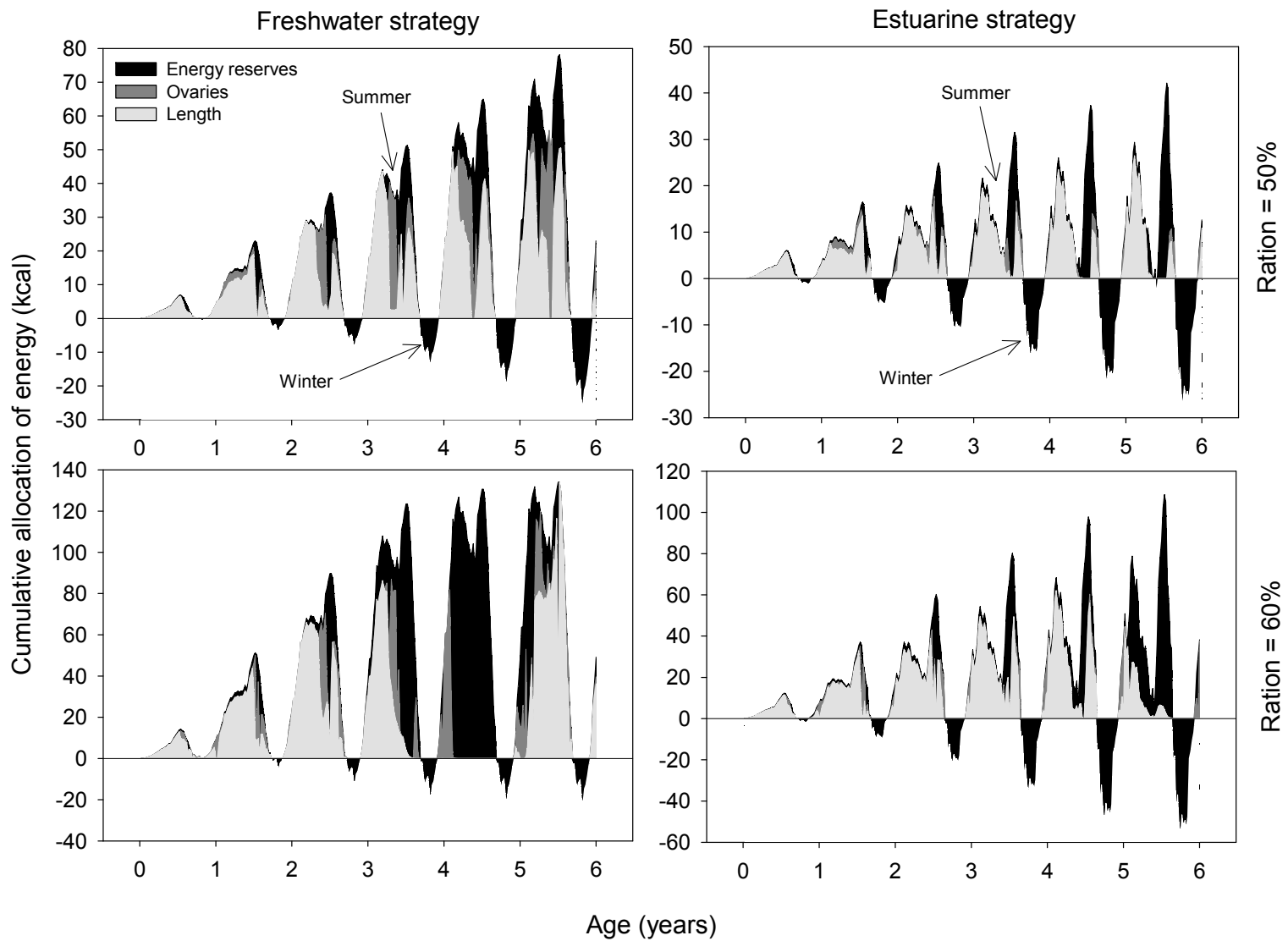


Figure 4.12

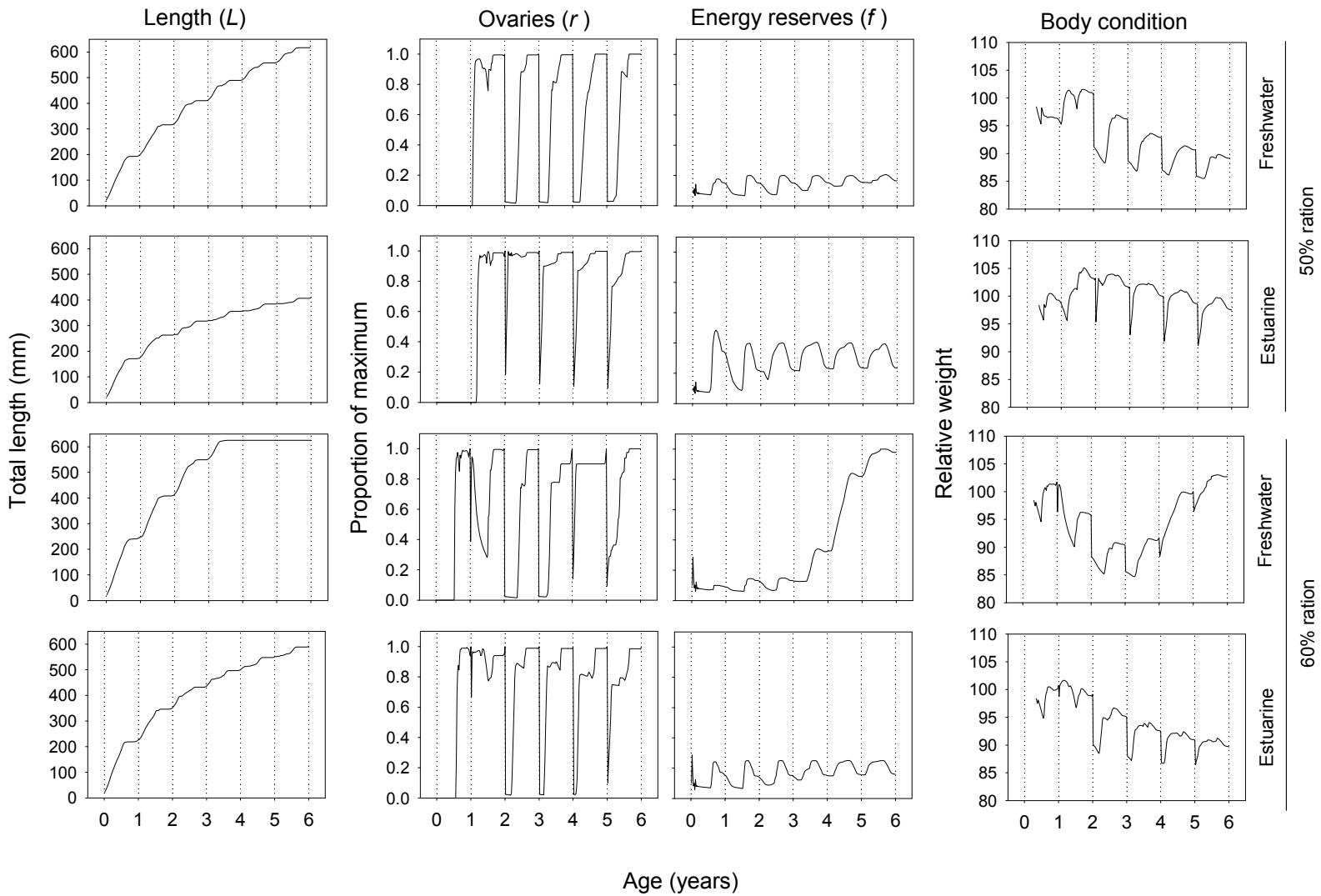


Figure 4.13

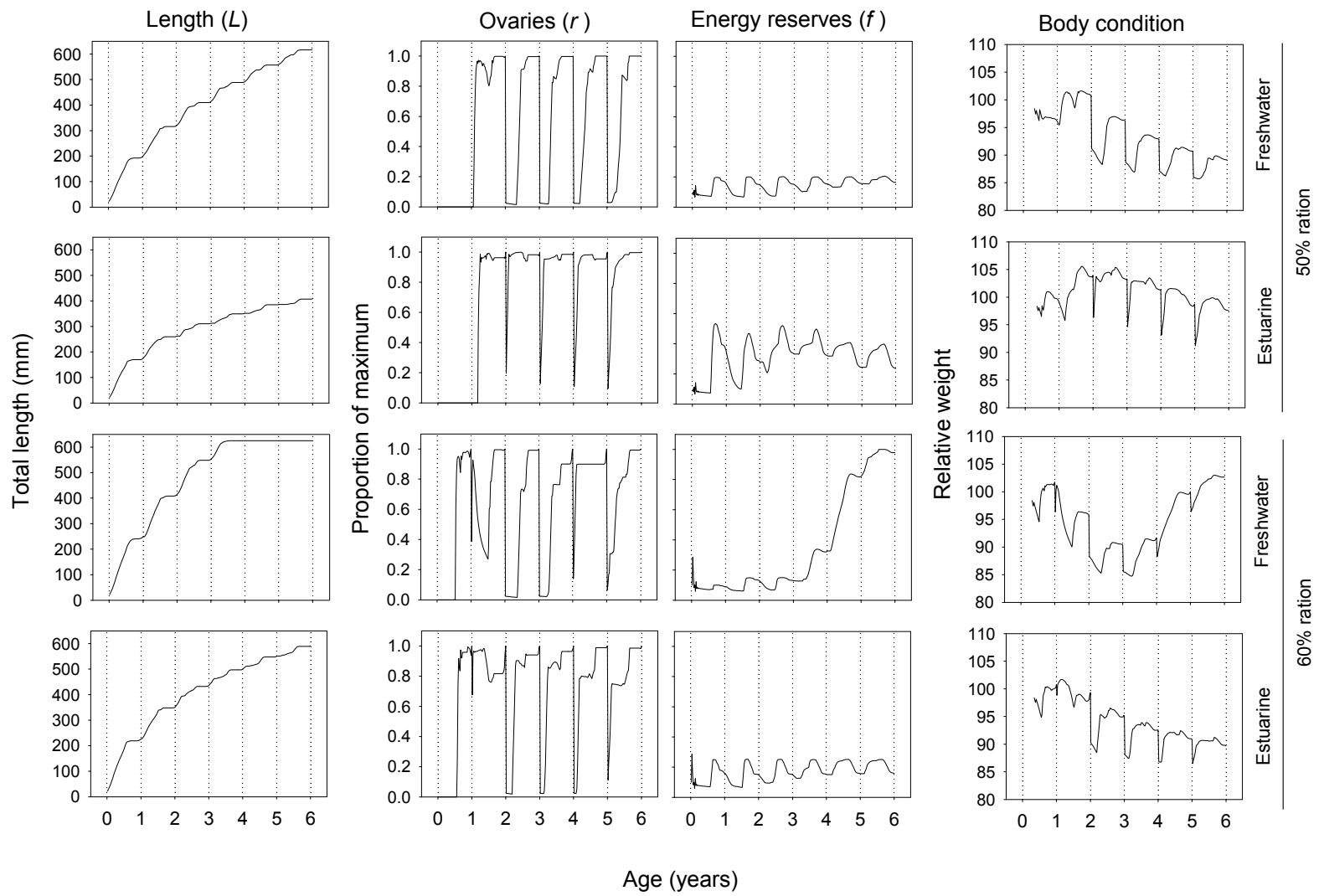


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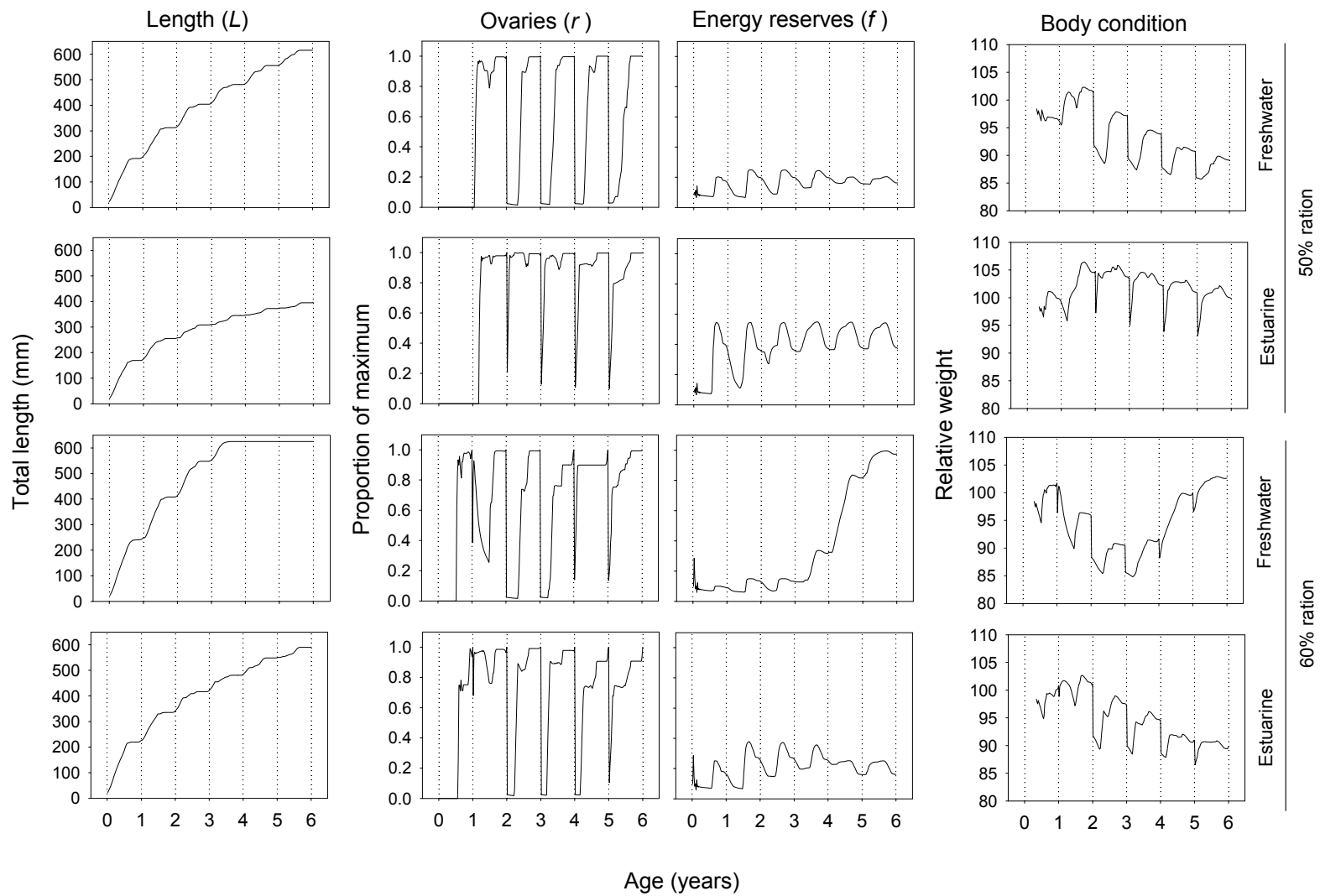


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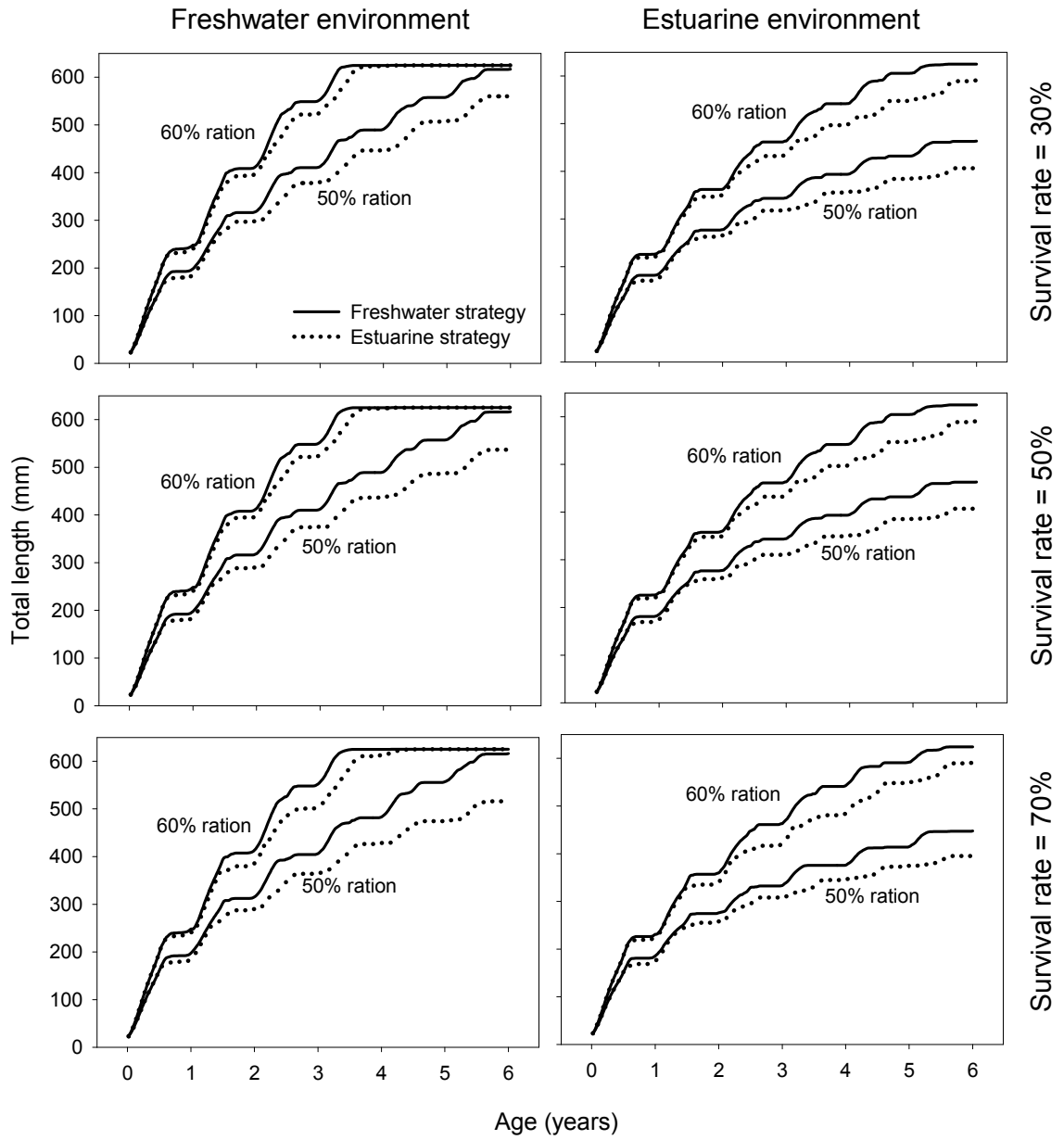


Figure 4.16

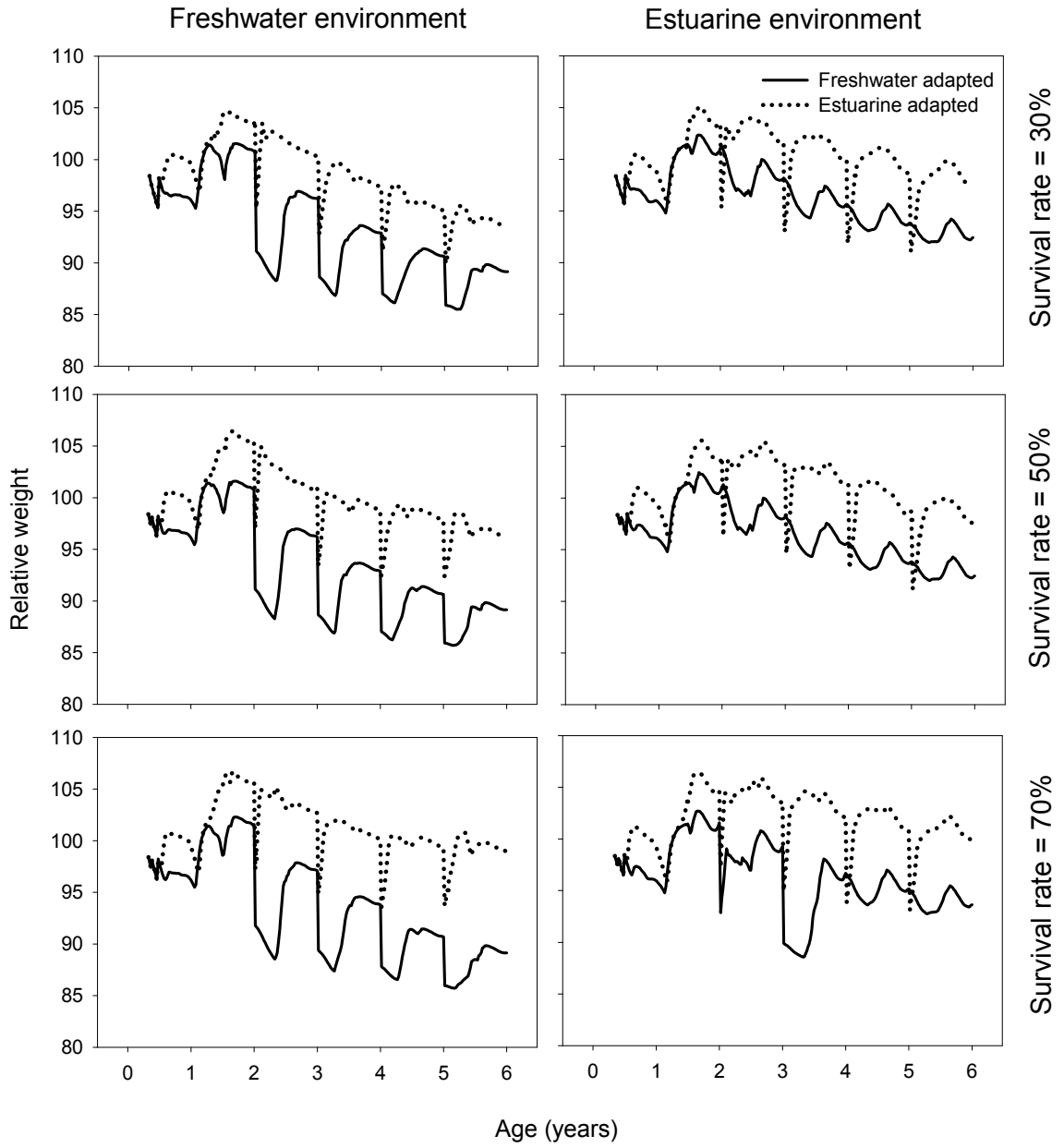


Figure 4.17

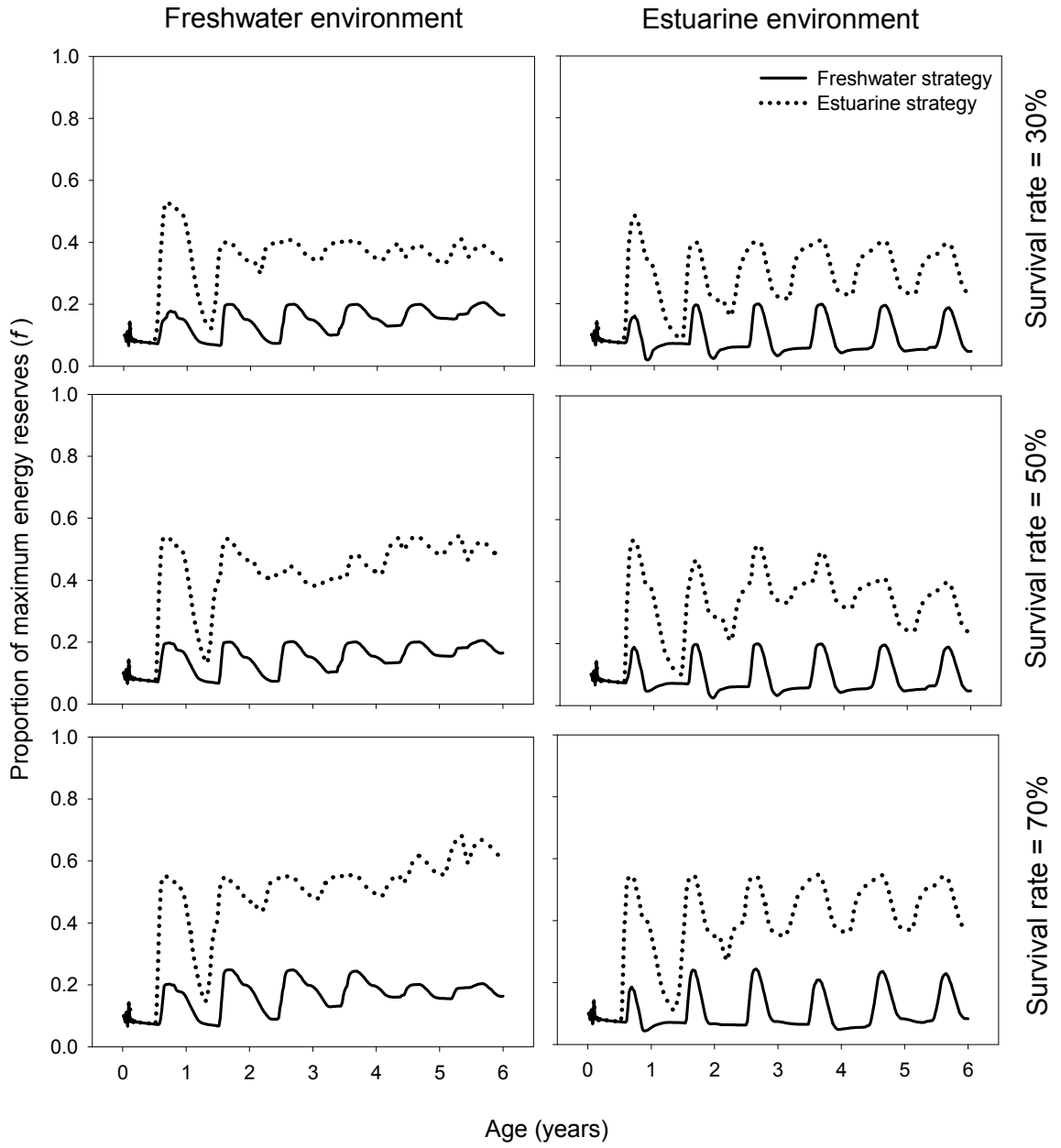


Figure 4.18

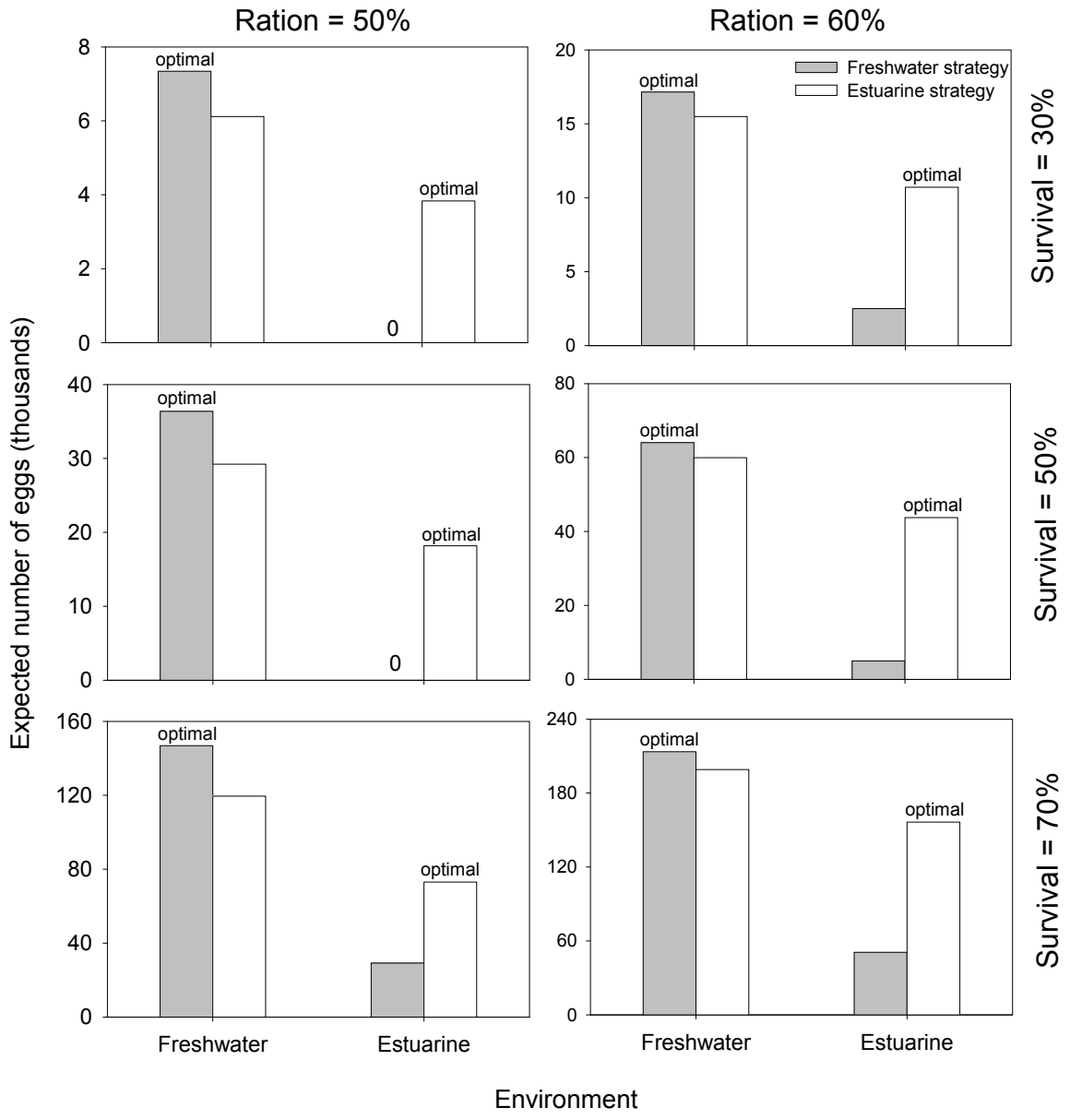


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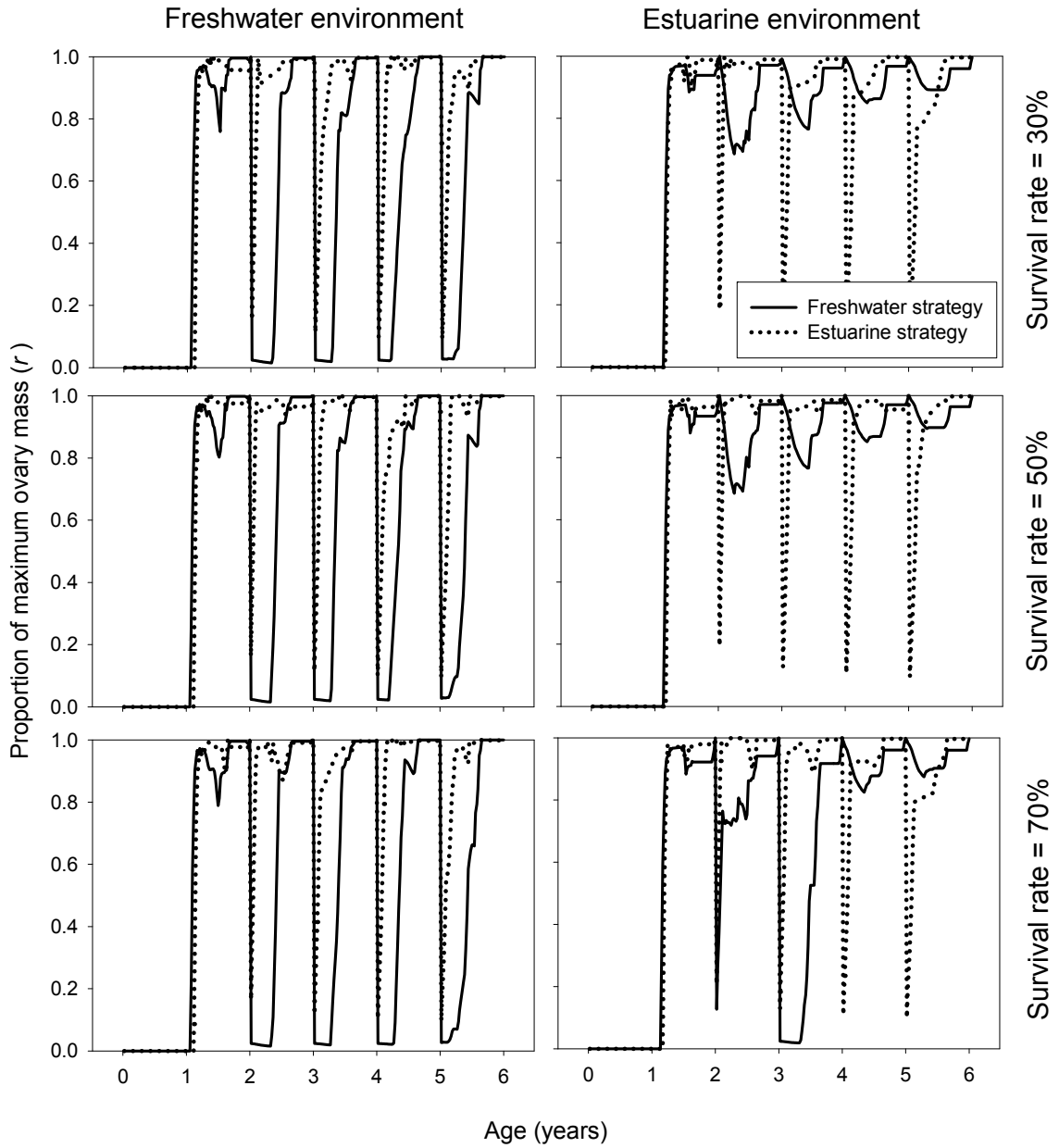


Figure 4.20

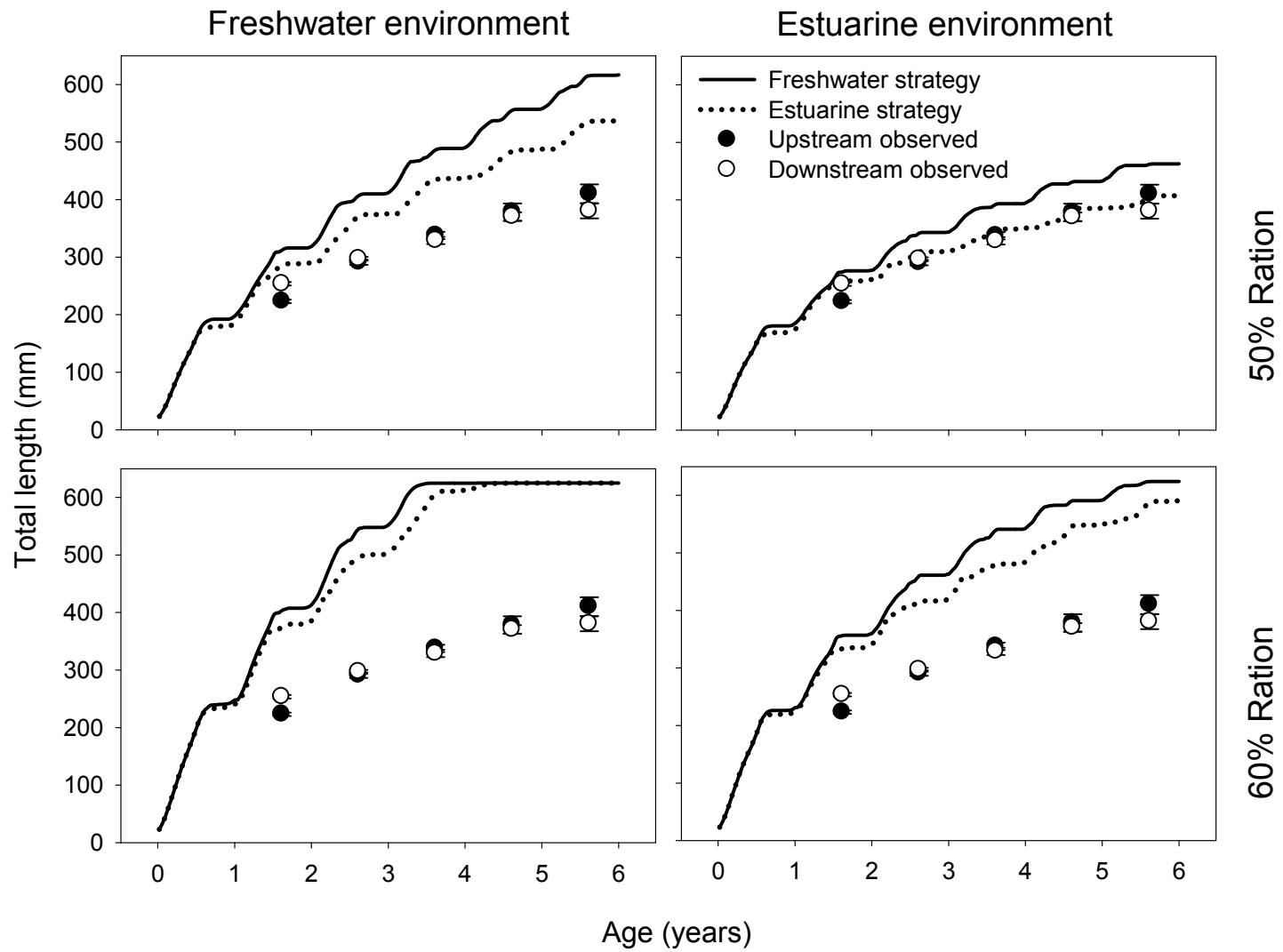


Figure 4.21

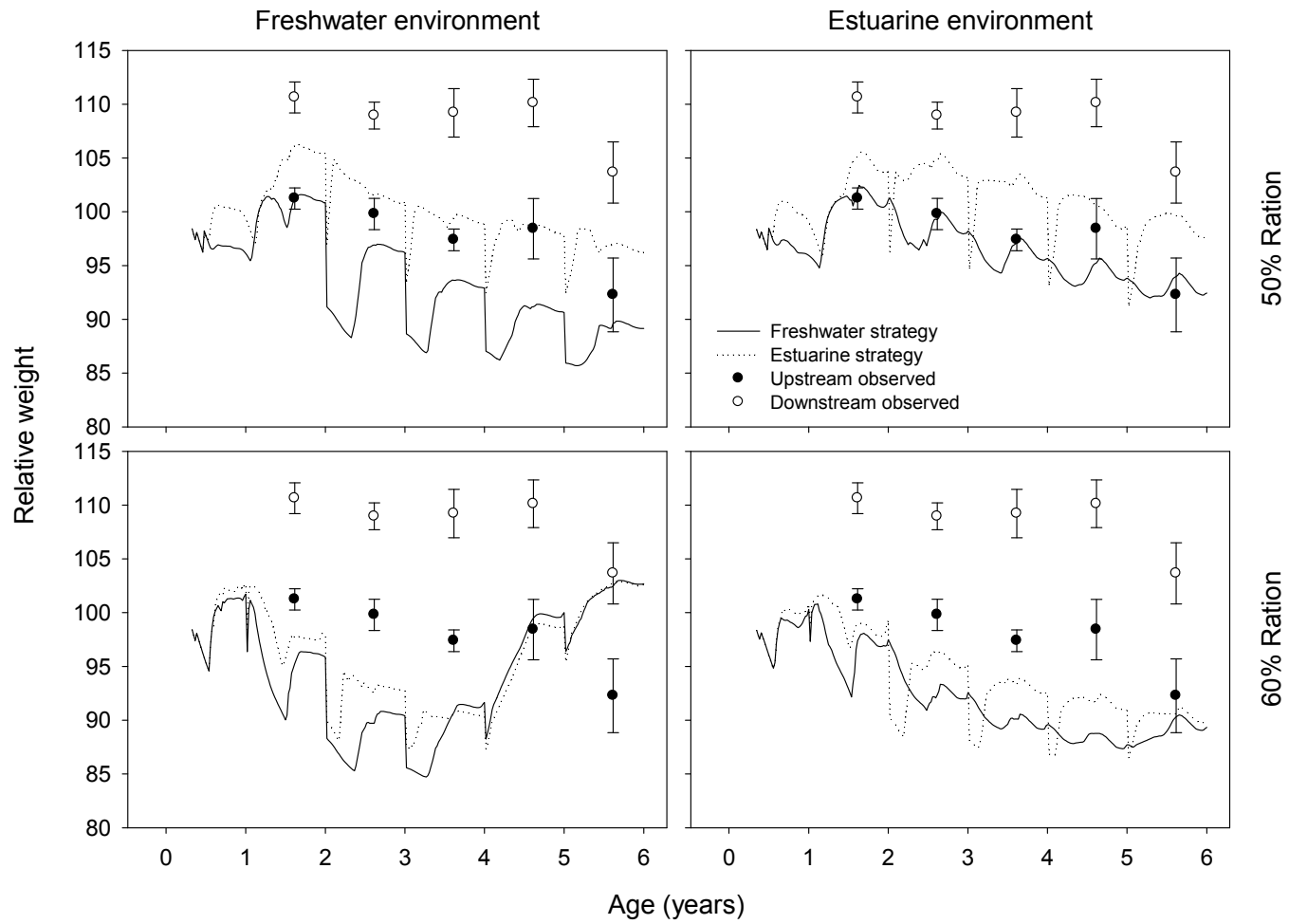


Figure 4.22

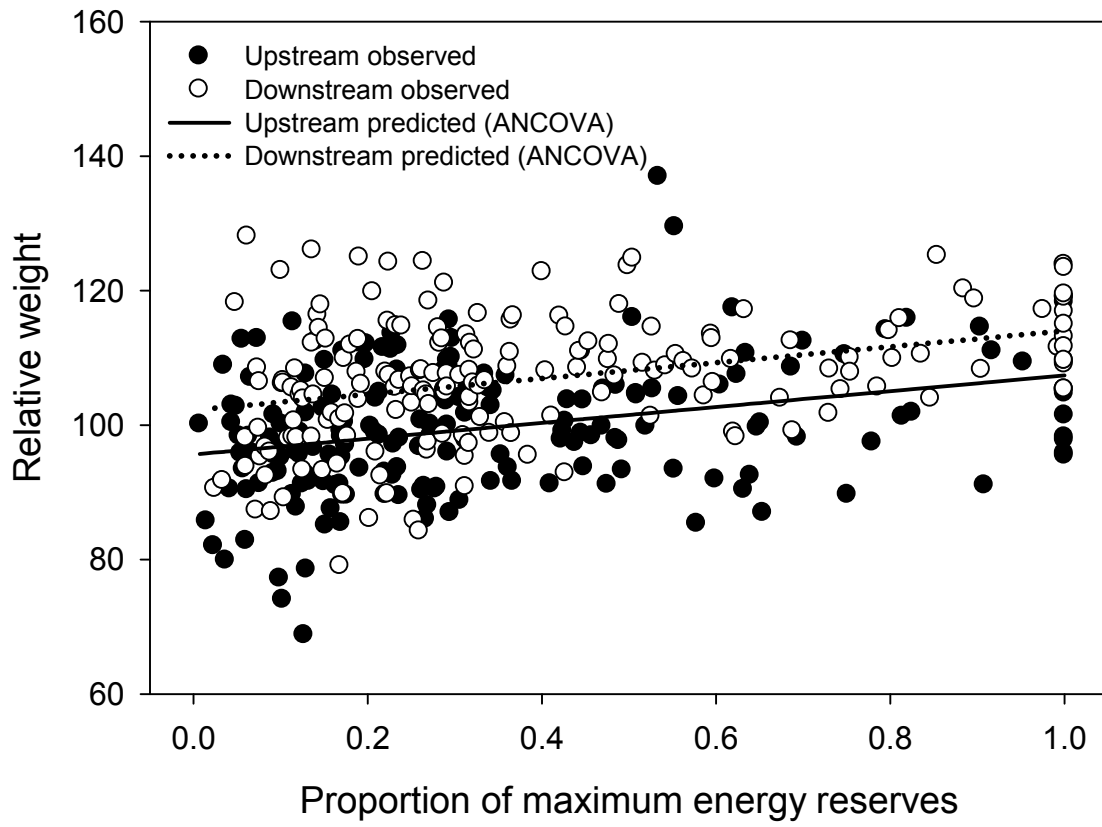


Figure 4.23

Appendix 1. Probability of blue crabs dominating the diet and probability of largemouth bass stomachs being empty

Methods

I used logistic regression to examine the effects of age, season-specific mean daily discharge, season, and all possible interactions on the odds of blue crabs dominating the diet of largemouth bass (PROC LOGISTIC; SAS Institute 2008). Fish were assigned to ages using size categories as described in the diet proportion determination section for the bioenergetics modeling. Individual fish that had at least 50% of their diet biomass consisting of crabs were considered dominated by crabs and were assigned a 1 for modeling purposes; otherwise fish were assigned a 0. Backward model selection was used to eliminate insignificant terms ($\alpha = 0.05$) from region-specific models and contrast statements were used to determine season-specific effects of age and discharge. The range of discharges observed within each season varied dramatically which made it difficult to use global models to conduct seasonal comparisons while correcting for age and discharge. Therefore, a model containing only the effect of season nested within region was used to determine whether seasonal differences existed within regions. Similarly, a model containing only the effect of region nested within season was used to determine whether season-specific odds of the diet being dominated by crabs were different between regions.

I also used logistic regression to examine the effects of age, season, and region, and all possible interactions on the probability of largemouth bass having an empty stomach. Backward model selection was used to determine the best model by sequentially eliminating insignificant terms ($\alpha = 0.05$). Contrast statements were used to

test whether season-specific regional differences existed in the odds of a largemouth bass stomach being empty while correcting for the effect of age.

Results

Backward model selection indicated that the odds of crabs dominating the diet of largemouth bass in the upstream region was affected by the main effects of age ($\chi_1^2 = 21.26$; $P < 0.001$), mean daily discharge ($\chi_1^2 = 4.55$; $P = 0.03$), and season ($\chi_3^2 = 36.94$; $P < 0.001$), as well as the interaction between discharge and season ($\chi_3^2 = 14.24$; $P = 0.003$) (Figure A.1). Across all seasons and discharge levels, the odds of crabs dominating the diet increased with age at rate of 30% (95% C.I. = 16 – 45%). Summer-specific mean daily discharge decreased the odds of crabs dominating the diet by 36% with every 500 $\text{m}^3 \cdot \text{s}^{-1}$ ($\chi_1^2 = 17.96$; $P < 0.001$; 95% C.I. = 22-48%), whereas discharge did not affect the odds during any other season ($\chi_1^2 \leq 0.81$; $P \geq 0.37$).

Backward model selection revealed that the three-way interaction among age, mean daily discharge, and season significantly affected the odds of crabs dominating the diet of largemouth bass in the downstream region ($\chi_3^2 = 14.23$; $P = 0.003$; Figure A.2); therefore all lower order interactions and main effect remained in the final model. The effect of age depended on season-specific mean daily discharge during the summer ($\chi_1^2 = 6.07$; $P = 0.01$) and fall ($\chi_1^2 = 4.98$; $P = 0.03$), and while it was insignificant during the spring ($\chi_1^2 = 3.23$; $P = 0.07$) this likely represented a biologically significant finding. During the spring the effect of age on the odds of crabs dominating the diet increased with discharge such that the odds increased at a rate of 6% and 70% with age at the lowest ($482 \text{ m}^3 \cdot \text{s}^{-1}$) and highest ($3976 \text{ m}^3 \cdot \text{s}^{-1}$) observed spring discharge, respectively; however, the effect of age was not significant at discharges below $1294 \text{ m}^3 \cdot \text{s}^{-1}$ ($P > 0.05$).

During the summer, the effect of age was highest at the lowest observed discharge (209 $\text{m}^3 \cdot \text{s}^{-1}$), increasing at a rate of 151% with age, and declined as discharge increased to only a 9% increase with age at the highest observed summer-specific discharge (2268 $\text{m}^3 \cdot \text{s}^{-1}$). Yet, at mean daily discharges above 1645 $\text{m}^3 \cdot \text{s}^{-1}$ age did not have a significant effect on the odds of crabs dominating largemouth bass diets during the summer ($P > 0.05$). Similar to the summer period, the effect of age decreased with increasing discharge, ranging from a 70% increase in odds with age at the lowest observed fall discharge (187 $\text{m}^3 \cdot \text{s}^{-1}$) to a 2% decrease with age at the highest observed fall discharge (1624 $\text{m}^3 \cdot \text{s}^{-1}$). The effect of age was not significant, however, at fall discharge levels greater than 1061 $\text{m}^3 \cdot \text{s}^{-1}$ ($P > 0.05$). Neither the main effects of age ($\chi_1^2 = 0.002$; $P = 0.96$), mean daily discharge ($\chi_1^2 = 0.18$; $P = 0.67$), nor the interaction between age and discharge ($\chi_1^2 = 0.008$; $P = 0.93$) affected the odds of crabs dominating largemouth bass diets during the winter.

The logistic model including only the effect of season nested within region on the odds of crabs dominating the diet of largemouth bass indicated that season-specific differences existed within each region ($\chi_7^2 = 217.23$; $P < 0.001$). In the upstream region, the odds of a crab-dominated diet were 2.6, 1.6, and 3.3 times higher during the summer than the spring, fall, and winter, respectively ($\chi_1^2 \geq 7.75$; $P \leq 0.005$; Figure A.3a.). The odds of crabs dominating the diet during the fall were 1.6 and 2.1 times higher than the spring and winter season ($\chi_1^2 \geq 7.08$; $P \leq 0.008$) and the odds were similar between the spring and winter ($\chi_1^2 = 1.64$; $P = 0.20$). In the downstream region the odds during the summer were 2.1, 2.2, and 2.6 times higher compared to the spring, fall, and winter, respectively ($\chi_1^2 \geq 25.46$; $P < 0.001$; Figure A.3b.). The odds of crabs dominating the

diet were similar among spring, fall, and winter ($\chi_1^2 \leq 2.71$; $P \geq 0.10$). The logistic model containing only the effects of region nested within season indicated that the season-specific odds of crabs dominating the diet of largemouth bass was different between regions ($\chi_7^2 = 217.23$; $P < 0.001$). The odds were 3.2, 2.6, 1.9, and 3.4 times higher in the downstream region compared to the upstream region during the spring, summer, fall, and winter, respectively ($\chi_1^2 \geq 17.45$; $P \leq 0.001$).

Backward model selection indicated that the best model describing the odds of largemouth bass having an empty stomach included the main effects of age ($\chi_1^2 = 30.68$; $P < 0.001$), season ($\chi_3^2 = 61.31$; $P < 0.001$), and region ($\chi_1^2 = 31.99$; $P < 0.001$), as well as the interaction between age and season ($\chi_3^2 = 20.91$; $P < 0.001$) and between region and season ($\chi_3^2 = 32.15$; $P < 0.001$). The odds of largemouth bass having an empty stomach increased at a rate of 29%, 20%, and 20% with age during the spring ($\chi_1^2 = 26.05$; $P < 0.001$; Figure A.4a), summer ($\chi_1^2 = 7.74$; $P = 0.005$; Figure A.4b), and fall ($\chi_1^2 = 9.49$; $P = 0.002$; Figure A.4c), respectively, but did not have an effect during the winter ($\chi_1^2 = 0.16$; $P = 0.69$; Figure A.4d). At any particular age the odds of observing an empty stomach was 1.4, 2.3, and 1.6 times higher in the upstream region compared to the downstream region during the spring ($\chi_1^2 = 6.95$; $P = 0.008$), summer ($\chi_1^2 = 27.83$; $P < 0.001$), and fall ($\chi_1^2 = 11.16$; $P < 0.001$), respectively. The odds were similar between regions during the winter period ($\chi_1^2 = 2.01$; $P = 0.16$). The odds of an empty stomach corrected for the effect of age was highest during the winter in the upstream ($\chi_1^2 \geq 8.41$; $P \leq 0.004$) and downstream region ($\chi_1^2 \geq 34.86$; $P < 0.001$). All other seasons had similar odds of observing a largemouth bass with an empty stomach in both regions ($\chi_1^2 \leq 2.86$; $P \geq 0.09$).

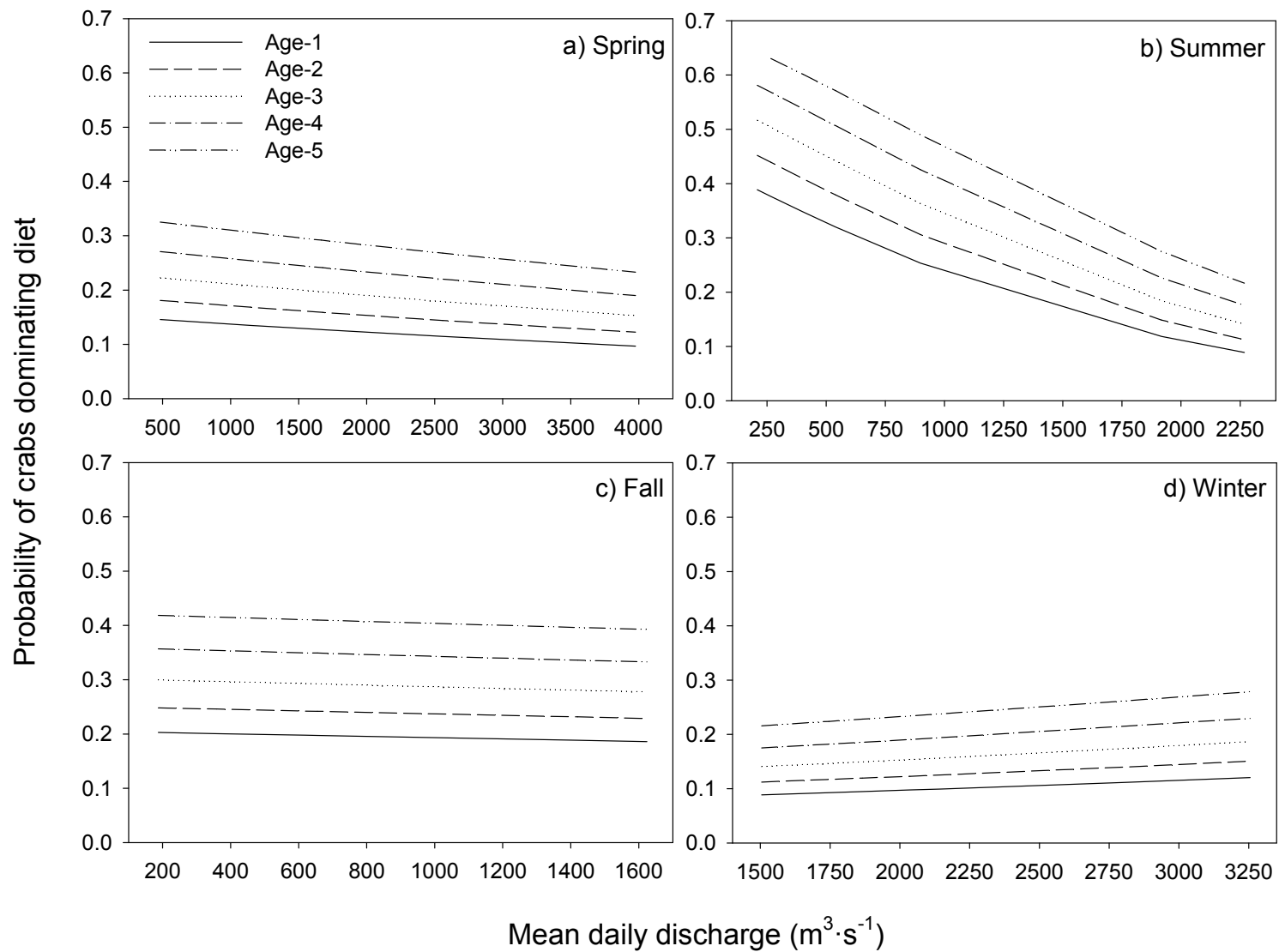


Figure A.1

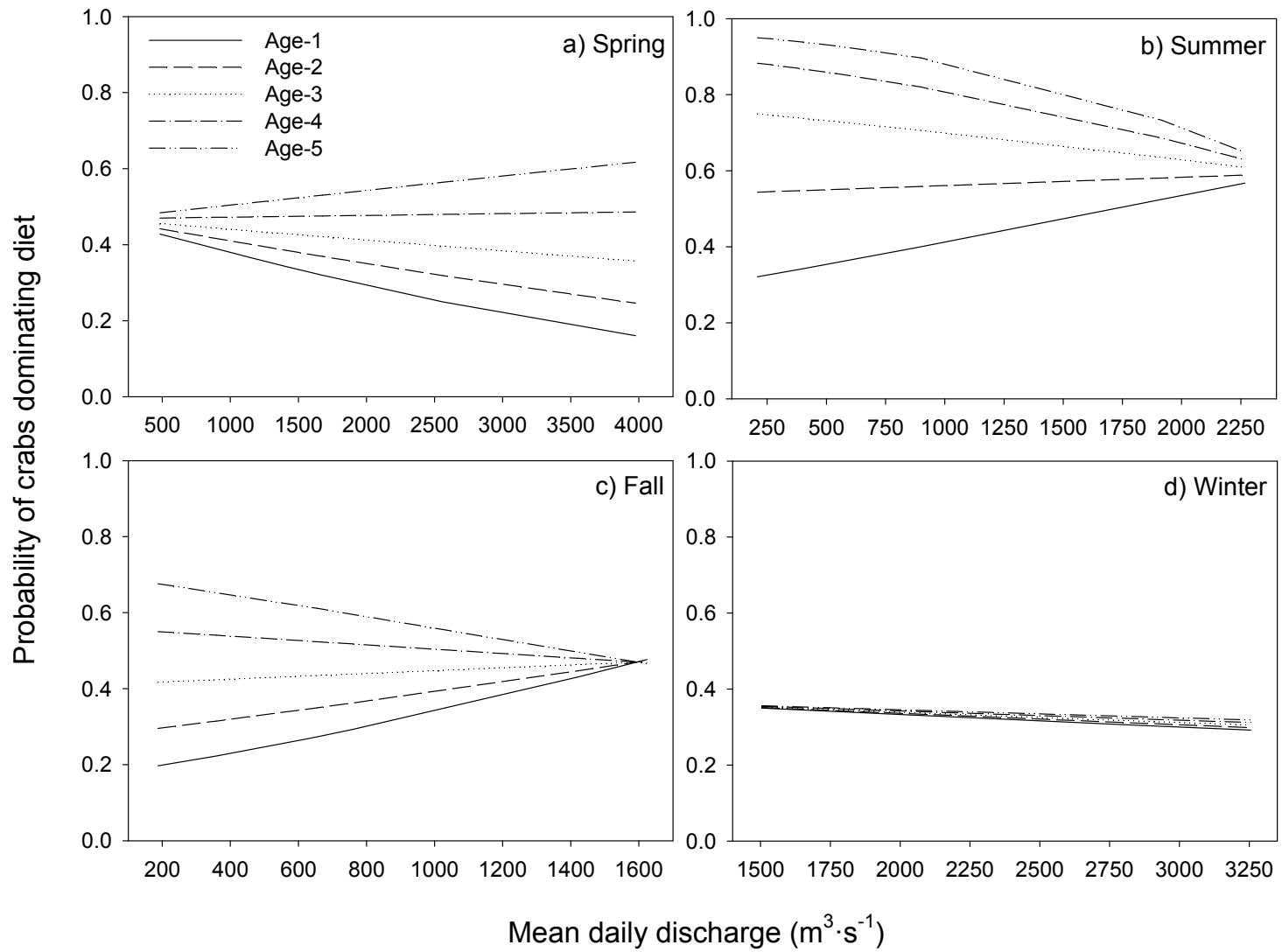


Figure A.2

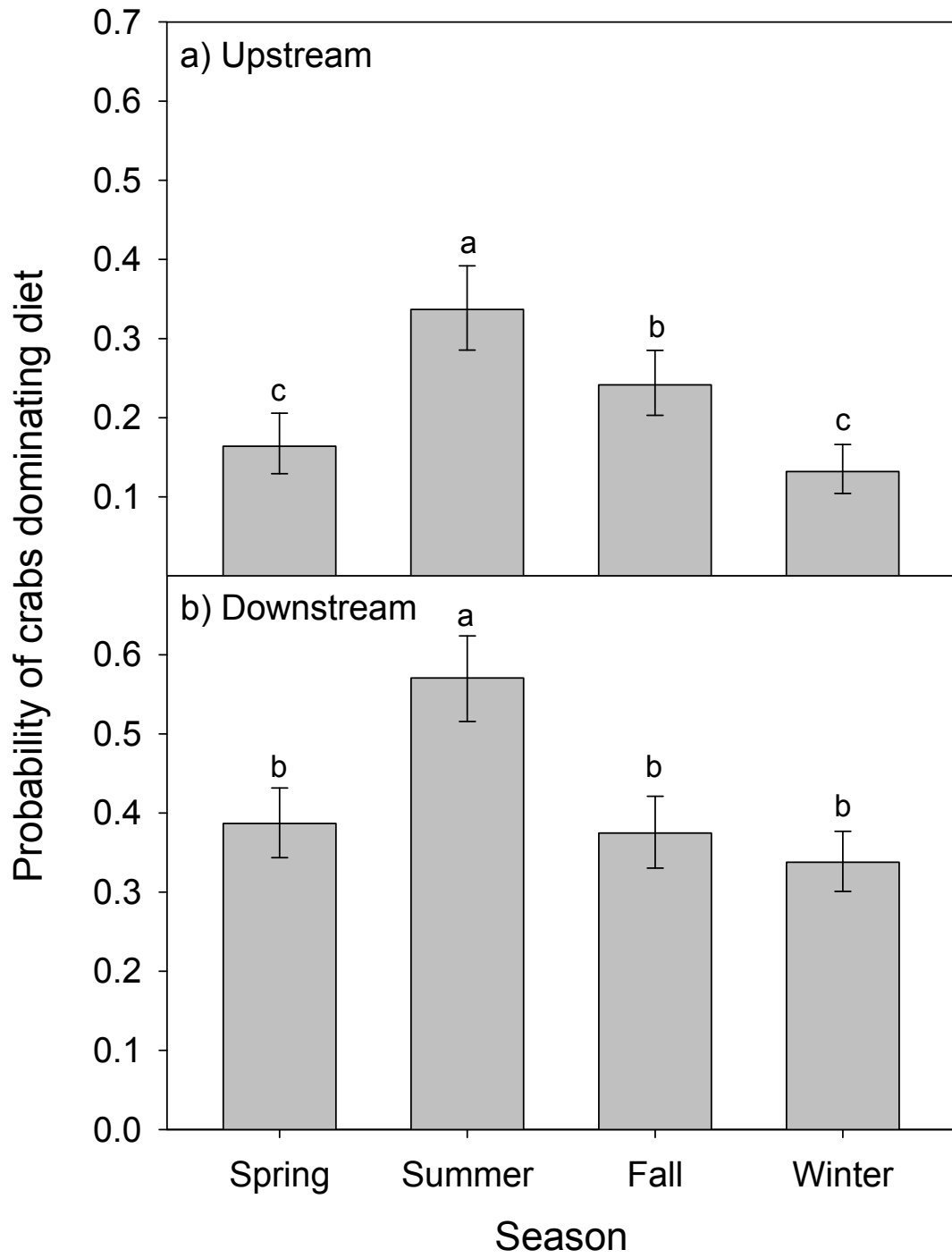


Figure A.3

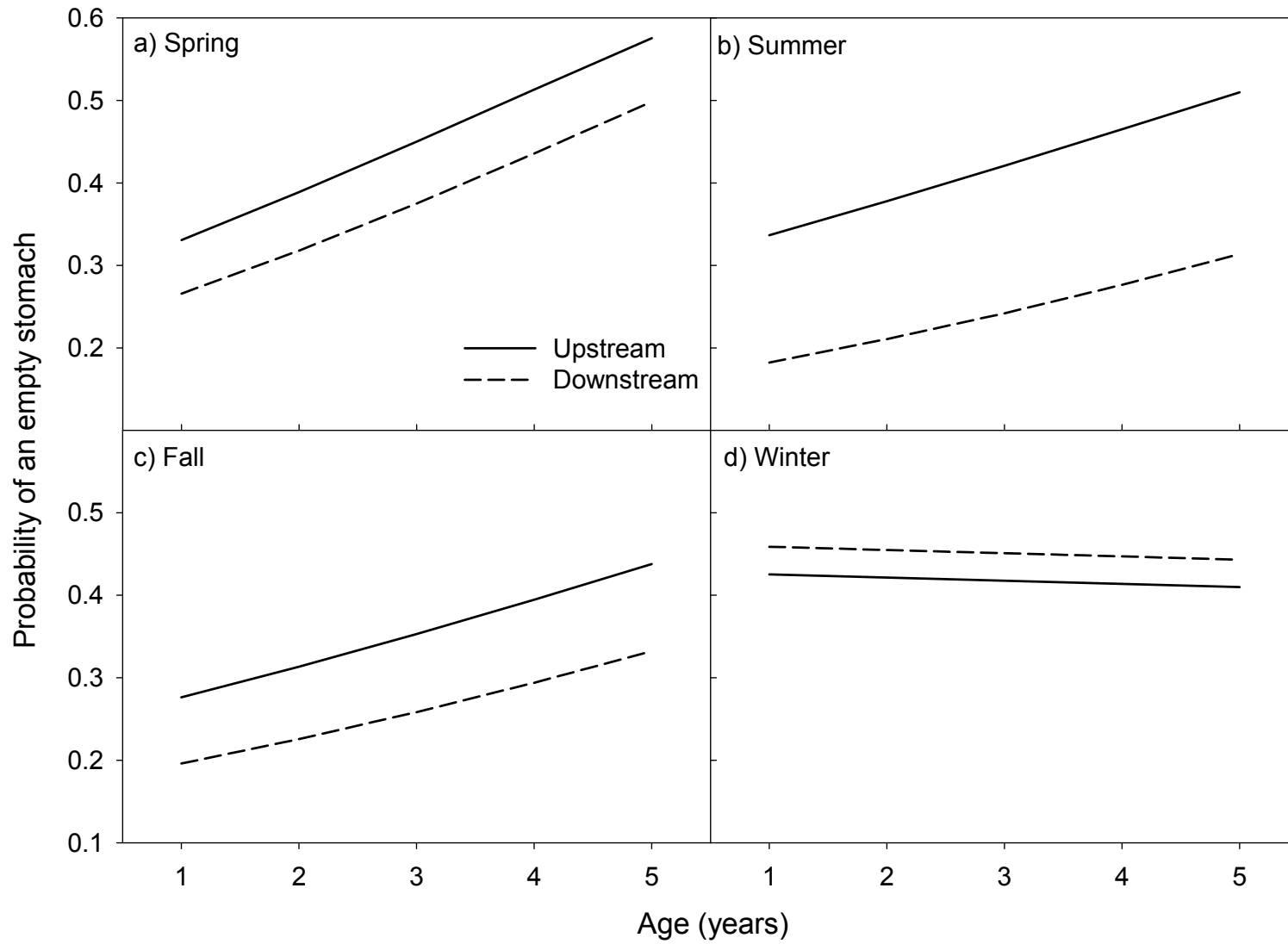


Figure A.4

Appendix 2. Visual Basics code used for bioenergetics simulations in Chapter III.

'Basic model run values

```
Private Const Cohort = 5
Private Const Start_day = 1
Private Const Final_day = 365
Private Const Prey_types = 7
Private Const AgeAtFirstRepro = 1
Private Const DayofSpawning = 365
```

'Parameter values for consumption function

```
Private Const CA = 0.33
Private Const CB = -0.325
Private Const CQ = 2.65
Private Const CTO = 27.5
Private Const CTM = 37
```

'Wisconsin bioenergetics respiration values

```
Private Const RA = 0.00279
Private Const RB = -0.355
Private Const RQ = 0.0811
Private Const RTO = 0.0196
Private Const RTM = 0
Private Const RTL = 0
Private Const RK1 = 1
Private Const RK4 = 0
Private Const ACT = 1
Private Const BACT = 0
Private Const SDA = 0.142
```

'Parameter values for Mobile Delta largemouth bass respiration

```
Private Const MTRD_RA = 0.003774
Private Const MTRD_RB = -0.2393
Private Const MTRD_RS = -0.00238
Private Const ISOTONIC = 9.2999
Private Const MTRD_RQ = 0.0375
```

'Parameter values for egestion and excretion

```
Private Const FA = 0.104
Private Const UA = 0.079
```

'Values for prey energy densities

```
Private Const ffish_ed = 1122.56 'Freshwater fish
Private Const efish_ed = 1191.98 'Estuarine fish
Private Const mfish_ed = 1108.49 'Marine fish
Private Const crab_ed = 594.57 'Blue crabs
```



```

Private Const shrimp_ed = 822.38 'Shrimp
Private Const cray_ed = 827.5 'Crayfish
Private Const invert_ed = 874.84 'Insects and others

```

'Arrays to store daily values and results from each formula

```

Dim Start_wt(1 To Cohort)
Dim Final_wt(1 To Cohort)
Dim temp(1 To Cohort, Start_day To Final_day)
Dim salinity(1 To Cohort, Start_day To Final_day)
Dim ffish_prop(1 To Cohort, Start_day To Final_day)
Dim efish_prop(1 To Cohort, Start_day To Final_day)
Dim mfish_prop(1 To Cohort, Start_day To Final_day)
Dim cray_prop(1 To Cohort, Start_day To Final_day)
Dim crab_prop(1 To Cohort, Start_day To Final_day)
Dim shrimp_prop(1 To Cohort, Start_day To Final_day)
Dim invert_prop(1 To Cohort, Start_day To Final_day)
Dim ave_prey_ed(1 To Cohort, Start_day To Final_day)
Dim pred_ed(1 To Cohort, Start_day To Final_day)
Dim Mass(1 To Cohort, Start_day - 1 To Final_day)
Dim CMAX_g(1 To Cohort, Start_day To Final_day)
Dim C_g(1 To Cohort, Start_day To Final_day)
Dim R_g(1 To Cohort, Start_day To Final_day)
Dim F_g(1 To Cohort, Start_day To Final_day)
Dim U_g(1 To Cohort, Start_day To Final_day)
Dim S_g(1 To Cohort, Start_day To Final_day)
Dim Perc_diff(1 To Cohort)
Dim p(1 To Cohort)
Dim final_p(1 To Cohort)
Dim iterations(1 To Cohort)
Dim Gonad_g(1 To Cohort, Start_day To Final_day)
Dim Resid_gonad_g(1 To Cohort, Start_day To Final_day)
Dim repro_costs(1 To Cohort, Start_day To Final_day)

```

'Subroutine to clear "Results" sheet prior to writing new output

```

Private Sub ClearResults()
    With Worksheets("Results")
        .Select
        .Range(.Cells(1, 1), .Cells(((10 * Final_day) + 1), (parms + 2))).Select
        Selection.ClearContents
    End With
    With Worksheets("Model Run")
        .Select
        .Range(.Cells(1, 6), .Cells(11, 10)).Select
        Selection.ClearContents
    End With
End Sub

```

'Subroutine to assign user-specified values to arrays

Private Sub model_parms()

For c = 1 To Cohort

For i = Start_day To Final_day

temp(c, i) = Worksheets("Temperature").Cells(i + 1, 2)

salinity(c, i) = Worksheets("Salinity").Cells(i + 1, 2)

ffish_prop(c, i) = Worksheets("Diet Proportions").Cells(i + 2, 2 + (c - 1) *
Prey_types)

efish_prop(c, i) = Worksheets("Diet Proportions").Cells(i + 2, 3 + (c - 1) *
Prey_types)

mfish_prop(c, i) = Worksheets("Diet Proportions").Cells(i + 2, 4 + (c - 1) *
Prey_types)

crab_prop(c, i) = Worksheets("Diet Proportions").Cells(i + 2, 5 + (c - 1) *
Prey_types)

shrimp_prop(c, i) = Worksheets("Diet Proportions").Cells(i + 2, 6 + (c - 1) *
Prey_types)

cray_prop(c, i) = Worksheets("Diet Proportions").Cells(i + 2, 7 + (c - 1) *
Prey_types)

invert_prop(c, i) = Worksheets("Diet Proportions").Cells(i + 2, 8 + (c - 1) *
Prey_types)

Next i

Start_wt(c) = Worksheets("Model Run").Cells(c + 1, 4)

Final_wt(c) = Worksheets("Model Run").Cells(c + 1, 5)

Next c

End Sub

'Function to determine maximum consumption (g/g/day)

Private Function MaximumConsumption(Mass)

MaximumConsumption = (CA * Mass ^ CB)

End Function

'Function to determine temperature-corrected consumption for a given proportion of maximum consumption

Private Function RealizedConsumption(CMAX, temp, pofCMAX)

If temp > CTM Then

RealizedConsumption = 0

Else: V = (CTM - temp) / (CTM - CTO)

Z = Log(CQ) * (CTM - CTO)

Y = Log(CQ) * (CTM - CTO + 2)

X = (Z ^ 2 * (1 + (1 + 40 / Y) ^ 0.5) ^ 2) / 400

temp_func = V ^ X * Exp(X * (1 - V))

RealizedConsumption = CMAX * temp_func * pofCMAX

End If

End Function

'Function to determine respiration (g O₂/g/day) using the Mobile Delta-derived equation

Private Function MTRD_Respiration(Mass, temp, salinity)

If temp > RTL Then

VEL = RK1 * Mass ^ RK4

Else: VEL = ACT * Mass ^ RK4 * Exp(BACT * temp)

End If

ACTIVITY = Exp(RTO * VEL)

MTRD_Respiration = MTRD_RA * (Mass ^ (MTRD_RB * Exp(MTRD_RS *
((salinity) * ((salinity - ISOTONIC) ^ 2)))) * Exp(MTRD_RQ
* temp) * ACTIVITY

End Function

'Function to determine egestion (g/g/day)

Private Function Egestion(g_consumed)

Egestion = FA * g_consumed

End Function

'Function to determine SDA (g/g/day)

Private Function SpecDynAct(g_consumed, g_egested)

SpecDynAct = SDA * (g_consumed - g_egested)

End Function

'Function to determine excretion (g/g/day)

Private Function Excretion(g_consumed, g_egested)

Excretion = UA * (g_consumed - g_egested)

End Function

'Function to determine the average prey energy density (cal/g) from seven different prey items

Private Function prey_ed(preylprop, preyled, prey2prop, prey2ed, prey3prop, prey3ed,
prey4prop, prey4ed, prey5prop, prey5ed, prey6prop, prey6ed, prey7prop, prey7ed)

prey_ed = (preylprop * preyled) + (prey2prop * prey2ed) + (prey3prop * prey3ed) +
(prey4prop * prey4ed) + (prey5prop * prey5ed) + (prey6prop * prey6ed) +
(prey7prop * prey7ed)

End Function

'Function for log base-10

Static Function Log10(X)

Log10 = Log(X) / Log(10#)

End Function

'Function to determine predator energy density (cal/g) as a function of body mass

Private Function PredEnergyDensity(DayofYear, Mass)

If 244 <= DayofYear <= 335 Then

Log_ED = 2.942 + 0.057 * Log10(Mass) 'If summer, then use this equation

Else: Log_ED = 2.918 + 0.057 * Log10(Mass) 'if not summer, use this equation

```

End If
PredEnergyDensity = 10 ^ Log_ED
End Function

```

'Function to determine the gonad mass (g) from the mass of the fish

```

Private Function Gonad_mass(Mass)
    Gonad_mass = Mass * 0.07 - 1.53
End Function

```

'Function to determine the residual gonad mass (g) of the fish post-spawn

```

Private Function Residual_gonad(Mass)
    Residual_gonad = Mass * 0.01 - 1.78
End Function

```

'Function to determine the cost of spawning (cal)

```

Private Function Spawning_cost(Age, DayofYear, Gonad_mass, Residual_gonad, Mass)
If Age >= AgeAtFirstRepro Then 'if the fish is old enough to spawn
    If DayofYear = DayofSpawning Then 'and it is the day of spawning
        GSI_max = 100 * (Gonad_mass / Mass) 'then estimate spawning cost
        GSI_resid = 100 * (Residual_gonad / Mass)
        Log_GonadED = 2.9952 + 0.3907 * Log10(GSI_max)
        Log_ResidED = 2.9952 + 0.3907 * Log10(Abs(GSI_resid))
        Spawning_cost = (Gonad_mass * (10 ^ Log_GonadED)) - (Residual_gonad * (10
            ^ Log_ResidED))
        Else: Spawning_cost = 0 'if it isn't the day of spawning, there is no cost
    End If
    Else: Spawning_cost = 0 'if the fish isn't old enough to spawn, there is no cost
End If
End Function

```

'Function to determine the mass at the next day after accounting for caloric gains and losses. Note that the constant of 3240 calories per gram of oxygen consumed was used to convert to calories (Elliot and Davidson 1975)

```

Private Function ChangeInMass(Mass, g_consumed, g_SDA, g_egested, g_excreted,
g_O2_respired, prey_energy_density, predator_energy_density, Spawning_cost)
    CaloriesGained = g_consumed * Mass * prey_energy_density
    CaloriesLost = ((g_SDA + g_egested + g_excreted) * Mass * prey_energy_density) +
        (g_O2_respired * Mass * 3240) + Spawning_cost
    ChangeInMass = (CaloriesGained - CaloriesLost) / predator_energy_density
End Function

```

'Subroutine that writes the results to the spreadsheets

```

Private Sub WriteResults(t)
For c = 1 To Cohort
    For i = Start_day To Final_day
        Worksheets("Results").Cells(1, 1) = "Cumulative Days"

```

Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 1) = (i + (c - 1) * (Final_day))
 Worksheets("Results").Cells(1, 2) = "Cohort Days"
 Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 2) = i
 Worksheets("Results").Cells(1, 3) = "Temperature"
 Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 3) = temp(c, i)
 Worksheets("Results").Cells(1, 4) = "Salinity"
 Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 4) = salinity(c, i)
 Worksheets("Results").Cells(1, 5) = "Total Consumption (g/g)"
 Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 5) = C_g(c, i)
 Worksheets("Results").Cells(1, 6) = "FW Fish Consumed (g/g)"
 Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 6) = ffish_prop(c, i) * C_g(c, i)
 Worksheets("Results").Cells(1, 7) = "Est Fish Consumed (g/g)"
 Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 7) = efish_prop(c, i) * C_g(c, i)
 Worksheets("Results").Cells(1, 8) = "Mar Fish Consumed (g/g)"
 Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 8) = mfish_prop(c, i) * C_g(c, i)
 Worksheets("Results").Cells(1, 9) = "Crabs Consumed (g/g)"
 Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 9) = crab_prop(c, i) * C_g(c, i)
 Worksheets("Results").Cells(1, 10) = "Shrimp Consumed (g/g)"
 Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 10) = shrimp_prop(c, i) * C_g(c, i)
 Worksheets("Results").Cells(1, 11) = "Crayfish Consumed (g/g)"
 Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 11) = cray_prop(c, i) * C_g(c, i)
 Worksheets("Results").Cells(1, 12) = "Inverts Consumed (g/g)"
 Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 12) = invert_prop(c, i) * C_g(c, i)
 Worksheets("Results").Cells(1, 13) = "Total Consumption (cal/g)"
 Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 13) = C_g(c, i) * ave_prey_ed(c, i)
 Worksheets("Results").Cells(1, 14) = "FW Fish Consumed (cal/g)"
 Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 14) = ffish_prop(c, i) * C_g(c, i) * ffish_ed
 Worksheets("Results").Cells(1, 15) = "Est Fish Consumed (cal/g)"
 Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 15) = efish_prop(c, i) * C_g(c, i) * efish_ed
 Worksheets("Results").Cells(1, 16) = "Mar Fish Consumed (cal/g)"
 Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 16) = mfish_prop(c, i) * C_g(c, i) * mfish_ed
 Worksheets("Results").Cells(1, 17) = "Crabs Consumed (cal/g)"
 Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 17) = crab_prop(c, i) * C_g(c, i) * crab_ed

```

Worksheets("Results").Cells(1, 18) = "Shrimp Consumed (cal/g)"
Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 18) = shrimp_prop(c,
i) * C_g(c, i) * shrimp_ed
Worksheets("Results").Cells(1, 19) = "Crayfish Consumed (cal/g)"
Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 19) = cray_prop(c, i) *
C_g(c, i) * cray_ed
Worksheets("Results").Cells(1, 20) = "Inverts Consumed (cal/g)"
Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 20) = invert_prop(c, i)
* C_g(c, i) * invert_ed
Worksheets("Results").Cells(1, 21) = "Respiration (cal/g)"
Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 21) = R_g(c, i) * 3240
Worksheets("Results").Cells(1, 22) = "Egestion (cal/g)"
Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 22) = F_g(c, i) *
ave_prey_ed(c, i)
Worksheets("Results").Cells(1, 23) = "SDA (cal/g)"
Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 23) = S_g(c, i) *
ave_prey_ed(c, i)
Worksheets("Results").Cells(1, 24) = "Excretion (cal/g)"
Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 24) = U_g(c, i) *
ave_prey_ed(c, i)
Worksheets("Results").Cells(1, 25) = "Gonad mass(g)"
Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 25) = Gonad_g(c, i)
Worksheets("Results").Cells(1, 26) = "Mass (g)"
Worksheets("Results").Cells(((i + 1) + (c - 1) * (Final_day)), 26) = Mass(c, i)

```

Next i

```

Worksheets("Model Run").Cells(1, 6) = "P-value"
Worksheets("Model Run").Cells(c + 1, 6) = final_p(c)
Worksheets("Model Run").Cells(1, 7) = "Iterations attempted"
Worksheets("Model Run").Cells(c + 1, 7) = iterations(c)
Worksheets("Model Run").Cells(1, 8) = "Predicted end wt (g)"
Worksheets("Model Run").Cells(c + 1, 8) = Mass(c, Final_day)

```

Next c

```

Worksheets("Results").Columns("A:AA").AutoFit 'autofits column widths
Worksheets("Model Run").Columns("A:H").AutoFit 'autofits column widths

```

End Sub

'Subroutine to determine proportion of maximum consumption for each cohort

Private Sub DeterminePvalues_Click()

Call ClearResults

Call model_parms

For c = 1 To Cohort 'loop through cohorts

Mass(c, Start_day - 1) = Start_wt(c) 'use the start weight from day = 0 to begin
'the process

iterations(c) = 0

p(c) = 0.5 'initial p-value to begin evaluating

Do

```

If p(c) > 1 Then 'if the new p-value is > 1 then provide this warning message
    MsgBox "The p-value exceeded 1 for cohort " & c & " on iteration " &
        iterations(c) & "."
End If
If p(c) < 0 Then 'if the new p-value is < 0 then provide this warning message
    MsgBox "The p-value is below 0 for cohort " & c & " on iteration " &
        iterations(c) & "."
End If
Select Case p(c) 'exit program if p-value is < 0 or > 1
    Case Is > 1: Exit Sub 'exit the Sub procedure if the new p-value is > 1
    Case Is < 0: Exit Sub 'exit the Sub procedure if the new p-value is < 0
End Select
For i = Start_day To Final_day 'loop through days within a cohort
    ave_prey_ed(c, i) = prey_ed(ffish_prop(c, i), ffish_ed, efish_prop(c, i),
        efish_ed, mfish_prop(c, i), mfish_ed, crab_prop(c, i), crab_ed, shrimp_prop(c,
        i), shrimp_ed, cray_prop(c, i), cray_ed, invert_prop(c, i), invert_ed)
    CMAX_g(c, i) = MaximumConsumption(Mass(c, i - 1))
    C_g(c, i) = RealizedConsumption(CMAX_g(c, i), temp(c, i), p(c))
    R_g(c, i) = MTRD_Respiration(Mass(c, i - 1), temp(c, i), salinity(c, i))
    F_g(c, i) = Egestion(C_g(c, i))
    S_g(c, i) = SpecDynAct(C_g(c, i), F_g(c, i))
    U_g(c, i) = Excretion(C_g(c, i), F_g(c, i))
    pred_ed(c, i) = PredEnergyDensity(i - 1, Mass(c, i - 1))
    Gonad_g(c, i) = Gonad_mass(Mass(c, i - 1))
    Resid_gonad_g(c, i) = Residual_gonad(Mass(c, i - 1))
    repro_costs(c, i) = Spawning_cost(c, i, Gonad_g(c, i), Resid_gonad_g(c, i),
        Mass(c, i - 1))
    Mass(c, i) = Mass(c, i - 1) + ChangeInMass(Mass(c, i - 1), C_g(c, i), S_g(c, i),
        F_g(c, i), U_g(c, i), R_g(c, i), ave_prey_ed(c, i), pred_ed(c, i),
        repro_costs(c, i))
Next i 'go to next day
    final_p(c) = p(c) 'this is the final p-value chosen if following criteria are met
    Perc_diff(c) = (100 * ((Mass(c, Final_day) - Final_wt(c)) / Final_wt(c)))
        'percent difference between observed and predicted growth
If Perc_diff(c) < 0 Then 'if the difference is negative
    p(c) = p(c) + (p(c) * (Abs(Perc_diff(c)) / 1000)) 'then try a larger p-value in
        'proportion to the percent
        'difference
    Else: p(c) = p(c) - (p(c) * (Abs(Perc_diff(c)) / 1000)) 'if it is positive then use a
        'smaller p-value in
        'proportion to the percent
        'difference

End If
iterations(c) = iterations(c) + 1 'add 1 to the number of iterations attempted for
        'proportion of maximum consumption
Loop Until Abs(Perc_diff(c)) <= 0.001 'keep attempting different p-values until the

```

'percent diff is within +/- 0.001%

```
Next c 'go to next cohort
Call WriteResults(t)
End Sub
```

'Subroutine to determine growth for each age separately based on a user-specified proportion of maximum consumption and start weights for each cohort

```
Private Sub AgeSpecificGrowth_Click()
Call ClearResults
Call model_parms
For c = 1 To Cohort 'loop through cohorts
  Mass(c, Start_day - 1) = Start_wt(c) 'use the start mass from day = 0 for each
                                     'cohort to begin the process
  For i = Start_day To Final_day 'loop through days within a cohort
    ave_pre_yed(c, i) = prey_ed(ffish_prop(c, i), ffish_ed, efish_prop(c, i), efish_ed,
                                mfish_prop(c, i), mfish_ed, crab_prop(c, i), crab_ed,
                                shrimp_prop(c, i), shrimp_ed, cray_prop(c, i), cray_ed,
                                invert_prop(c, i), invert_ed)
    CMAX_g(c, i) = MaximumConsumption(Mass(c, i - 1))
    C_g(c, i) = RealizedConsumption(CMAX_g(c, i), temp(c, i), p(c))
    R_g(c, i) = MTRD_Respiration(Mass(c, i - 1), temp(c, i), salinity(c, i))
    F_g(c, i) = Egestion(C_g(c, i))
    S_g(c, i) = SpecDynAct(C_g(c, i), F_g(c, i))
    U_g(c, i) = Excretion(C_g(c, i), F_g(c, i))
    pred_ed(c, i) = PredEnergyDensity(i - 1, Mass(c, i - 1))
    Gonad_g(c, i) = Gonad_mass(Mass(c, i - 1))
    Resid_gonad_g(c, i) = Residual_gonad(Mass(c, i - 1))
    repro_costs(c, i) = Spawning_cost(c, i, Gonad_g(c, i), Resid_gonad_g(c, i),
                                     Mass(c, i - 1))
    Mass(c, i) = Mass(c, i - 1) + ChangeInMass(Mass(c, i - 1), C_g(c, i), S_g(c, i),
                                                F_g(c, i), U_g(c, i), R_g(c, i), ave_pre_yed(c, i), pred_ed(c, i),
                                                repro_costs(c, i))
  Next i 'go to next day
Next c 'go to next cohort
Call WriteResults(t)
End Sub
```

'Subroutine to predict lifetime growth based on a user-specified age-specific proportion of maximum consumption and a single starting weight

```
Private Sub LifetimeGrowth_Click()
Call ClearResults
Call model_parms
For c = 1 To Cohort 'loop through cohorts
  Mass(1, Start_day - 1) = Start_wt(1) 'use the start weight from day = 0 for cohort 1
  If c > 1 Then 'if the cohort number is greater than one
    Mass(c, Start_day - 1) = Mass(c - 1, Final_day) 'then use the final mass of the
```


'previous cohort as the starting
'mass for the current cohort

End If

For i = Start_day To Final_day 'loop through days within a cohort

ave_pre_y_ed(c, i) = prey_ed(ffish_prop(c, i), ffish_ed, efish_prop(c, i), efish_ed,
mfish_prop(c, i), mfish_ed, crab_prop(c, i), crab_ed,
shrimp_prop(c, i), shrimp_ed, cray_prop(c, i), cray_ed,
invert_prop(c, i), invert_ed)

CMAX_g(c, i) = MaximumConsumption(Mass(c, i - 1))

C_g(c, i) = RealizedConsumption(CMAX_g(c, i), temp(c, i), p(c))

R_g(c, i) = MTRD_Respiration(Mass(c, i - 1), temp(c, i), salinity(c, i))

F_g(c, i) = Egestion(C_g(c, i))

S_g(c, i) = SpecDynAct(C_g(c, i), F_g(c, i))

U_g(c, i) = Excretion(C_g(c, i), F_g(c, i))

pred_ed(c, i) = PredEnergyDensity(i - 1, Mass(c, i - 1))

Gonad_g(c, i) = Gonad_mass(Mass(c, i - 1))

Resid_gonad_g(c, i) = Residual_gonad(Mass(c, i - 1))

repro_costs(c, i) = Spawning_cost(c, i, Gonad_g(c, i), Resid_gonad_g(c, i),
Mass(c, i - 1))

Mass(c, i) = Mass(c, i - 1) + ChangeInMass(Mass(c, i - 1), C_g(c, i), S_g(c, i),
F_g(c, i), U_g(c, i), R_g(c, i), ave_pre_y_ed(c, i), pred_ed(c, i),
repro_costs(c, i))

Next i 'go to the next day

Next c 'go to the next cohort

Call WriteResults(t)

End Sub

Appendix 3. Visual Basics code for optimal energy allocation model using backward iteration (Chapter IV)

'Model run parameters

```
Private Const Cohort = 10 'total number of cohorts/age groups
Private Const Start_week = 1 'initial week of simulation
Private Const Final_week = 52 'final week of simulation
Private Const PofCmax = 0.6 'proportion of maximum consumption (set to 0.5 or 0.6)
Private Const Soma_ED = 1081 'lean body mass energy density that is used for
    'determining growth in length (Barziza and Gatlin 2000)
Private Const Fat_ED = 8693.991 'energy density of lipids (Brett 1995)
Private Const Ave_prej_ED = 1000 'average prey energy density
```

'Parameter values for consumption

```
Private Const CA = 0.33
Private Const CB = -0.325
Private Const CQ = 2.65
Private Const CTO = 27.5
Private Const CTM = 37
```

'WI bioenergetic respiration values

```
Private Const RA = 0.00279
Private Const RB = -0.355
Private Const RQ = 0.0811
Private Const RTO = 0.0196
Private Const RTM = 0
Private Const RTL = 0
Private Const RK1 = 1
Private Const RK4 = 0
Private Const ACT = 1
Private Const BACT = 0
Private Const SDA = 0.142
```

'Parameter values for MTRD bass respiration

```
Private Const MTRD_RA = 0.003774
Private Const MTRD_RB = -0.2393
Private Const MTRD_RS = -0.00238
Private Const ISOTONIC = 9.2999
Private Const MTRD_RQ = 0.0375
```

'Parameter values for egestion/excretion

```
Private Const FA = 0.104
Private Const UA = 0.079
```

'Various sizes for the model to evaluate

Private Const minTL = 10 'minimum TL to evaluate

Private Const maxTL = 625 'maximum TL to evaluate

Private Const TLstep = 15 'step size for TL

Private Const TLarray = ((maxTL - minTL) / TLstep) 'determines the total number of
'elements in the total length array
'based on TL step size

Private Const gminprop = 0 'minimum proportion of ovaries (as an index)

Private Const gmaxprop = 10 'maximum proportion of ovaries (as an index)

Private Const fminprop = 0 'minimum proportion of fat reserves (as an index)

Private Const fmaxprop = 10 'maximum proportion of fat reserves (as an index)

Private Const nsigma = 10 'number of divisions for allocation

Private Const gmin = 0 'smallest possible ovary size

Private Const fmin = 0 'smallest possible amount of fat = death

Private Const smax = (10 ^ -5.2687) * (maxTL ^ 3.1498) 'maximum lean body mass
possible

Private Const outfile30\$ = "C:\Documents and Settings\glovedc\Desktop\oea results
(surv = 0.3, ration = " & PofCmax & ").txt" 'filename to export to if survival rate is 30%

Private Const outfile50\$ = "C:\Documents and Settings\glovedc\Desktop\oea results
(surv = 0.5, ration = " & PofCmax & ").txt" 'filename to export to if survival rate is 50%

Private Const outfile70\$ = "C:\Documents and Settings\glovedc\Desktop\oea results
(surv = 0.7, ration = " & PofCmax & ").txt" 'filename to export to if survival is 70%

'Arrays used to keep track of calculations and results

Dim temp(Start_week To Final_week) 'Keeps track of the daily temperature values

Dim salinity(Start_week To Final_week) 'Keeps track of the daily salinity values

Dim ft(0 To 1, 0 To TLarray, gminprop To gmaxprop, fminprop To fmaxprop, 0 To 1)

'ft(Probability of salt, TL, Gonad mass, Fat reserves, 0) = current fitness

'ft(Probability of salt, TL, Gonad mass, Fat reserves, 1) = future fitness

Dim rhs0(0 To nsigma, 0 To nsigma) 'keeps track of value of right hand side of dynamic
programming equation until all are evaluated (freshwater environment)

Dim rhs1(0 To nsigma, 0 To nsigma) 'keeps track of value of right hand side of dynamic
programming equation until all are evaluated (salty environment)

Dim sigmasstar(0 To 1, 1 To Cohort, Start_week To Final_week, 0 To TLarray,
gminprop To gmaxprop, fminprop To fmaxprop)

'optimal allocation of energy to somatic tissue given probability of salt with states TL,
'gonad proportion of max, and energy reserves as a proportion of max

Dim sigmagstar(0 To 1, 1 To Cohort, Start_week To Final_week, 0 To TLarray,
gminprop To gmaxprop, fminprop To fmaxprop)

'optimal allocation of energy to ovaries given probability of salt with states TL, gonad
'proportion of max, and energy reserves as a proportion of max

Dim sigmafstar(0 To 1, 1 To Cohort, Start_week To Final_week, 0 To TLarray,
gminprop To gmaxprop, fminprop To fmaxprop)

'optimal allocation of energy to fat reserves given probability of salt with states TL,
'gonad proportion of max, and energy reserves as a proportion of max

'Assigns parameter values to arrays for bioenergetics model from worksheets

```
Private Sub model_parms()  
  For i = Start_week To Final_week  
    temp(i) = Worksheets("Temperature").Cells(i + 1, 2)  
    salinity(i) = Worksheets("Salinity").Cells(i + 1, 2)  
  Next i  
End Sub
```

'Bioenergetics model to determine net calories available for allocation on the ith week for the cth cohort

```
Private Function Net_Calories(Total_mass, temp, salinity, PofCmax, prey_ED)  
  'consumption (g/g/day)  
  CMAX = (CA * Total_mass ^ CB)  
  V = (CTM - temp) / (CTM - CTO)  
  Z = Log(CQ) * (CTM - CTO)  
  Y = Log(CQ) * (CTM - CTO + 2)  
  x = (Z ^ 2 * (1 + (1 + 40 / Y) ^ 0.5) ^ 2) / 400  
  temp_func = V ^ x * Exp(x * (1 - V))  
  g_consumed = CMAX * temp_func * PofCmax  
  'respiration (g O2/g/day)  
  If temp > RTL Then  
    VEL = RK1 * Total_mass ^ RK4  
  Else: VEL = ACT * Total_mass ^ RK4 * Exp(BACT * temp)  
  End If  
  ACTIVITY = Exp(RTO * VEL)  
  g_O2_respired = MTRD_RA * (Total_mass ^ (MTRD_RB * Exp(MTRD_RS *  
    ((salinity) * ((salinity - ISOTONIC) ^ 2)))) * Exp(MTRD_RQ *  
    temp) * ACTIVITY  
  'egestion (g/g/day)  
  g_egested = FA * g_consumed  
  'SDA (g/g/day)  
  g_SDA = SDA * (g_consumed - g_egested)  
  'excretion (g/g/day)  
  g_excreted = UA * (g_consumed - g_egested)  
  'Function to determine the net energy available for growth after accounting for caloric  
  gains and losses. The constant of 3240 calories per gram of oxygen consumed is used  
  to convert to calories (Elliot and Davidson 1975)  
  CaloriesGained = (g_consumed * Total_mass * prey_ED) 'cal/day  
  CaloriesLost = (((g_SDA + g_egested + g_excreted) * Total_mass * prey_ED) +  
    (Total_mass * (g_O2_respired * 3240))) 'cal/day  
  Net_Calories = 7 * (CaloriesGained - CaloriesLost) 'cal/week  
End Function
```

'Static function to determine log base 10 values

Static Function Log10(x)

Log10 = Log(x) / Log(10#)

End Function

'Conversion between total length to somatic tissue (lean body mass) based on Barziza and Gatlin (2000)

Private Function TLtoSoma(Total_length)

Log10LBM = -5.2687 + 3.1498 * Log10(Total_length)

TLtoSoma = (10 ^ Log10LBM)

End Function

'Conversion between somatic tissue to total length based on based on Barziza and Gatlin (2000)

Private Function SomatoTL(Soma_mass)

LogTL = (Log10(Soma_mass) + 5.2687) / 3.1498

SomatoTL = 10 ^ LogTL

End Function

'Maximum mass of ovaries for a given length fish less than 203 mm TL have zero gonad mass

Private Function Max_Gonad(Total_length)

If Total_length >= 203 Then

Max_Gonad = Total_length * 0.3933 - 79.8083

Else: Max_Gonad = 0

End If

End Function

'Predicts the caloric density of the ovaries from the mass of the ovaries the caloric density of ovaries is based on the maximum ovary mass for the fish rather than giving them the option to grow ovarian tissue at a discounted rate

Private Function Gonad_ED(Total_length)

maxg = Max_Gonad(Total_length)

If maxg > 0 Then

Gonad_ED = (10 ^ 2.8418) * (maxg ^ 0.2441)

End If

End Function

'Predicts the residual gonad mass of the fish after spawning based on total length

Private Function Residual_gonad(Total_length)

Residual_gonad = Total_length * 0.0094 - 1.8859

End Function

'Maximum mass of lipids for a given total length based on Barziza and Gatlin (2000) data

```
Private Function Max_Fat(Total_length)
  Ln_max = -17.9973 + 3.815 * Log(Total_length)
  Max_Fat = Exp(Ln_max)
End Function
```

'Determines fecundity from ovary size. If size is less than 210 then fecundity is negative

```
Private Function Fecundity(Gonad_mass)
  x = 988.21 * Gonad_mass - 2558.1
  If x >= 0 Then
    Fecundity = x
  Else: Fecundity = 0
  End If
End Function
```

'Determines the change in somatic mass based on the net calories available and the proportion of energy devoted to somatic growth constrained not to lose somatic mass

```
Private Function Change_in_soma(Soma_ED, Net_Calories, ssigma)
  If Net_Calories >= 0 Then
    Change_in_soma = (Net_Calories * (ssigma / nsigma)) / Soma_ED
  Else: Change_in_soma = 0
  End If
End Function
```

'Determines the change in gonad mass based on the net calories available and the proportion of energy devoted to gonad growth, yet constrained not to lose gonad mass

```
Private Function Change_in_gonad(Total_length, Gonad_ED, Net_Calories, gsigma)
  If Net_Calories >= 0 And Total_length >= 203 Then
    Change_in_gonad = (Net_Calories * (gsigma / nsigma)) / Gonad_ED
  Else: Change_in_gonad = 0
  End If
End Function
```

'Determines the change in fat mass based on the net calories available and the proportion of energy devoted to fat growth. If net calories positive then add fat, if negative lose fat

```
Private Function Change_in_fat(Fat_ED, Net_Calories, fsigma)
  If Net_Calories >= 0 Then
    Change_in_fat = (Net_Calories * (fsigma / nsigma)) / Fat_ED
  Else: Change_in_fat = Net_Calories / Fat_ED
  End If
End Function
```

```

'General constraint function
Private Function chop(xxx, low, high)
chop = xxx
If xxx < low Then chop = low
If xxx > high Then chop = high
End Function

```

'This subroutine initializes F(Prob of salt,t,g,f,T,T), i.e., the probability of survival to terminal time based on current states

```

Private Sub TermTime()
For Salt_index = 0 To 1 Step 1 'Loop through salt absence/presence
  For t = 0 To TLarray Step 1 'Loop through total length index
    For g = gminprop To gmaxprop Step 1 'Loop through gonad index
      ft(Salt_index, t, g, 0, 1) = 0 'future fitness for fat = 0 is 0
      For f = fminprop + 1 To fmaxprop Step 1
        ft(Salt_index, t, g, f, 1) = 1 'assign future survival to 1 for all fat reserves
          'greater than zero
      Next f
      For f = fminprop To fmaxprop Step 1
        ft(Salt_index, t, g, f, 0) = 0 'set current survival to zero
      Next f
    Next g
  Next t
Next Salt_index
End Sub

```

'Converts the annual survival rate to weekly survival rate

```

Private Function beta(Surv)
  beta = (Surv) ^ (1 / 52)
End Function

```

'Finds the allocation strategy with greatest expected fitness by returning position of greatest element of the array (returns length allocation only)

```

Private Function maxsigma(ww())
  big = ww(0, 0) 'begin with all allocation to fat as best
  ssigmabig = 0 'allocation to length at this point is zero
  gsigmabig = 0 'allocation to gonads at this point it zero
  For i = 0 To nsigma Step 1
    For j = (nsigma - i) To 0 Step -1 'step backward through gonad allocation to
      'ensure that they don't put too much into
      'ovaries
    If ww(i, j) >= big Then 'if new value is >= to previous value, then
      big = ww(i, j) 'big=new value
      ssigmabig = i 'new allocation to length
      gsigmabig = j 'new allocation to gonads
    End If
  Next j
Next i

```

```

    Next j
  Next i
  maxssigma = ssigmabig
End Function

```

'Finds the allocation strategy with greatest expected fitness by returning position of greatest element of the array (returns gonad allocation only)

```

Private Function maxgsigma(ww())
  big = ww(0, 0) 'begin with all allocation to fat as best
  ssigmabig = 0 'allocation to length at this point is zero
  gsigmabig = 0 'allocation to gonads at this point it zero
  For i = 0 To nsigma Step 1
    For j = (nsigma - i) To 0 Step -1 'step backward through gonad allocation to
      'ensure that they don't put too much into
      'ovaries
      If ww(i, j) >= big Then 'if new value is >= to previous value, then
        big = ww(i, j) 'big=new value
        ssigmabig = i 'new allocation to length
        gsigmabig = j 'new allocation to gonads
      End If
    Next j
  Next i
  maxgsigma = gsigmabig
End Function

```

'Converts TL index to TL value

```

Private Function TLind2val(index)
  TLind2val = minTL + (index * TLstep)
End Function

```

'Converts gonad index to gonad mass

```

Private Function gind2val(index, Total_length)
  If index >= 0 And index <= 5 Then
    gind2val = index * 0.15 * Max_Gonad(Total_length)
  Else: gind2val = ((index * 0.05) + 0.5) * Max_Gonad(Total_length)
  End If
End Function

```

'Converts fat index to fat mass

```

Private Function find2val(index, Total_length)
  If index >= 0 And index <= 5 Then
    find2val = index * 0.05 * Max_Fat(Total_length)
  Else: find2val = ((index * 0.15) - 0.5) * Max_Fat(Total_length)
  End If
End Function

```


'Converts TL value to TL index

Private Function TLval2ind(Total_length)

 x = (Total_length - minTL) / TLstep

 If x > 0 Then TLval2ind = x

 If x <= 0 Then TLval2ind = 0 'had to do this due to small rounding errors

End Function

'Converts gonad mass to gonad index based on a two-piece regression

Private Function gval2ind(gonad_value, Total_length)

 If Max_Gonad(Total_length) > 0 Then

 gonad_prop = gonad_value / Max_Gonad(Total_length)

 Else: gonad_prop = 0

 End If

 If gonad_prop >= 0 And gonad_prop <= 0.75 Then

 gval2ind = (gonad_prop / 0.15)

 Else: gval2ind = ((gonad_prop - 0.5) / 0.05)

 End If

End Function

'Converts fat mass to fat index based on a two-piece regression

Private Function fval2ind(fat_value, Total_length)

 fat_prop = fat_value / Max_Fat(Total_length)

 If fat_prop >= 0 And fat_prop <= 0.25 Then

 fval2ind = (fat_prop / 0.05)

 Else: fval2ind = ((fat_prop + 0.5) / 0.15)

 End If

End Function

'Trilinear interpolation function to estimate fitness for non-indexed state values

Private Function interp3D(Salt_index, NewTL, Newgmass, Newfmass)

NewTL_i = Int(TLval2ind(NewTL)) 'integer value of new TL

Newgmass_i = Int(gval2ind(Newgmass, NewTL)) 'integer value of new gonad mass

Newfmass_i = Int(fval2ind(Newfmass, NewTL)) 'integer value of new fat mass

TLLo = TLind2val(NewTL_i) 'convert integer value to actual TL

gLo = gind2val(Newgmass_i, NewTL) 'convert integer value to actual gonad mass

fLo = find2val(Newfmass_i, NewTL) 'convert integer value to actual fat mass

 If NewTL >= maxTL Then 'if TL too high, knocks it back down to maximum

 NewTL = maxTL 'and adjusts everything else, i.e., TLLo and TLHi

 TLLo = TLind2val((TLval2ind(NewTL) - 1)) 'TL of one index lower

 NewTL_i = TLval2ind(TLLo) 'index of this lower TL

 TLHi = maxTL 'TL of the biggest index

 Else: TLHi = TLind2val(NewTL_i + 1) 'if not maxTL then give me the value of the next highest index

End If

```
If Newgmass >= Max_Gonad(NewTL) Then 'same as above, but for gonads
  Newgmass = Max_Gonad(NewTL)
  gLo = gind2val((gval2ind(Max_Gonad(NewTL), NewTL) - 1), NewTL)
  Newgmass_i = gval2ind(gLo, NewTL)
  gHi = Max_Gonad(NewTL)
Else: gHi = gind2val((Newgmass_i + 1), NewTL)
End If
```

```
If Newfmass >= Max_Fat(NewTL) Then 'same as above, but for fat
  Newfmass = Max_Fat(NewTL)
  fLo = find2val((fval2ind(Max_Fat(NewTL), NewTL) - 1), NewTL)
  Newfmass_i = fval2ind(fLo, NewTL)
  fHi = Max_Fat(NewTL)
Else: fHi = find2val((Newfmass_i + 1), NewTL)
End If
```

```
TLf = (NewTL - TLLo) / (TLHi - TLLo)
ff = (Newfmass - fLo) / (fHi - fLo)
'add a special case for when gLo = 0 and gHi = 0 for fish < 203 mm TL
If gHi > gLo Then
  gf = (Newgmass - gLo) / (gHi - gLo)
Else: gf = 0
End If
```

```
ione = ft(Salt_index, NewTL_i, Newgmass_i, Newfmass_i, 1) * (1 - ff) + ft(Salt_index,
  NewTL_i, Newgmass_i, Newfmass_i + 1, 1) * ff
itwo = ft(Salt_index, NewTL_i, Newgmass_i + 1, Newfmass_i, 1) * (1 - ff) +
  ft(Salt_index, NewTL_i, Newgmass_i + 1, Newfmass_i + 1, 1) * ff
jone = ft(Salt_index, NewTL_i + 1, Newgmass_i, Newfmass_i, 1) * (1 - ff) +
  ft(Salt_index, NewTL_i + 1, Newgmass_i, Newfmass_i + 1, 1) * ff
jtwo = ft(Salt_index, NewTL_i + 1, Newgmass_i + 1, Newfmass_i, 1) * (1 - ff) +
  ft(Salt_index, NewTL_i + 1, Newgmass_i + 1, Newfmass_i + 1, 1) * ff
```

```
wone = ione * (1 - gf) + itwo * gf
wtwo = jone * (1 - gf) + jt看 * gf
```

```
interp3D = wone * (1 - TLf) + wtwo * TLf
End Function
```

```

'This program determines the optimal allocation strategy using backward iteration
Private Sub OptimalAllocation_Click()
For Survival_index = 0 To 2 Step 1
If Survival_index = 0 Then
    Surv = 0.3
    Open outfile30$ For Output As #1
End If
If Survival_index = 1 Then
    Surv = 0.5
    Open outfile50$ For Output As #1
End If
If Survival_index = 2 Then
    Surv = 0.7
    Open outfile70$ For Output As #1
End If
Call model_parms 'input model parameters
Call TermTime 'initialize terminal time
For C = Cohort To 1 Step -1 'step backward through cohorts/years
For i = Final_week To Start_week Step -1 'step backward through weeks
For t = 0 To TLarray 'loop through total lengths
    TL = TLind2val(t) 'convert TL index to TL value
    Somatic_mass = TLtoSoma(TL) 'convert TL to lean body mass value
For g = gminprop To gmaxprop 'loop through possible gonad sizes for a given
    'length
For f = fminprop + 1 To fmaxprop 'loop through possible fat masses for a
    'given length
    Fat_mass = find2val(f, TL) 'convert fat index to fat mass value

'if it is spawning week, and gonads are maxed at beginning of week, fat
'mass is > 0, and they at least 210 mm TL, the fish can spawn
If i = Final_week And TL >= 210 And Fat_mass > 0 And g = gmaxprop
Then
    Offspring = Fecundity(gind2val(g, TL)) 'current fitness payoff
    Gonad_mass = Residual_gonad(TL) 'replace gonad mass with post-
        'spawn gonad mass
    Else: Offspring = 0 'otherwise no offspring are produced and we don't
        'redifine gonad or total mass
    Gonad_mass = gind2val(g, TL)
End If
Total_mass = Somatic_mass + Gonad_mass + Fat_mass 'sum for total
    'mass

'Determine net calories available for allocation in freshwater environment
'versus salt environment
NetCals_salt = Net_Calories(Total_mass, temp(i), salinity(i), PofCmax,
    Ave_preying_ED)

```

```

NetCals_fresh = Net_Calories(Total_mass, temp(i), 0, PofCmax,
                             Ave_pre_y_ED)
For ssigma = 0 To nsigma 'loop through allocation toward lean body mass
  For gsigma = 0 To (nsigma - ssigma) 'loop through allocation to gonads
    '(minus the amount already
    'devoted to lean body mass)
    fsigma = nsigma - ssigma - gsigma 'determine allocation to fat
    'through subtraction

'determine new states if environment is fresh
Sp = chop((Somatic_mass + Change_in_soma(Soma_ED,
    NetCals_fresh, ssigma)), Somatic_mass, smax) 'new somatic
    'mass (S)

TLp = SomatoTL(Sp) 'new TL (TL)
Gp = chop((Gonad_mass + Change_in_gonad(TLp,
    Gonad_ED(TLp), NetCals_fresh, gsigma)), Gonad_mass,
    Max_Gonad(TLp)) 'new gonad mass (G)
Fp = chop((Fat_mass + Change_in_fat(Fat_ED, NetCals_fresh,
    fsigma)), fmin, Max_Fat(TLp)) 'new fat mass (F)
Total_massp = Sp + Gp + Fp 'new total mass (M)

'determine new states if environment is salty
Spp = chop((Somatic_mass + Change_in_soma(Soma_ED,
    NetCals_salt, ssigma)), Somatic_mass, smax) 'new somatic
    'mass (S")

TLpp = SomatoTL(Spp) 'new TL (TL")
Gpp = chop((Gonad_mass + Change_in_gonad(TLpp,
    Gonad_ED(TLpp), NetCals_salt, gsigma)), Gonad_mass,
    Max_Gonad(TLpp)) 'new gonad mass (G")
Fpp = chop((Fat_mass + Change_in_fat(Fat_ED, NetCals_salt,
    fsigma)), fmin, Max_Fat(TLpp)) 'new fat mass (F")
Total_masspp = Spp + Gpp + Fpp 'new total mass (M")

'determine expected fitness based on current states
fresh_rhs = interp3D(0, TLp, Gp, Fp)
salt_rhs = interp3D(1, TLpp, Gpp, Fpp)
rhs0(ssigma, gsigma) = Offspring + (beta(Surv) * fresh_rhs)
rhs1(ssigma, gsigma) = Offspring + (beta(Surv) * salt_rhs)
'constrain allocation to gonads to zero if total length is less than 205
'allocation toward gonads under 203 mm would result in negative
'gonad size due to the maximum ovary size constraint
'set to 205 because this is one of the stored arrays. if set to 203,
'forward interpolation allows for allocation
'to gonads at the next lowest state
If TL <= 205 And gsigma > 0 Then
  rhs0(ssigma, gsigma) = 0

```

```

        rhs1(ssigma, gsigma) = 0
    End If
Next gsigma
Next ssigma

'determine optimal allocation for freshwater environment
sigmasstar(0, C, i, t, g, f) = maxssigma(rhs0()) 'provide the array position
                                                'of the strategy that
                                                'maximizes fitness

sigmagstar(0, C, i, t, g, f) = maxgsigma(rhs0())
sigmafstar(0, C, i, t, g, f) = (nsigma - sigmasstar(0, C, i, t, g, f) -
                                sigmagstar(0, C, i, t, g, f))

'assign max expected fitness to f(states,t,T)
ft(0, t, g, f, 0) = rhs0(sigmasstar(0, C, i, t, g, f), sigmagstar(0, C, i, t, g, f))

'determine optimal allocation for salty environment
sigmasstar(1, C, i, t, g, f) = maxssigma(rhs1()) 'provide the array position
                                                'of the strategy that
                                                'maximizes fitness

sigmagstar(1, C, i, t, g, f) = maxgsigma(rhs1())
sigmafstar(1, C, i, t, g, f) = (nsigma - sigmasstar(1, C, i, t, g, f) -
                                sigmagstar(1, C, i, t, g, f))

'assign max expected fitness to f(states,t,T)
ft(1, t, g, f, 0) = rhs1(sigmasstar(1, C, i, t, g, f), sigmagstar(1, C, i, t, g, f))

'write optimal decision to a file
For Salt_index = 0 To 1
    Write #1, C, i, Salt_index, t, g, f, sigmasstar(Salt_index, C, i, t, g, f),
    sigmagstar(Salt_index, C, i, t, g, f), sigmafstar(Salt_index, C, i, t, g, f),
    ft(Salt_index, t, g, f, 0)
Next Salt_index
Next f
Next g
Next t
'assigns current expected fitness (t) to future (t+1) and resets current expected
'fitness to 0
For Salt_index = 0 To 1
    For t = 0 To TLarray
        For g = gminprop To gmaxprop
            For f = fminprop To fmaxprop
                ft(Salt_index, t, g, f, 1) = ft(Salt_index, t, g, f, 0) 'set current to future
                ft(Salt_index, t, g, f, 0) = 0 'reset current fitness to zero
            Next f
        Next g
    Next t
Next Salt_index

```

```
Next i
Next C
Close #1
Next Survival_index
End Sub
```

Appendix 4. Additional Visual Basics code required to determine growth trajectories based on the predetermined optimal energy allocation strategy using forward iteration (Chapter IV)

```
Private Const nReps = 1 'number of replicate model runs
Private Const nfish = 1 'number of fish per replicate
```

'Filename to import predetermined optimal energy allocation from

```
Private Const infile$ = "C:\Users\Dave\Documents\Dissertation\Chapter 3 - Life
history\dynamic programs\Final model used\oea results (surv = " & Surv & ", ration = "
& pofCMAX & ", age effect = " & AgeEffect & ").txt"
```

'These arrays keep track of the states for the forward iteration

```
Dim TL2(1 To nfish, 0 To 1, 1 To Cohort, Start_week To Final_week)
Dim Somatic_mass(1 To nfish, 0 To 1, 1 To Cohort, Start_week To Final_week)
Dim Gonad_mass(1 To nfish, 0 To 1, 1 To Cohort, Start_week To Final_week)
Dim Fat_mass(1 To nfish, 0 To 1, 1 To Cohort, Start_week To Final_week)
Dim Total_mass(1 To nfish, 0 To 1, 1 To Cohort, Start_week To Final_week)
Dim NetCals(1 To nfish, 0 To 1, 1 To Cohort, Start_week To Final_week)
Dim ssigma(1 To nfish, 0 To 1, 1 To Cohort, Start_week To Final_week)
Dim gsigma(1 To nfish, 0 To 1, 1 To Cohort, Start_week To Final_week)
Dim fsigma(1 To nfish, 0 To 1, 1 To Cohort, Start_week To Final_week)
Dim Repro_output(1 To nfish, 0 To 1, 1 To Cohort) 'egg production for each fish within
'a cohort
Dim Cohort_eggs(1 To nReps, 0 To 1, 1 To Cohort) 'total egg production for each cohort
'within a repetition
Dim Total_eggs(1 To nReps, 0 To 1) 'total egg production across cohorts for each
'repitation
Dim Rep_ave_eggs(1 To nReps, 0 To 1) 'average egg production across cohorts for each
'repitation
Dim Cumulative_eggs(0 To 1) 'total egg production across all repetitions
Dim Ave_eggs(0 To 1) 'average egg production across repetitions
Dim Rep_X2(0 To nReps, 0 To 1) 'squared error of egg production for each repetition
Dim Sum_of_squares(0 To 1) 'sum of squares estimate of egg production across
'repitations
Dim SE(0 To 1) 'standard error of mean egg production across repetitions
```

'This function interpolates allocation decisions to lean body mass when TL, Gonad mass, and fat mass are non-indexed states

```
Private Function interpssigma(Expectation, C, i, TL, Gonadmass, Fatmass, maxgmass,
maxfmass)
```

```
TL_i = Int(TLval2ind(TL)) 'index of next lowest TL state
```

```
Gonadmass_i = Int(gval2ind(Gonadmass, TL)) 'index of next lowest gonad state
```

```
Fatmass_i = Int(fval2ind(Fatmass, TL)) 'index of next lowest fat state
```

TLLo = TLind2val(TL_i) 'TL value of this next lowest state
 gLo = gind2val(Gonadmass_i, TL) 'gonad value of this next lowest state
 fLo = find2val(Fatmass_i, TL) 'fat value of this next lowest state

If TL >= maxTL Then 'if state too high, knocks it back down to maximum
 TL = maxTL 'and adjusts everything else, e.g., TLLo and TLHi
 TLLo = TLind2val(TLval2ind(maxTL) - 1)
 TL_i = TLval2ind(TLLo)
 TLHi = maxTL
 Else: TLHi = TLind2val(TL_i + 1)
 End If

If Gonadmass >= maxgmass Then 'same as above
 Gonadmass = maxgmass
 gLo = gind2val((gval2ind(maxgmass, TL) - 1), TL)
 Gonadmass_i = gval2ind(gLo, TL)
 gHi = maxgmass
 Else: gHi = gind2val((Gonadmass_i + 1), TL)
 End If

If Fatmass >= maxfmass Then 'same as above
 Fatmass = maxfmass
 fLo = find2val((fval2ind(maxfmass, TL) - 1), TL)
 Fatmass_i = fval2ind(fLo, TL)
 fHi = maxfmass
 Else: fHi = find2val((Fatmass_i + 1), TL)
 End If

TLf = (TL - TLLo) / (TLHi - TLLo)
 ff = (Fatmass - fLo) / (fHi - fLo)
 'add a special case for when gLo = 0 and gHi = 0 for fish < 203 mm TL
 If gHi > gLo Then
 gf = (Gonadmass - gLo) / (gHi - gLo)
 Else: gf = 0
 End If

ione = sigmasstar(Expectation, C, i, TL_i, Gonadmass_i, Fatmass_i) * (1 - ff) +
 sigmasstar(Expectation, C, i, TL_i, Gonadmass_i, Fatmass_i + 1) * ff
 itwo = sigmasstar(Expectation, C, i, TL_i, Gonadmass_i + 1, Fatmass_i) * (1 - ff) +
 sigmasstar(Expectation, C, i, TL_i, Gonadmass_i + 1, Fatmass_i + 1) * ff
 jone = sigmasstar(Expectation, C, i, TL_i + 1, Gonadmass_i, Fatmass_i) * (1 - ff) +
 sigmasstar(Expectation, C, i, TL_i + 1, Gonadmass_i, Fatmass_i + 1) * ff
 jtwo = sigmasstar(Expectation, C, i, TL_i + 1, Gonadmass_i + 1, Fatmass_i) * (1 - ff) +
 sigmasstar(Expectation, C, i, TL_i + 1, Gonadmass_i + 1, Fatmass_i + 1) * ff

wone = ione * (1 - gf) + itwo * gf


```
wtwo = jone * (1 - gf) + jtwo * gf
interpssigma = wone * (1 - TLf) + wtwo * TLf
```

End Function

'This function interpolates allocation decisions to gonads when TL, Gonad mass, and fat mass are non-indexed states

Private Function interpgsigma(Expectation, C, i, TL, Gonadmass, Fatmass, maxgmass, maxfmass)

```
TL_i = Int(TLval2ind(TL)) 'index of next lowest TL state
Gonadmass_i = Int(gval2ind(Gonadmass, TL)) 'index of next lowest gonad state
Fatmass_i = Int(fval2ind(Fatmass, TL)) 'index of next lowest fat state
```

```
TLLo = TLind2val(TL_i) 'TL value of this next lowest state
gLo = gind2val(Gonadmass_i, TL) 'gonad value of this next lowest state
fLo = find2val(Fatmass_i, TL) 'fat value of this next lowest state
```

If TL >= maxTL Then 'if state too high, knocks it back down to maximum

TL = maxTL 'and adjusts everything else, e.g., TLLo and TLHi

TLLo = TLind2val(TLval2ind(maxTL) - 1)

TL_i = TLval2ind(TLLo)

TLHi = maxTL

Else: TLHi = TLind2val(TL_i + 1)

End If

If Gonadmass >= maxgmass Then 'same as above

Gonadmass = maxgmass

gLo = gind2val((gval2ind(maxgmass, TL) - 1), TL)

Gonadmass_i = gval2ind(gLo, TL)

gHi = maxgmass

Else: gHi = gind2val((Gonadmass_i + 1), TL)

End If

If Fatmass >= maxfmass Then 'same as above

Fatmass = maxfmass

fLo = find2val((fval2ind(maxfmass, TL) - 1), TL)

Fatmass_i = fval2ind(fLo, TL)

fHi = maxfmass

Else: fHi = find2val((Fatmass_i + 1), TL)

End If

TLf = (TL - TLLo) / (TLHi - TLLo)

ff = (Fatmass - fLo) / (fHi - fLo)

'add a special case for when gLo = 0 and gHi = 0 for fish < 203 mm TL

If gHi > gLo Then

```

    gf = (Gonadmass - gLo) / (gHi - gLo)
Else: gf = 0
End If

ione = sigmagstar(Expectation, C, i, TL_i, Gonadmass_i, Fatmass_i) * (1 - ff) +
      sigmagstar(Expectation, C, i, TL_i, Gonadmass_i, Fatmass_i + 1) * ff
itwo = sigmagstar(Expectation, C, i, TL_i, Gonadmass_i + 1, Fatmass_i) * (1 - ff) +
      sigmagstar(Expectation, C, i, TL_i, Gonadmass_i + 1, Fatmass_i + 1) * ff
jone = sigmagstar(Expectation, C, i, TL_i + 1, Gonadmass_i, Fatmass_i) * (1 - ff) +
      sigmagstar(Expectation, C, i, TL_i + 1, Gonadmass_i, Fatmass_i + 1) * ff
jtwo = sigmagstar(Expectation, C, i, TL_i + 1, Gonadmass_i + 1, Fatmass_i) * (1 - ff) +
      sigmagstar(Expectation, C, i, TL_i + 1, Gonadmass_i + 1, Fatmass_i + 1) * ff

wone = ione * (1 - gf) + itwo * gf
wtwo = jone * (1 - gf) + jt看 * gf
interpgsigma = wone * (1 - TLf) + wtwo * TLf

```

End Function

'Subroutine to input optimal energy allocation strategy from text file

```

Private Sub OptEnergy()
Do While Not EOF(2)
    Input #2, C
    Input #2, i
    Input #2, Expectation
    Input #2, t
    Input #2, g
    Input #2, f
    Input #2, sigmasstar(Expectation, C, i, t, g, f), sigmagstar(Expectation, C, i, t, g, f),
    sigmafstar(Expectation, C, i, t, g, f)
    Input #2, fitness 'don't need this for forward iteration, thus not assigned to an array
Loop
End Sub

```

'Subroutine to provide initial states for forward iteration and allows for a distribution of initial states to be specified if desired

```

Private Sub InitState(Expectation)
For x = 1 To nfish
    TL2(x, Expectation, 1, Start_week) = 23 'Initial TL fixed to 23 mm
    Somatic_mass(x, Expectation, 1, Start_week) = TLtoSoma(TL2(x, Expectation, 1,
        Start_week))
    Gonad_mass(x, Expectation, 1, Start_week) = 0 'Initial gonad fixed to 0 g
    Fat_mass(x, Expectation, 1, Start_week) = find2val(2, TL2(x, Expectation, 1,
        Start_week)) 'Initial fat = 10% of max
    Total_mass(x, Expectation, 1, Start_week) = Somatic_mass(x, Expectation, 1,

```

```
Start_week) + Gonad_mass(x,  
Expectation, 1, Start_week) +  
Fat_mass(x, Expectation, 1, Start_week)
```

```
Next x  
End Sub
```

'Subroutine to write expected lifetime fitness results to a spreadsheet

```
Private Sub WriteResults(Prob_of_salinity)  
Worksheets("Model Run").Cells(1, 5) = nReps  
Worksheets("Model Run").Cells(2, 5) = nfish  
Worksheets("Model Run").Cells(3, 5) = Surv  
Worksheets("Model Run").Cells(4, 5) = pofCMAX
```

'Write average reproductive output for each combination

```
For Expectation = 0 To 1  
Worksheets("Model Run").Cells(8 + Expectation, 5 + Prob_of_salinity) =  
Ave_eggs(Expectation)  
For rep = 1 To nReps  
For C = 1 To Cohort  
Worksheets("Egg Production by Cohort").Cells(1 + 15 * Expectation + 30 *  
Prob_of_salinity, 1) = "Probability of salinity = " & Prob_of_salinity & "  
Expected probability = " & Expectation  
Worksheets("Egg Production by Cohort").Cells(2 + 15 * Expectation + 30 *  
Prob_of_salinity, 1) = "Cohort"  
Worksheets("Egg Production by Cohort").Cells((C + 2) + 15 * Expectation + 30 *  
Prob_of_salinity, 1) = C  
Worksheets("Egg Production by Cohort").Cells(2 + 15 * Expectation + 30 *  
Prob_of_salinity, rep + 1) = "Rep = " & rep  
Worksheets("Egg Production by Cohort").Cells((C + 2) + 15 * Expectation + 30 *  
Prob_of_salinity, rep + 1) = Cohort_eggs(rep, Expectation, C)  
Next C  
Worksheets("Egg Production by Cohort").Cells(13 + 15 * Expectation + 30 *  
Prob_of_salinity, 1) = "Sum"  
Worksheets("Egg Production by Cohort").Cells(13 + 15 * Expectation + 30 *  
Prob_of_salinity, rep + 1) = Total_eggs(rep, Expectation)  
Worksheets("Egg Production by Cohort").Cells(14 + 15 * Expectation + 30 *  
Prob_of_salinity, 1) = "Average per individual (N = " & nfish & ")"  
Worksheets("Egg Production by Cohort").Cells(14 + 15 * Expectation + 30 *  
Prob_of_salinity, rep + 1) = Rep_ave_eggs(rep, Expectation)  
Next rep  
Next Expectation  
End Sub
```

'Subroutine that writes states through time to a spreadsheet

```
Private Sub WriteStates(Prob_of_salinity)  
If Prob_of_salinity = 0 Then 'if freshwater write results to this sheet
```

```

enviro = "fresh"
Else: enviro = "salt"
End If
Worksheets("States through time (" & enviro & ")).Cells(1, 1) = "Cumulative weeks"
Worksheets("States through time (" & enviro & ")).Cells(1, 2) = "Cohort weeks"
For Expectation = 0 To 1 'expectation = 0 is freshwater strategy; = 1 is estuarine strategy
'write titles
Worksheets("States through time (" & enviro & ")).Cells(1, 3 + Expectation) = "TL ("
& Expectation & ")"
Worksheets("States through time (" & enviro & ")).Cells(1, 5 + Expectation) =
"pofGmax (" & Expectation & ")"
Worksheets("States through time (" & enviro & ")).Cells(1, 7 + Expectation) =
"pofFmax (" & Expectation & ")"
Worksheets("States through time (" & enviro & ")).Cells(1, 9 + Expectation) = "Soma
mass (" & Expectation & ")"
Worksheets("States through time (" & enviro & ")).Cells(1, 11 + Expectation) =
"Gonad mass (" & Expectation & ")"
Worksheets("States through time (" & enviro & ")).Cells(1, 13 + Expectation) = "Fat
mass (" & Expectation & ")"
Worksheets("States through time (" & enviro & ")).Cells(1, 15 + Expectation) =
"Total mass (" & Expectation & ")"
Worksheets("States through time (" & enviro & ")).Cells(1, 17 + Expectation) =
"ssigma (" & Expectation & ")"
Worksheets("States through time (" & enviro & ")).Cells(1, 19 + Expectation) =
"gsigma (" & Expectation & ")"
Worksheets("States through time (" & enviro & ")).Cells(1, 21 + Expectation) =
"fsigma (" & Expectation & ")"
Worksheets("States through time (" & enviro & ")).Cells(1, 23 + Expectation) =
"Num of larvae expected (" & Expectation & ")"
Worksheets("States through time (" & enviro & ")).Cells(1, 25 + Expectation) = "Net
Cals (" & Expectation & ")"
Worksheets("States through time (" & enviro & ")).Cells(1, 27 + Expectation) =
"Condition (" & Expectation & ")"
For C = 1 To Cohort
For i = Start_week To Final_week
'write states through time
x = 1
Worksheets("States through time (" & enviro & ")).Cells((i + 1) + ((C - 1) *
Final_week), 1) = i + ((C - 1) * Final_week)
Worksheets("States through time (" & enviro & ")).Cells((i + 1) + ((C - 1) *
Final_week), 2) = i
Worksheets("States through time (" & enviro & ")).Cells((i + 1) + ((C - 1) *
Final_week), 3 + Expectation) = TL2(x, Expectation, C, i)
If Max_Gonad(TL2(x, Expectation, C, i)) > 0 Then

```

```

Worksheets("States through time (" & enviro & ")").Cells((i + 1) + ((C - 1) *
Final_week), 5 + Expectation) = Gonad_mass(x, Expectation, C, i) /
Max_Gonad(TL2(x, Expectation, C, i))
Else: Worksheets("States through time (" & enviro & ")").Cells((i + 1) + ((C -
1) * Final_week), 5 + Expectation) = 0
End If
Worksheets("States through time (" & enviro & ")").Cells((i + 1) + ((C - 1) *
Final_week), 7 + Expectation) = Fat_mass(x, Expectation, C, i) / Max_Fat(TL2(x,
Expectation, C, i))
Worksheets("States through time (" & enviro & ")").Cells((i + 1) + ((C - 1) *
Final_week), 9 + Expectation) = Somatic_mass(x, Expectation, C, i)
Worksheets("States through time (" & enviro & ")").Cells((i + 1) + ((C - 1) *
Final_week), 11 + Expectation) = Gonad_mass(x, Expectation, C, i)
Worksheets("States through time (" & enviro & ")").Cells((i + 1) + ((C - 1) *
Final_week), 13 + Expectation) = Fat_mass(x, Expectation, C, i)
Worksheets("States through time (" & enviro & ")").Cells((i + 1) + ((C - 1) *
Final_week), 15 + Expectation) = Total_mass(x, Expectation, C, i)
Worksheets("States through time (" & enviro & ")").Cells((i + 1) + ((C - 1) *
Final_week), 17 + Expectation) = ssigma(x, Expectation, C, i)
Worksheets("States through time (" & enviro & ")").Cells((i + 1) + ((C - 1) *
Final_week), 19 + Expectation) = gsigma(x, Expectation, C, i)
Worksheets("States through time (" & enviro & ")").Cells((i + 1) + ((C - 1) *
Final_week), 21 + Expectation) = fsigma(x, Expectation, C, i)
If i = Final_week Then
Worksheets("States through time (" & enviro & ")").Cells((i + 1) + ((C - 1) *
Final_week), 23 + Expectation) = Repro_output(x, Expectation, C)
Else: Worksheets("States through time (" & enviro & ")").Cells((i + 1) + ((C - 1)
* Final_week), 23 + Expectation) = 0
End If
Worksheets("States through time (" & enviro & ")").Cells((i + 1) + ((C - 1) *
Final_week), 25 + Expectation) = NetCals(x, Expectation, C, i)
If TL2(x, Expectation, C, i) >= 150 Then
Worksheets("States through time (" & enviro & ")").Cells((i + 1) + ((C - 1) *
Final_week), 27 + Expectation) = 100 * (Total_mass(x, Expectation, C, i) / (10
^ (-5.528 + (3.273 * Log10(TL2(x, Expectation, C, i))))))
End If
Next i
Next C
Next Expectation
End Sub

```

'Program used to determine expected lifetime fitness of various strategies in freshwater (Prob_of_salinity = 0) and saltwater (Prob_of_salinity = 1). This program also estimates states through time in either a completely fresh or an estuarine environment for both a freshwater and estuarine allocation strategy (i.e., a theoretical reciprocal transplant experiment)

Private Sub ForwardIteration_Click()

Randomize Timer

Call model_parms 'inputs salinity and temperature

Open infile\$ For Input As #2 'opens file for reading optimal decisions

Call OptEnergy

'loop through freshwater (Prob_of_salinity = 0) and salinity environments

(Prob_of_salinity = 1)

For Prob_of_salinity = 0 To 1 Step 1

'loop through strategies in terms of their expectation of salinity occurring on any given week

For Expectation = 0 To 1 Step 1

Cumulative_eggs(Expectation) = 0 'initial number of offspring produced across all repetitions for determining mean

For rep = 1 To nReps 'loop through repetitions

Call InitState(Expectation) 'get initial states

Total_eggs(rep, Expectation) = 0 'initial number of offspring produced for a population within each repetition

For C = 1 To Cohort 'loop through cohorts

Cohort_eggs(rep, Expectation, C) = 0 'initial number of offspring produced for a cohort summed across fish

For x = 1 To nfish 'loop through fish

For i = Start_week To Final_week Step 1

salty = Rnd 'draw a random number each year to set salty/fresh

If salty > Prob_of_salinity Then

Environment = 0 'current environment is fresh

Else: Environment = 1 'current environment is salty

End If

TL = TL2(x, Expectation, C, i) 'TL at time i for the Cth cohort

s = Somatic_mass(x, Expectation, C, i) 'Somatic mass at time i for the Cth cohort

g = Gonad_mass(x, Expectation, C, i) 'Gonad mass at i for the Cth cohort

f = Fat_mass(x, Expectation, C, i) 'Fat mass at i for the Cth cohort

TM = Total_mass(x, Expectation, C, i) 'Total mass at i for the Cth cohort

gmax = Max_Gonad(TL)

If gmax > 0 Then

pofGmax = Round(g, 4) / Round(gmax, 4)

Else: pofGmax = 0

End If

If i = 52 And TL >= 210 And pofGmax = 1 And f > 0 Then

'if above conditions are met, then spawn

Repro_output(x, Expectation, C) = (Fecundity(g)) * (Surv ^ C) 'by
 including survival here it becomes expected reproduction for an
 individual (i.e., l_{xmx})
 'ovaries shrink to post-spawn mass
 g = Residual_gonad(TL)
 'redefine total mass with new gonad mass
 TM = s + g + f
 Else: Repro_output(x, Expectation, C) = 0 'if above conditions not
 'satisfied they don't spawn

End If

If f = 0 And i = Final_week And C < 10 Then

Fat_mass(x, Expectation, C + 1, Start_week) = 0 'once fat is zero,
 'always zero (i.e.,
 'dead) and stop
 'growing

TL2(x, Expectation, C + 1, Start_week) = TL2(x, Expectation, C, i)
 Somatic_mass(x, Expectation, C + 1, Start_week) = Somatic_mass(x,
 Expectation, C, i)
 Gonad_mass(x, Expectation, C + 1, Start_week) = Gonad_mass(x,
 Expectation, C, i)
 Total_mass(x, Expectation, C + 1, Start_week) = Total_mass(x,
 Expectation, C, i)

End If

If f = 0 And i >= Start_week And i < Final_week Then

Fat_mass(x, Expectation, C, i + 1) = 0 'once fat is zero, always zero
 '(i.e., dead) and stop growing

TL2(x, Expectation, C, i + 1) = TL2(x, Expectation, C, i)
 Somatic_mass(x, Expectation, C, i + 1) = Somatic_mass(x, Expectation,
 C, i)
 Gonad_mass(x, Expectation, C, i + 1) = Gonad_mass(x, Expectation, C,
 i)

Total_mass(x, Expectation, C, i + 1) = Total_mass(x, Expectation, C, i)

End If

If f > 0 Then 'if fish x is alive then

'determine strategy via trilinear interpolation based on current states

ssigma(x, Expectation, C, i) = interpssigma(Expectation, C, i, TL, g, f,
 Max_Gonad(TL), Max_Fat(TL))

gsigma(x, Expectation, C, i) = interpgsigma(Expectation, C, i, TL, g, f,
 Max_Gonad(TL), Max_Fat(TL))

fsigma(x, Expectation, C, i) = nsigma - ssigma(x, Expectation, C, i) -
 gsigma(x, Expectation, C, i)

'determine calories available for allocation

If Environment = 0 Then NetCals(x, Expectation, C, i) =

Net_Calories(TM, temp(i), 0, pofC_{MAX}, Ave_pre_{ED})

```

If Environment = 1 Then NetCals(x, Expectation, C, i) =
    Net_Calories(TM, temp(i), salinity(i), pofCMAX, Ave_preys_ED)
'Determine new states for the following week
'bbb = Rnd 'generate a random value between 0 and 1 to evaluate
whether fish lives or dies (stochastic only)
If i = Final_week And C < 10 Then
    Somatic_mass(x, Expectation, C + 1, Start_week) = Chop(s +
        Change_in_soma(Soma_ED, NetCals(x, Expectation, C, i),
            ssigma(x, Expectation, C, i)), s, smax)
    TL2(x, Expectation, C + 1, Start_week) =
        SomatoTL(Somatic_mass(x, Expectation, C + 1, Start_week))
    Gonad_mass(x, Expectation, C + 1, Start_week) = Chop(g +
        Change_in_gonad(TL2(x, Expectation, C + 1, Start_week),
            Gonad_ED(TL2(x, Expectation, C + 1, Start_week)),
            NetCals(x, Expectation, C, i), gsigma(x, Expectation, C, i)),
            gmin, Max_Gonad(TL2(x, Expectation, C + 1, Start_week)))
    Fat_mass(x, Expectation, C + 1, Start_week) = Chop(f +
        Change_in_fat(Fat_ED, NetCals(x, Expectation, C, i),
            fsigma(x, Expectation, C, i)), fmin, Max_Fat(TL2(x,
            Expectation, C + 1, Start_week)))
    Total_mass(x, Expectation, C + 1, Start_week) = Somatic_mass(x,
        Expectation, C + 1, Start_week) + Gonad_mass(x, Expectation,
        C + 1, Start_week) + Fat_mass(x, Expectation, C + 1,
        Start_week)
    'If bbb > beta(Surv) Then 'if random value is > weekly survival rate
    'Fat_mass(x, Expectation, C + 1, Start_week) = 0 'then fish x dies
    and fat mass goes to zero
    'End If
End If
If i >= Start_week And i < Final_week Then
    Somatic_mass(x, Expectation, C, i + 1) = Chop(s +
        Change_in_soma(Soma_ED, NetCals(x, Expectation, C, i),
            ssigma(x, Expectation, C, i)), s, smax)
    TL2(x, Expectation, C, i + 1) = SomatoTL(Somatic_mass(x,
        Expectation, C, i + 1))
    Gonad_mass(x, Expectation, C, i + 1) = Chop(g +
        Change_in_gonad(TL2(x, Expectation, C, i + 1),
            Gonad_ED(TL2(x, Expectation, C, i + 1)), NetCals(x,
            Expectation, C, i), gsigma(x, Expectation, C, i)), gmin,
            Max_Gonad(TL2(x, Expectation, C, i + 1)))
    Fat_mass(x, Expectation, C, i + 1) = Chop(f +
        Change_in_fat(Fat_ED, NetCals(x, Expectation, C, i),
            fsigma(x, Expectation, C, i)), fmin, Max_Fat(TL2(x,
            Expectation, C, i + 1)))

```



```

        Total_mass(x, Expectation, C, i + 1) = Somatic_mass(x, Expectation,
            C, i + 1) + Gonad_mass(x, Expectation, C, i + 1) + Fat_mass(x,
            Expectation, C, i + 1)
        'If bbb > beta(Surv) Then 'if random value is > weekly survival rate
        'Fat_mass(x, Expectation, C, i + 1) = 0 'then fish x dies and fat
        mass goes to zero
        'End If
    End If
End If
Next i
'determine total egg production for each cohort (sum across fish)
Cohort_eggs(rep, Expectation, C) = Cohort_eggs(rep, Expectation, C) +
    Repro_output(x, Expectation, C)
Next x
'Determine total egg production of all cohorts for this repetition
Total_eggs(rep, Expectation) = Total_eggs(rep, Expectation) +
    Cohort_eggs(rep, Expectation, C)
Next C
Rep_ave_eggs(rep, Expectation) = Total_eggs(rep, Expectation) / nfish
Cumulative_eggs(Expectation) = Cumulative_eggs(Expectation) +
    Rep_ave_eggs(rep, Expectation)
Next rep
'determine average egg production across reps
Ave_eggs(Expectation) = Cumulative_eggs(Expectation) / nReps
'determine standard error of egg production
Sum_of_squares(Expectation) = 0 'initial sum of squares of offspring
For rep = 1 To nReps
    Rep_X2(rep, Expectation) = (Ave_eggs(Expectation) - Rep_ave_eggs(rep,
        Expectation)) ^ 2
    Sum_of_squares(Expectation) = Sum_of_squares(Expectation) + Rep_X2(rep,
        Expectation)
Next rep
SE(Expectation) = Sqr(Sum_of_squares(Expectation) / (nReps - 1)) / Sqr(nReps)
Next Expectation
Call WriteResults(Prob_of_salinity)
Call WriteStates(Prob_of_salinity)
Next Prob_of_salinity
Close #2
End Sub

```