

**ENERGY ALLOCATION OF LARGEMOUTH BASS (*Micropterus salmoides*): THE
INTERACTIVE EFFECTS OF SEASON AND RATION**

by

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Abstract

Young-of-year (YOY) fish differentially allocate energy towards growth of various dimensions and tissue types. In temperate environments, several size-selective sources of mortality (e.g., overwinter starvation and predation) have driven adaptation through season-specific energy allocation strategies in YOY fish. However, the degree to which observed patterns in energy allocation are the product of ration-dependent plasticity rather than hard-wired life-history traits is largely unknown. We conducted two experiments to evaluate the role of ration and season on energy allocation of YOY largemouth bass (*Micropterus salmoides*). Through a controlled laboratory experiment in 2006, growth and condition of largemouth bass were monitored under four ration treatments. Repeated measures ANOVA indicated the effect of ration treatment was significant for relative weight ($F_{3,9.41} = 9.973$, $p = 0.003$) but not for wet weight ($F_{3,6.41} = 2.082$, $p = 0.198$) or total length ($F_{3,6.41} = 0.967$, $p = 0.462$). A second study conducted in outdoor experimental raceways in 2006 and 2007 evaluated the effects of ration (mediated by stocking density and raceway position) and season on patterns of energy allocation during summer and fall. Analyses of covariance found significant differences in length-adjusted dry weight among treatments in August and September of 2006 and 2007, but no significant difference among treatments in October of 2006 ($F_{2,67} = 2.627$, $p = 0.080$) and 2007 ($F_{3,56} = 2.994$, $p = 0.14$). These experiments demonstrate the existence of a tradeoff associated with allocating energy to structure or storage tissue and suggest that ration mediates the extent to which fish must respond to this tradeoff with seasonal shifts in energy allocation pattern.

Introduction

Growth patterns in fishes vary across species, life-stages, and environments (Pepin 1991; Winemiller and Rose 1992; Schultz and Conover 1997; Searcy and Sponaugle 2000). Early life growth patterns interact with size-specific survival processes to strongly influence spatial and temporal patterns of recruitment and production of young fishes (Werner and Gilliam 1984; Houde 1997; Sogard 1997). Elucidating growth processes can thereby contribute to understanding variation in year class strength and can inform stocking and harvesting practices. While intra-specific growth variation is largely attributable to direct environmental influences (e.g., temperature, prey availability), factors which influence behavior and energy allocation may also contribute towards growth variation.

Predation, starvation risk, environmental conditions, and growth patterns during the juvenile stage interact to determine survival and year class strength in fish, particularly freshwater species (Houde 1994). These factors vary temporally such that fish experience different survival pressures throughout their first year of life (Ludsin and DeVries 1997). During the early summer when most juvenile temperate fishes are still of very small body size and prey resources are relatively high, predation is a significant source of mortality. Survival during this stage is believed to be mediated by growth rate, independent of tissue composition, where fish that attain the greatest size the quickest have the best chance of survival (Tonn et al. 1994; Persson et al. 1996; Sogard 1997; Post et al. 1999; Meekan et al. 2006). In contrast, vulnerability to overwinter mortality is likely dependent not only on size, but also somatic energy stores and mass-specific metabolism (Fullerton et al. 2000; Garvey et al. 2004; Biro et al. 2005). Therefore, the

shift from a strategy of energy allocation towards size independent of tissue composition to one selecting for high energy tissue mass confers a survival advantage for young-of-year fish (Booth and Keast 1986; Hurst and Conover 2003; Garvey et al. 2004).

The amount of energy available for growth is energy consumed less excretion, egestion, and metabolic losses (Kooijman 2000). Available energy can be allocated to various somatic tissues yielding changes in size, energy content, body shape, and condition. Body mass is composed of various tissue classes (e.g., lipid, muscle, nerve, and skeletal tissue) which may be divided into more specific categories based on function or chemical structure. Due to the difficulty of analyzing each of these tissue categories independently, it is useful to consider fish as composed of a combination of structural and storage tissues. In this conceptual model, growth in structural tissues is expressed by growth in length and low energy body mass. Energy allocated to structure would increase the size (length) of the fish and its capacity for soft tissue mass, but would be less available for catabolism. Growth in storage is associated with growth in girth and high energy tissues as well as mass (Brown and Murphy 1991; Jonas et al. 1996; Brown and Murphy 2004). Energy from these tissues would then be available for catabolism during periods of starvation but the tissues themselves would not contribute to length. Due to limitations on energy intake and behavioral responses to sources of mortality (Werner and Anholt 1993), fish cannot allocate energy to simultaneously maximize growth in all dimensions and tissue types. This points to the existence of a tradeoff between allocating energy to growth in body size independent of energy (structure) and allocating energy to growth of highly energy dense tissues (storage) (Hurst and Conover 2003).

As young-of-year fish are exposed to size-selective starvation and predation, an appropriate energy allocation strategy is critical for survival. Ontogenetic energy allocation patterns are characterized by increased capacity for storage with increases in body size, often presented as allometric scaling of storage mass with length (Sogard and Spencer 2004). Beyond allometric growth, a potential strategy by which juvenile fish may cope with temporal variation in mortality risk is via variable energy allocation pattern through ontogeny (Post and Parkinson 2001). Seasonally variable energy allocation patterns have been documented for many species of fish including largemouth bass *Micropterus salmoides*, striped bass *Morone saxatilis*, and rainbow trout *Oncorhynchus mykiss* (Adams et al. 1982; Hurst and Conover 2003; Biro et al. 2005). Early during their first summer, young north-temperate fishes may allocate energy to structural tissue growth in order to escape gape limits of size-selective predators (Sogard and Spencer 2004). These fish stay relatively lean and invest relatively little in storage growth in favor of attaining a larger size. Prior to the onset of winter, fish begin to allocate a larger proportion of energy to storage at the expense of structure. These energy reserves may limit starvation and disease related mortality while decreasing the necessity for risk taking behavior associated with foraging in a time of low prey abundance (Garvey et al. 2004; Slater et al. 2007).

In addition to seasonally and ontogenetically determined energy allocation, there is evidence that consumption patterns (type and amount of food) also influence energy allocation (Skalski et al. 2005). Depending on food availability and environmental conditions (e.g., temperature), fish may consume more energy than necessary to maintain metabolism, and can allocate surplus energy toward the growth of various

somatic tissues (Johnson et al. 2002). With increasing consumption rate, somatic energy density may increase, which is indicative of increased storage tissue (Brett et al. 1969; Elliott 1976). Conversely, fishes undergoing starvation have been found to decrease in storage tissue and somatic energy density (Niimi 1972; Breck 2008). Therefore, one would expect a fish feeding near its maximum consumption rate to build a greater proportion of high energy tissues than one feeding at lower ration.

Ration can also affect growth through a compensatory response characterized by a period of increased consumption and growth efficiency after a period of low ration or starvation (e.g., Broekhuizen et al. 1994; Nieceza and Metcalfe 1997). For example, Skalski et al. (2005) found that the compensatory response to variable ration was the product of a shift in energy allocation pattern via changes in growth efficiency and maintenance metabolism in addition to variable energy intake (consumption) for juvenile hybrid striped bass (*Morone saxatilis x chrysops*).

The largemouth bass is a common sport fish species in North America which has a long history of intense exploitation, propagation, and scientific study. As a nest guarding species, egg and larval stage largemouth bass are less vulnerable to predation than many other species. However, after emerging from the nest young bass are exposed to variable growth conditions and mortality sources, including size-dependent predation and overwinter mortality (Post et al. 1998). The intensity of these mortality sources may be tempered by appropriate energy allocation strategies in this species, and thereby young largemouth bass are useful study organisms for exploring the effects of ration and season on energy allocation patterns.

The objective of this study was to evaluate the combined effects of ration and season on energy allocation by young largemouth bass. A short-term laboratory experiment was conducted to test for a season-independent ration effect on energy allocation. In addition, largemouth bass were reared in semi-natural outdoor raceways under two ration treatments to determine the effect of ration on seasonal energy allocation pattern.

Methods

Study site and design

Experiments with young-of-year bass were conducted during 2006 and 2007 at the Michigan Department of Natural Resources Saline Fisheries Research Station in Saline, MI. Resident populations of adult largemouth bass, maintained in 17 ~0.25-hectare ponds of 1-m average depth (Breck 1996), served as brood stock for experimental fish. Experiments were conducted in 40-liter tanks and in semi-natural raceways measuring 36.5 m long by 5 m wide and adjusted to 0.5 m mean depth (Merna and Queener 1977). Raceways are arranged in a sequence of three pairs, with inflow spilling into common collection reservoirs before spilling into each pair from upstream to downstream (Figure 1). Each raceway has a gravel and silt bottom, cement dividers on three sides, one natural shoreline, and an aquatic macroinvertebrate community that provides a natural prey base for juvenile fish. Between experiments in 2006 and 2007, riparian vegetation along these raceways was cut back as part of routine site maintenance such that there was markedly less riparian cover in 2007 than in 2006.

Adult largemouth bass were allowed to nest and spawn during the spring, and juveniles were allowed to grow to a reasonable size for handling (i.e., >40 mm). Young-of-year largemouth bass were collected for experimentation in early- to mid-July and immediately divided between raceway (2006 and 2007) and tank (2006) experiments. During each study year only one rearing pond was drained for juvenile fish collection to minimize variation in initial size, condition, and hatch date.

Ration study

The purpose of the ration study was to compare energy allocation patterns among fish that differed in ration level. Beginning on 19 July 2006, young-of-year largemouth bass were individually marked with visible implant elastomer tags, held in 24 40-liter tanks (6 fish per tank) at ambient temperature and photoperiod, and exposed to four feeding treatments to investigate the effect of ration on energy allocation pattern. In the preliminary phase of the experiment, fish were fed frozen chironomids at either high or low rations to produce differences in condition between two groups of fish. Feeding was maintained at initial levels until mean weights, relative weights, and lengths were significantly different among treatments (ANOVA, $\alpha = 0.05$). After 26 days, ration was re-assigned such that half of the high-ration tanks were switched to low ration and vice versa, resulting in four feeding treatments: High-High (HH), High-Low (HL), Low-Low (LL), and Low-High (LH). On a regular basis, individual fish were removed from tanks and length and weight were measured.

Ration was set as a proportion of maximum daily ration, calculated using a bioenergetics model for largemouth bass (Rice et al. 1983). Maximum ration was calculated for each fish in a tank and summed to determine total tank ration. Initially, high ration was defined as $1.0 \times$ maximum ration and low ration was defined as $0.5 \times$ maximum ration. However, these feeding levels did not result in adequate growth rates, and on day 12 (1 August), feeding treatments were altered and high ration was defined as $2.0 \times$ maximum ration and low ration was defined as $0.75 \times$ maximum ration. Live fish were measured (total length to 1 mm; wet weight to 0.01 g) weekly through day 26 (15 August), then every 3-4 days through the end of the experiment on day 46 (2

September). Relative weight (W_r) was calculated for each individual at each date using methods described in Murphy et al. (1991). At the end of the experiment, fish were sacrificed, measured as above, and dried to a constant dry weight (70 °C for approximately 3 days).

Seasonal raceway study

The purpose of the seasonal raceway study was to investigate the effect of ration and season on energy allocation pattern. Young-of-year bass were planted and reared in semi-natural raceways under two ration treatments. A sub-sample of fish from each raceway was taken monthly to quantify size and condition. Size and condition metrics were then compared across treatment and season to examine the relative effects of season and ration on energy allocation. Prior to planting young-of-year largemouth bass, raceways were drained, all fish were removed, and raceways were refilled immediately in order to remove potential predators and competitors while maintaining the resident aquatic macroinvertebrate community.

Raceway position and stocking densities were selected to produce two treatment types, high ration and low ration, designed to control food availability for young-of-year largemouth bass. We assumed that a) more potential prey (primarily limited to large zooplankton) would be transported to upstream raceways than those downstream such that position further upstream would have a positive effect on individual ration, and b) density of young-of-year fish would be negatively related to individual ration through behavioral and competitive interactions (Tonn et al. 1994). In the high ration treatment, 170 young-of-year largemouth bass were stocked into each of the furthest upstream raceways. In the low ration treatment, 500 young-of-year bass were stocked into each

of the pair of raceways immediately downstream from the high ration treatment. The high ration treatment was therefore characterized by low stocking density and upstream raceway position, whereas the low ration treatment was characterized by high stocking density and downstream raceway position (Figure 1).

During 2006 and 2007, raceways were stocked with young-of-year largemouth bass in early- to mid-July (21 July 2006; 9 July 2007), and then removed in late-October (27 October 2006; 26 October 2007). On a monthly basis, subsamples of fish were collected from each raceway with a seine net, and at the end of experiments, raceways were drained and surviving fish were retrieved. After collection, fish were sacrificed, frozen and later thawed, measured (length, 1 mm; wet weight, 0.01 g), and dried to a constant dry weight at 70°C (3 days). In addition, prior to drying fish in 2007, stomach contents were removed, diet items were identified (to family or order) and enumerated, and diet dry weight was quantified (after drying at 70°C for 3 days).

Quantifying condition

Tissue weight in fishes is expected to increase with length in a pattern consistent with the following equation:

$$W = aL^b$$

This relationship can be log-transformed to give the linear relationship

$$\log_e W = \log_e a + b(\log_e TL).$$

To analyze energy allocation and the relative amount of structural and storage tissues in largemouth bass, we employed metrics of condition dependent on this relationship (e.g., relative weight, W_r , and length-adjusted total dry weight, DW_{adj}) that have been shown

to closely match physiological state and energy content of fishes (Brown and Murphy 2004).

For the ration study, we calculated relative wet weight (W_r), or the proportion of observed wet weight (W) to standard weight (W_s), which is that expected for a given length.

$$W_r = 100 (W W_s^{-1})$$

The standard weight equation we used to derive this metric was taken from Wege and Anderson (1978) where $\log_{10} W = -5.316 + 3.191(\log_{10} TL)$. Though a length bias has been found for this equation such that relative weight generally increases with increasing lengths (Murphy et al. 1991), our analysis covered a sufficiently small range of largemouth bass lengths that this bias was minimized.

For the raceway study, strong relationships existed between $\log_e TL$ and \log_e dry weight (DW) as well as between $\log_e TL$ and \log_e Joules (J). Because of these strong relationships, we analyzed the amount of DW relating to TL (length-adjusted \log_e total dry weight, hereafter referred to as DW_{adj}) in the context of analyses of covariance (ANCOVA). This statistical routine corrects the dependent variable (\log_e total DW) for the effect of the covariate ($\log_e TL$) and calculates a mean DW_{adj} and associated variance for each group in the analysis. More detail is given in the data analysis section below.

Percent dry weight (%DW), total energy (J) and energy density ($J g^{-1}$) were calculated for comparison with our length-dependent metrics of condition. Percent dry weight (%DW) is the percentage of fish wet weight made up of dry weight, and energy density is the amount of energy (Joules) per gram of fish wet weight. Energy density is

a useful indicator of amount of storage tissue (Salam and Davies 1994) and is strongly associated with %DW in fish (Hartman and Brandt 1995).

Energy density (J g^{-1} wet weight) was measured using a Parr isoperibol bomb calorimeter at the Lake Michigan Field Station (Muskegon, MI) of the Great Lakes Environmental Research Laboratory (National Oceanographic and Atmospheric Administration). In 2006, a subsample of 10 largemouth bass was selected randomly from 0.5 standard deviation length bins across all treatments and dates for the purpose of measuring energy density from a wide variety of fish ($N = 49$). In 2007, 10 random individuals were selected from each sampling treatment during each sampling date ($N = 159$).

Data analysis

To explore how measures of body size and condition influence energy and to justify using weight and length to analyze energy allocation patterns, we performed a series of simple linear regression (SLR) and forward stepwise linear regression (FSR) analyses to relate body size (length, wet weight, and dry weight) and condition measures (percent dry weight, relative weight [W_r]) to total body energy and energy density. Because stomach contents were removed prior to energy determination in 2007, analyses were performed separately for 2006 and 2007. For FSR analysis, percent dry weight, total length, dry weight, and W_r were potential explanatory variables for energy density; percent dry weight, W_r , \log_e total length, and \log_e dry weight were potential explanatory variables for total body energy. For both tests, criterion for inclusion was set at $\alpha = 0.01$.

For the ration experiment, mean total length, wet weight, and relative weight were tracked over time for each tank. Mean daily growth rates for wet weight ($\text{g g}^{-1} \text{ day}^{-1}$) were calculated across tanks for each treatment type during initial and final ration phases of the experiment in order to determine the effect of treatment on compensatory growth and energy allocation. To test for the effect of ration on mean size (length and weight) and condition (relative weight) by tank over the course of the experiment, repeated measures analysis of variance was conducted with a between-subjects effect of treatment type, a within-subjects effect of time, and their interaction. A Huynh-Feldt covariance structure was employed to adjust degrees of freedom and correct for violations of sphericity. Bonferroni adjusted post-hoc comparisons were used to calculate significant differences in mean length, weight, and relative weight between treatments at each observation date (Figure 2). Because post-hoc tests evaluated within-date differences, Bonferroni adjusted pairwise comparisons were conducted without adjustments to model covariance structure. Final %DW was calculated for each treatment to further describe condition and compare to W_r . Pearson's r was calculated to quantify the strength of the relationship between tank mean values for final W_r and final %DW and analyses of variance with Tukey post-hoc tests were used to determine differences in size (length, weight) and condition (W_r , %DW) of bass among treatment type.

Experimental facilities limited us to two replicates for each raceway and treatment type during both 2006 and 2007. Differences in growth of fish were evident between replicates. Thus, we a posteriori adopted a raceway-specific analytical

approach to investigate the effect of season and ration on energy allocation pattern in young-of-year largemouth bass.

We used analysis of covariance (ANCOVA) with dry weight (\log_e DW) as the dependent variable and length (\log_e TL) as the covariate to investigate ration- and season-mediated departures from power function relationships ($W = aL^b$) between length and tissue mass (Hurst and Conover 2003; Höök and Pothoven, in press). Prior to ANCOVAs we tested for homogeneity of slopes, and excluded individual data subsets which violated this assumption.

During the 2007 raceway experiment, we removed and weighed stomach contents to validate the effect of our treatments on individual ration. If fish in the high ration treatment were indeed subject to higher individual ration, we would expect to find greater average size-specific diet dry weight in those fish compared with low ration treatment fish. We then performed Kruskal-Wallis analysis of variance by ranks for differences in total diet dry weight (TDW) and fish weight adjusted diet dry weight (DPW) to test for significant differences in individual ration by treatment, as Shapiro-Wilk tests ($\alpha = 0.05$) indicated non-normal distributions for TDW and DPW.

Results

Quantifying Condition

Relationships between measures of condition and energy were explored to justify analysis of energy allocation patterns based on length and weight. Dry weight and %DW were strong predictors of total body energy and energy density, respectively. The dependent variables most highly correlated with \log_e total Joules and energy density were \log_e DW and %DW, respectively (Table 1). High r^2 values (0.807 to 0.997) were evident despite the narrow size range of fish (35 to 160 mm) and treatment-mediated differences in growth and condition. FSR results were consistent with the results above. For both years, the best models for predicting energy density included only %DW and the best models for predicting total energy included \log_e DW and \log_e TL (Table 2).

Ration study

Ration level had a significant impact on growth and condition of young-of-year largemouth bass in tank experiments. Prior to the feeding change, length and weight increased steadily in all treatments and diverged slowly among treatments (Figures 2 a-b). However, there was near immediate divergence in W_r after feeding treatments were applied (Figure 2c). Fish fed high ration grew in length and weight at a faster rate, in addition to increasing in girth and condition, producing fish of larger length and weight and increased relative weight. Fish fed low ration continued to grow (increase in length and weight), but preferentially allocated energy toward structure as opposed to storage, i.e., decreased W_r .

On day 26 (15 August 2006), fish from high and low feeding treatments were sufficiently different to apply the feeding change (ANOVA comparing W_r : $F_{3,19} = 42.819$,

$p < 0.001$; W: $F_{3,19} = 8.548$, $p = 0.001$; TL: $F_{3,19} = 3.871$, $p = 0.026$). After the feeding treatment switch, HL fish responded by remaining at relatively high W_r while slowing growth in length and weight. LH fish responded with a marked increase in W_r and compensatory growth. The effect of treatment type across the ration experiment was significant for W_r ($F_{3,9.41} = 9.973$, $p = 0.003$) but not for wet weight ($F_{3,6.41} = 2.082$, $p = 0.198$) or total length ($F_{3,6.41} = 0.967$, $p = 0.462$). However, the interactive effect of time and treatment was significant for all three measures at $p < 0.001$, indicating temporal differences in the effect of treatment type, driven by responses to temporal shifts in ration. There was no difference in mean daily growth rate in $g\ g^{-1}\ day^{-1}$ between HL and HH treatments or between LH and LL during the initial ration treatment (Figure 3). After the feeding switch, HL and LL fish grew at similar rates but the compensatory response in LH treatment fish resulted in a significantly higher growth rate for LH fish than HH fish during the final phase (Figure 3). Final W_r and %DW were significantly correlated across all tanks ($r = 0.678$; $p < 0.001$) while final W_r , DW, and %DW differed significantly by treatment (W_r : $F_{3,19} = 23.831$, $p < 0.001$; DW: $F_{3,19} = 8.376$, $p = 0.001$; %DW: $F_{3,19} = 8.762$, $p = 0.001$). Post-hoc tests indicated that measures for the LL treatment were significantly lower than all other treatments (Tukey post-hoc tests, $\alpha = 0.05$) while these variables were similar across the remaining 3 treatments.

Seasonal raceway study

Prior to analysis of energy allocation pattern, the ability of ration treatments to generate differential feeding patterns was evaluated for 2007 samples. Mean values of total diet dry weight (TDW) and dry weight-specific diet dry weight (DPW) (Figure 4) were generally higher for high-ration treatments than low-ration treatments. Kruskal-

Wallis comparison indicated that TDW on day-of-year (DOY) 214 (2 August) and 250 (7 September), and DPW on DOY 214 differed significantly among treatments (TDW DOY 214, $H = 29.708$, $p < 0.05$; TDW DOY 250, $H = 19.756$, $p < 0.05$; DPW DOY 214, $H = 22.228$, $p < 0.05$). We also observed differences in diet items found in stomachs by treatment, with a higher incidence of larger prey items (Odonata, Baetidae, Decapoda) in high-ration raceways and smaller prey items (Copepoda, Notonecta, Diptera) in low-ration raceways. This observation was likely significant due to the association of larger prey items with higher energy density and greater foraging efficiency. These results indicated that the combination of raceway position and stocking density as ration treatments was a successful means of manipulating relative consumption rates for young-of-year largemouth bass.

The length and weight of largemouth bass increased over the raceway experiment in all treatments (Figure 5). Measures of condition (W_r and %DW) also changed through the course of the experiment, though specific patterns in these measures were difficult to discern (Figure 6). For W_r , this may be due to reduced predictive ability of the standard weight equation for fish below the 150-mm minimum TL recommended for application (Murphy et al. 1991). During both years, ANCOVA results indicated seasonal differences in length-adjusted dry weight (DW_{adj}) for each treatment (Table 3; Figure 7). The seasonal pattern of energy allocation generally produced an increase in DW_{adj} in raceways over the course of the experiment such that there were significant differences in this measure across season in 2006 ($H1^*$: $F_{2,65} = 24.819$, $p < 0.001$; $H2$: $F_{3,84} = 8.686$, $p < 0.001$; L1: $F_{3, 115} = 71.531$, $p < 0.001$; L2: $F_{3,119} = 40.808$, $p < 0.001$) and 2007 ($H2^*$: $F_{2,55} = 5.353$, $p = 0.008$; L1: $F_{3, 124} = 22.620$, $p < 0.001$; L2:

$F_{3,107} = 15.769$, $p < 0.001$). The single exception was raceway H1 in 2007 for which differences in DW_{adj} were marginally insignificant among months ($F_{3,72} = 2.369$, $p = 0.078$). The September sampling date was excluded from the H1 2006 and H2 2007 ANCOVAs due to significant differences in slope between $\log_e TL$ and $\log_e DW$, thereby confounding ANCOVA interpretation.

Raceway-mediated differences in DW_{adj} were evident in ANCOVAs conducted across treatments for each sampling date (Table 4; Figure 8). During August, DW_{adj} was significantly larger for high-ration treatments than low-ration treatments in 2006 ($F_{3,114} = 59.197$, $p < 0.001$) and 2007 ($F_{3,116} = 9.489$, $p < 0.001$). In September of both years, values of DW_{adj} were still higher in high ration raceways, but to a somewhat lesser degree than in August (2006: $F_{3,59} = 12.003$, $p < 0.001$; 2007: $F_{3,96} = 4.572$, $p = 0.005$). Variance between means decreased further in October such that there was no significant difference in mean DW_{adj} in 2006 ($F_{2,67} = 2.627$, $p = 0.080$) and 2007 ($F_{3,56} = 2.994$, $p = 0.141$). Raceway L1 was excluded from September 2007 ANCOVA due to a significant difference in slope between $\log_e TL$ and $\log_e DW$.

Discussion

There is considerable variation in growth and energy allocation throughout ontogeny in fishes (Wuenschel et al. 2006). This variation is expressed by changes in growth rates, allometric growth of body structures, and changes in proximate composition. These changes may result from hard-wired life history mechanisms that are genetically predetermined (Garvey et al. 2000; Munch and Conover 2002), or they may be driven by environmental influences (e.g., food availability and temperature) (Adams et al. 1982; Slaughter et al. 2008). Largemouth bass and most other temperate fish species undergo considerable changes in body dimensions and composition during their first year of life. In particular, many studies have shown that young-of-year fish contain relatively high lipid concentration and energy density just prior to their first winter (Flath and Diana 1985; Ludsin and DeVries 1997; Hurst and Conover 2003). It has also been shown that the tissues of larval and early juvenile fish are primarily composed of water and protein and include very little energy reserve tissue (Wuenschel et al. 2006).

The recognition of a shift in body dimensions and composition over the first summer in young-of-year temperate fishes has long been established, but the underlying mechanisms remain unclear. This work indicates that ration and season interact to determine energy allocation pattern in juvenile largemouth bass during their first year of life. The ration experiment demonstrated that changes in food consumption can lead to short-term changes in energy allocation patterns. Whereas growth in length was relatively unresponsive to changes in ration during the short term, growth in weight and girth changed nearly immediately with ration. A compensatory growth response was also observed for fish switched from low to high ration (LH treatment). This may

suggest an additional mode of energy regulation and an allocation pattern characterized by changes in feeding behavior and metabolic demands as observed in other studies (Broekhuizen et al. 1994; Skalski et al. 2005).

The outdoor raceway experiment produced a shift in condition from relatively low DW_{adj} early in the season to relatively high DW_{adj} later in the season (Figure 5). This is indicative of a change in seasonal energy allocation pattern for young-of-year largemouth bass from one initially prioritizing structural growth to one prioritizing storage growth prior to winter. Ration treatment (density and raceway position) appeared to affect the extent of these seasonal changes in condition. During August of 2006 and 2007, there were significant differences in DW_{adj} between low-ration and high-ration treatment fish. This difference decreased steadily in both years such that there were no significant differences in DW_{adj} between ration treatments by October of 2006 and 2007 (Figure 8). This indicates that ration mediates the degree to which a tradeoff exists between growth in storage and growth in structure and that the extent of this tradeoff may interact strongly with season to determine the relative amount of energy fish allocate to structural or storage tissues.

The best model for total energy and dry weight generated by the forward stepwise regression analysis in this study would be expected not to include both \log_e length and \log_e dry weight due to the high positive correlation between dry weight and length. However, it is worth noting that in the final model for both 2006 and 2007 the effect of dry weight is positive, but the additive effect of total length on total energy is negative. This suggests that through both years of this study, at a given dry weight, fish

of greater length tended to be of lower energy, which agrees with our assumption that there is a tradeoff between growth in structure (length) and storage (weight and energy).

Analysis of largemouth bass stomach contents during 2007 resulted in strong differences among raceways in TDW and DPW. Differences were particularly apparent early in the season. Though there were not significant differences between feeding treatments at the later dates in the experiment, weight-specific maintenance metabolism and consumption have been shown to decrease with increasing body size in fish (Clarke and Johnston 1999). Since high-ration treatment fish at later dates were of greater body size, similar TDW and DPW between treatments still indicate the presence of a greater amount of energy available for growth in high-ration fish during this experiment.

Many studies of proximate composition and energy allocation of young-of-year fish have focused on energy reserve depletion overwinter and its effect on recruitment to age 1 (Miranda and Hubbard 1994; Post et al. 1998; Garvey et al. 2004). In such studies, it is implied that changes in energy allocation pattern over the first summer prior to winter are genetically hard-wired. However, various modeling and experimental studies including this study indicate that energy allocation pattern through the first year of life is complex and appears to involve multiple factors, genetic and environmental (Heulett et al. 1995; Post and Parkinson 2001; Sogard and Spencer 2004).

In a study of energy allocation of juvenile sablefish (*Anoplopoma fimbria*), Sogard and Spencer (2004) found that low ration and low temperature produced a tradeoff between growth in structure and growth in lipid resulting in delayed growth of lipid in favor of immediate growth in length. Further, the authors posited that energy allocation

pattern in juvenile sablefish was dependent on body size and tradeoffs mediated by ration and temperature. Similarly, our ration experiment found that ration affected energy allocation pattern and, more importantly, that energy was preferentially allocated to structure rather than storage at low ration. This general pattern was observed in spite of extensive differences in the early life history of sablefish, a pelagic marine species characterized by rapid juvenile growth and a limited capacity for compensatory growth (Sogard and Olla 2001), and largemouth bass, a warm freshwater species exhibiting parental care and a high capacity for compensatory growth as documented in the LH treatment of the ration experiment in this study. For eastern mosquitofish (*Gambusia holbrooki*), another species exhibiting high parental investment and relatively advanced-stage free-swimming larvae, energy allocation patterns from birth to 40 days of age were also characterized by initial growth in length at the expense of lipid reserves (Heulett et al. 1995). These ex situ studies of energy allocation were conducted for a sufficient length of time to see distinct patterns (Sogard and Spencer 2004: 15 weeks; Heulett et al. 1995: 40 days; this study: 46 days) but necessarily excluded environmental variation and seasonal cues that can influence energy allocation patterns.

For young-of-year largemouth bass reared in outdoor semi-natural raceways under high and low feeding treatments, the pattern outlined above of 'preferential' energy allocation to structural tissues did not hold throughout the growing season. Raceway study results mirrored ration study results only early in the growing season. During the summer, raceway fish preferentially allocated energy to growth in length before girth in a pattern consistent with results from the ration experiment. Similarities

were expected since the ration study was conducted concurrently with the early portion of the raceway study in 2006 and fish were sampled from the same source population only 2 days apart. However, during fall, fish in both treatments grew to similar length-adjusted dry weight (DW_{adj}) under both ration treatments in all raceways despite significant differences in total length. This indicates that energy allocation pattern had shifted and fish were growing preferentially in storage tissue with the onset of winter regardless of length.

These growth patterns suggested the existence of a tradeoff associated with allocating energy to structure or storage mass. Specifically, low ration led to a more severe tradeoff between allocating energy to growth in structural versus storage tissues. Essentially, there was a change in energy allocation priorities throughout the summer and fall. This resulted in fish allocating a significantly lower proportion of energy to storage tissue early in the season and a significantly higher proportion to storage late in the season. High-ration fish tended to express the same seasonal energy allocation pattern, but allocated a higher proportion of available energy to the lower priority tissue class. In fact, high ration fish in 2006 appeared to avoid forgoing growth in storage for growth in structure early in the season altogether. (Figure 7). Size-dependent, ontogenetic, and genotypic patterns in energy allocation pattern of young fish have been observed in prior studies (Munch and Conover 2002; Garvey and Marschall 2003; Wuenschel et al. 2006). Though these factors are undoubtedly important determinants, our study indicates that energy allocation patterns are also mediated by seasonal environmental cues and food availability.

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Table 1) Regression model coefficients and fits for simple linear regression analysis.
 Note: PDW represents fraction dry weight.

Year Class 2006	α	SE	p	β	SE	p	r^2
$\log_e(J) = \alpha + \beta(\log_e(DW))$	9.920	0.006	<0.001	1.016	1.011	<0.001	0.995
$\log_e(J) = \alpha + \beta(\log_e(TL))$	-4.074	0.502	<0.001	3.262	0.117	<0.001	0.943
$\log_e(DW) = \alpha + \beta(\log_e(TL))$	-14.582	0.225	<0.001	3.442	0.053	<0.001	0.928
$J g^{-1} = \alpha + \beta(PDW)$	-842.2	371.0	0.028	24,322	1,737	<0.001	0.807
Year Class 2007	α	SE	p	β	SE	p	r^2
$\log_e(J) = \alpha + \beta(\log_e(DW))$	9.914	0.004	<0.001	1.034	0.005	<0.001	0.997
$\log_e(J) = \alpha + \beta(\log_e(TL))$	-5.104	0.207	<0.001	3.627	0.050	<0.001	0.971
$\log_e(DW) = \alpha + \beta(\log_e(TL))$	-15.457	0.130	<0.001	3.636	0.032	<0.001	0.974
$J g^{-1} = \alpha + \beta(PDW)$	-755.0	85.88	<0.001	24,085	500.0	<0.001	0.948

Table 2) Results of forward stepwise regression analysis for \log_e total energy (J) and energy density($J g^{-1}$).

		Model	n	r^2
Energy Density	2006	$J g^{-1} = -842.2 + 24,322(PDW)$	49	0.807
	2007	$J g^{-1} = -755.0 + 24,085(PDW)$	158	0.948
Total Energy	2006	$\log_e(J) = 13.52 + 1.27(\log_e(DW)) - 0.844(\log_e(TL))$	49	0.994
	2007	$\log_e(J) = 11.72 + 1.15(\log_e(DW)) - 0.425(\log_e(TL))$	158	0.997

Table 3) Results of analysis of covariance with $\log_e(\text{total length})$ as a covariate testing for between-month differences in H1, H2, L1, and L2 raceways in 2006 and 2007.

			SSE	df	MSE	F	Sig.
DW 2006	H1	Month	0.250	2	0.125	24.819	< 0.001
		\log_e Total Length	1.732	1	1.732	343.765	< 0.001
		Error	0.328	65	0.005		
	H2	Month	0.182	3	0.061	8.686	< 0.001
		\log_e Total Length	3.727	1	3.727	533.095	< 0.001
		Error	0.587	85	0.007		
	L1	Month	1.043	3	0.348	71.531	< 0.001
		\log_e Total Length	4.388	1	4.388	902.924	< 0.001
		Error	0.559	115	0.005		
	L2	Month	0.720	3	0.240	40.808	< 0.001
		\log_e Total Length	7.404	1	7.404	1,259.527	< 0.001
		Error	0.700	119	0.006		
DW 2007	H1	Month	0.044	3	0.015	2.369	0.078
		\log_e Total Length	5.055	1	5.055	824.591	< 0.001
		Error	0.441	72	0.006		
	H2	Month	0.070	2	0.035	5.353	0.008
		\log_e Total Length	4.568	1	4.568	698.728	< 0.001
		Error	0.360	55	0.007		
	L1	Month	0.622	3	0.207	22.620	< 0.001
		\log_e Total Length	7.867	1	7.867	858.720	< 0.001
		Error	1.136	124	0.009		
	L2	Month	0.659	3	0.220	15.769	< 0.001
		\log_e Total Length	5.828	1	5.828	418.397	< 0.001
		Error	1.490	107	0.014		

Table 4) Results of analysis of covariance with $\log_e(\text{total length})$ as a covariate testing for between-raceway differences in dry weight (DW) in August (Aug), September (Sep), and October (Oct) for 2006 and 2007.

			SSE	df	MSE	F	Sig.
DW 2006	Aug	Raceway	1.149	3	0.383	59.197	<0.001
		\log_e Total Length	4.728	1	4.728	730.788	<0.001
		Error	0.738	114	0.006		
	Sep	Raceway	0.179	3	0.060	12.003	<0.001
		\log_e Total Length	1.727	1	1.727	348.330	<0.001
		Error	0.293	59	0.005		
	Oct	Raceway	0.027	2	0.008	2.627	0.080
		\log_e Total Length	8.132	1	8.132	1591.394	<0.001
		Error	0.342	67	0.005		
DW 2007	Aug	Raceway	0.311	3	0.104	9.489	<0.001
		\log_e Total Length	7.137	1	7.137	652.866	<0.001
		Error	1.268	116	0.011		
	Sep	Raceway	0.137	3	0.046	4.572	0.005
		\log_e Total Length	3.694	1	3.694	370.900	<0.001
		Error	0.956	96	0.010		
	Oct	Raceway	0.023	3	0.008	1.892	0.141
		\log_e Total Length	1.747	1	1.747	424.510	<0.001
		Error	0.230	56	0.004		

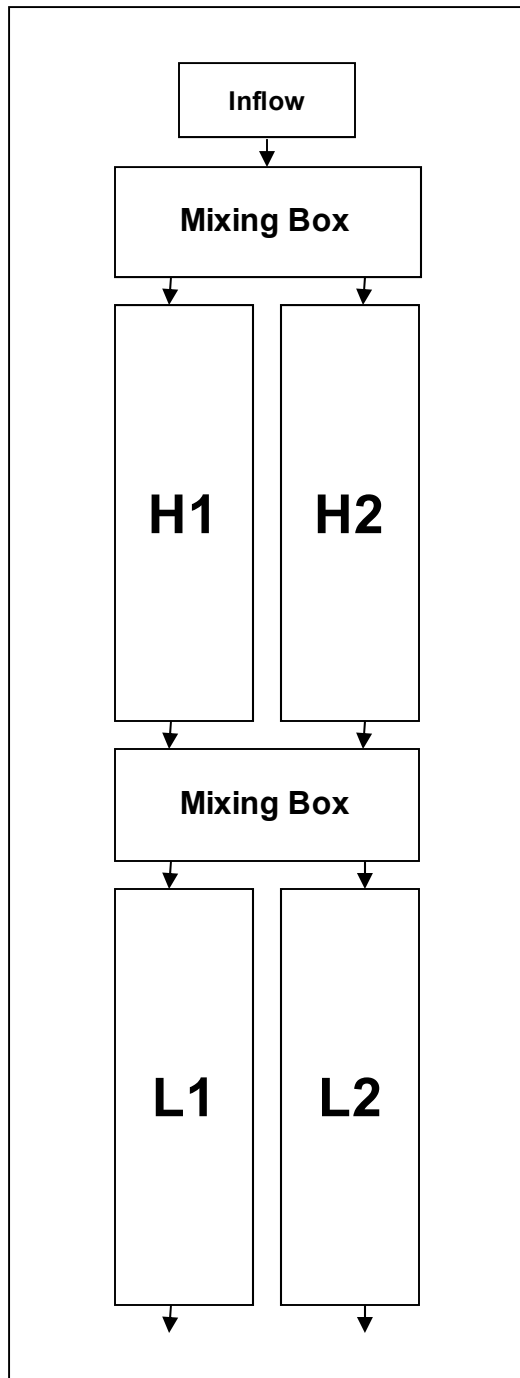


Figure 1) Diagram of raceways and treatment orientation at the Michigan DNR Fisheries Research Station in Saline, MI. H1 and H2 are the two high-ration raceways, which were each stocked with 170 young-of-year largemouth bass; L1 and L2 are the two low-ration raceways, which were each stocked with 500 young-of-year largemouth bass. Each raceway is approximately 36.5 m long, 5 m wide, and adjusted to a mean depth of 0.5 m. Screens at the upstream and downstream end of each raceway confine the fish.

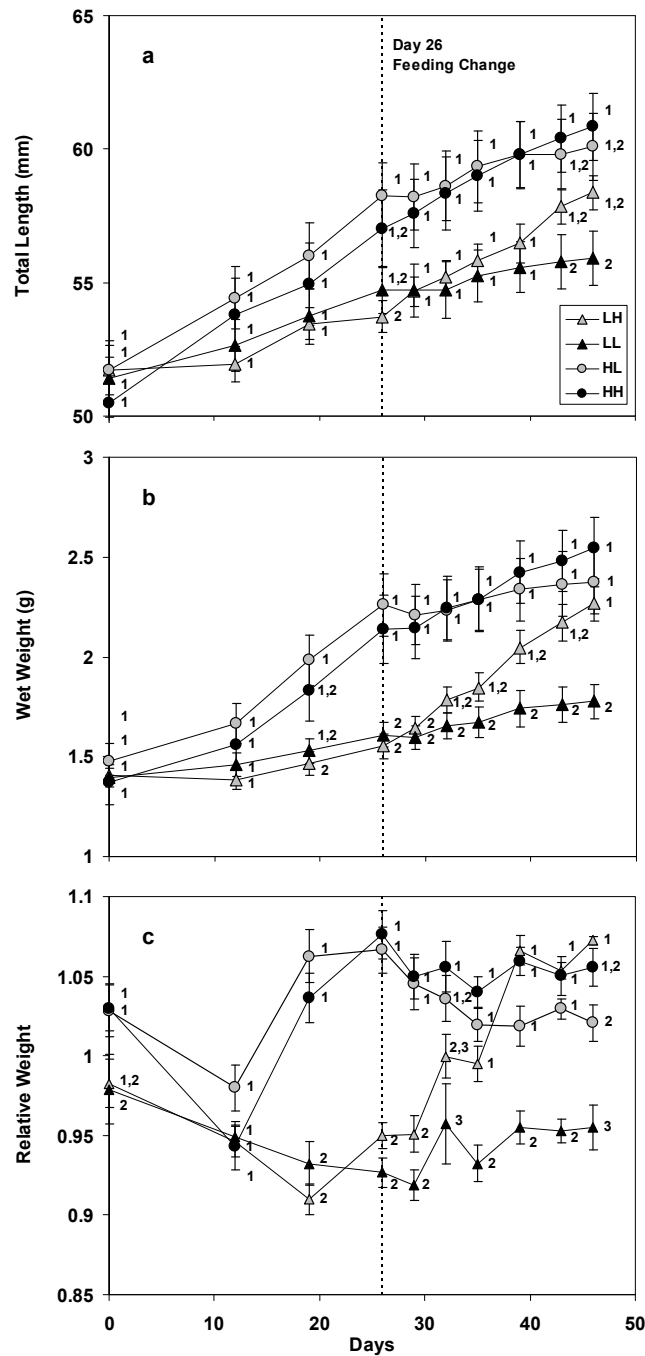


Figure 2) Means (\pm standard error) for a) length (mm), b) wet weight (g), and c) relative weight by treatment type for each date measured in indoor tank experiments. Grey triangles represent the low-high treatment (LH), solid triangles represent the low-low treatment (LL), grey circles represent the high-low treatment (HL), and solid circles represent the high-high treatment (HH). The dotted vertical line at day 26 represents the date at which the feeding change was applied to transitional treatments (LH and HL). Numbers denote homogenous subsets at each observation date derived from Bonferroni adjusted pairwise post-hoc tests ($\alpha = 0.05$).

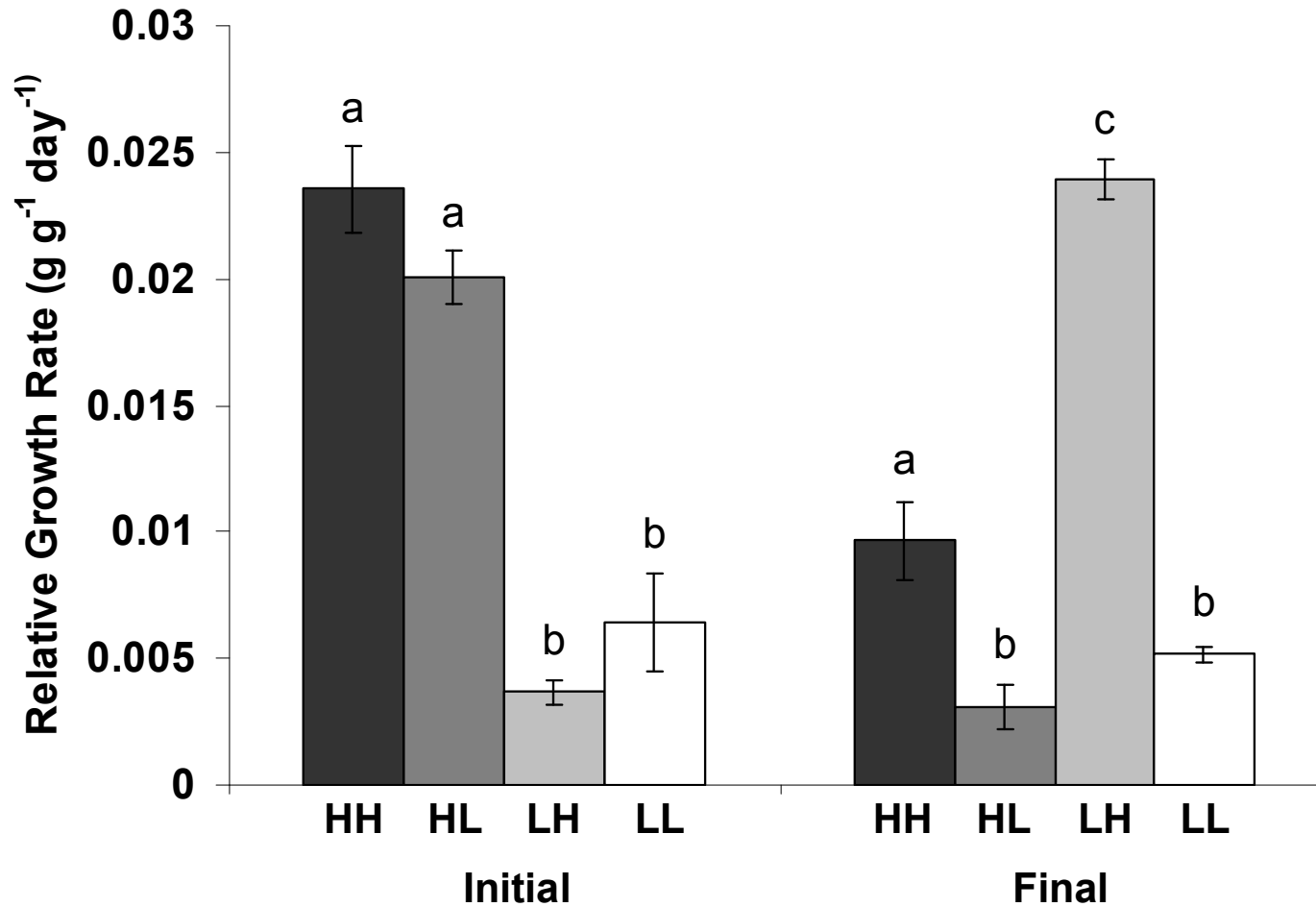


Figure 3) Mean (\pm standard error) growth rate ($\text{g wet weight g}^{-1} \text{ day}^{-1}$) for initial and final ration treatments in each of the four treatment types. Growth rates for initial ration phase were calculated for the time interval from Day 0 to 26. Growth rates for final ration phase were calculated for the time interval from Day 26 to 46. Letters denote Tukey homogenous subsets within treatment phases.

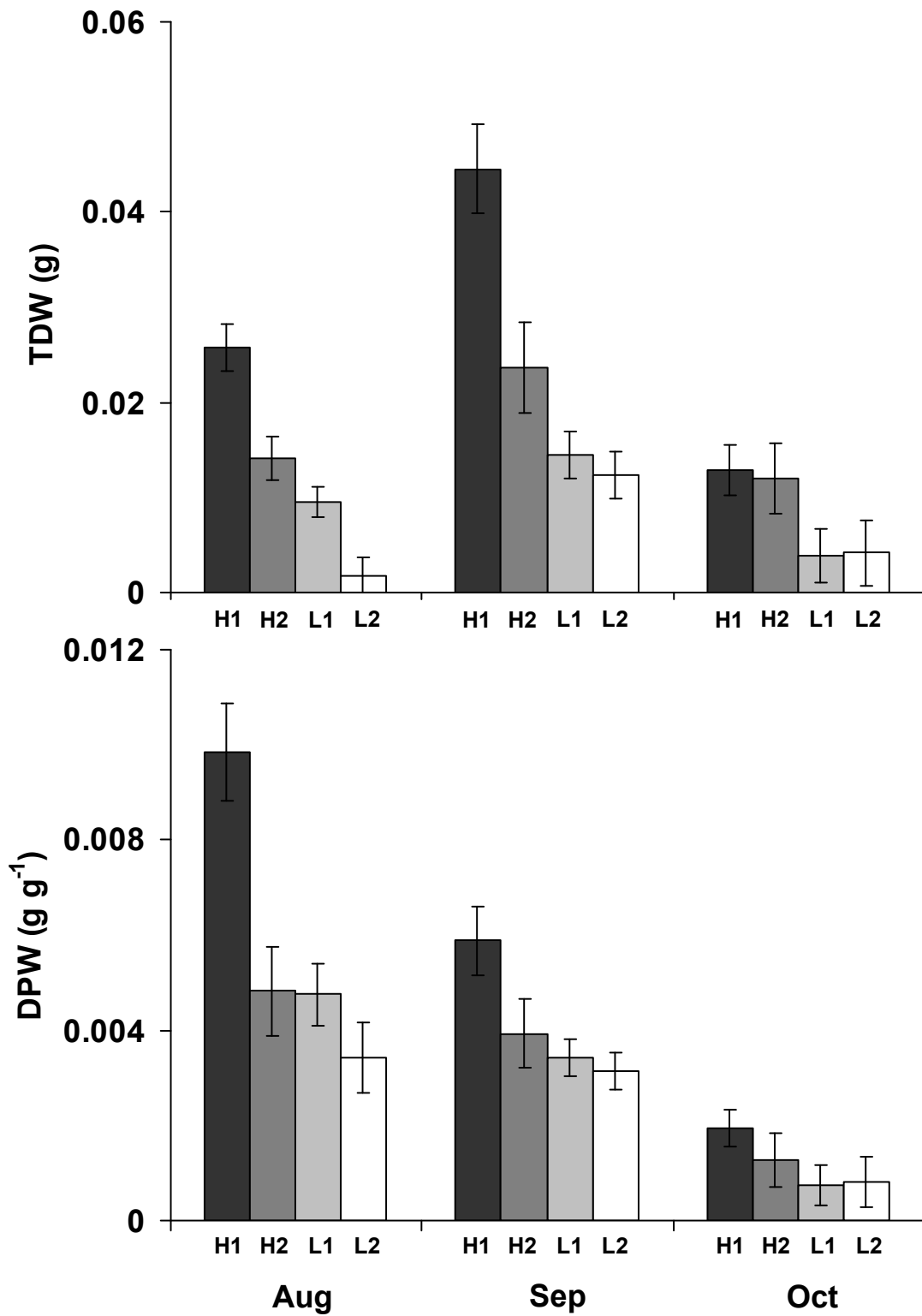


Figure 4) Mean dry weight (g) and fish weight specific dry weight (g g⁻¹) of diet contents (\pm standard error) found in the stomachs of young-of-year largemouth bass by raceway during August, September, and October, 2007.

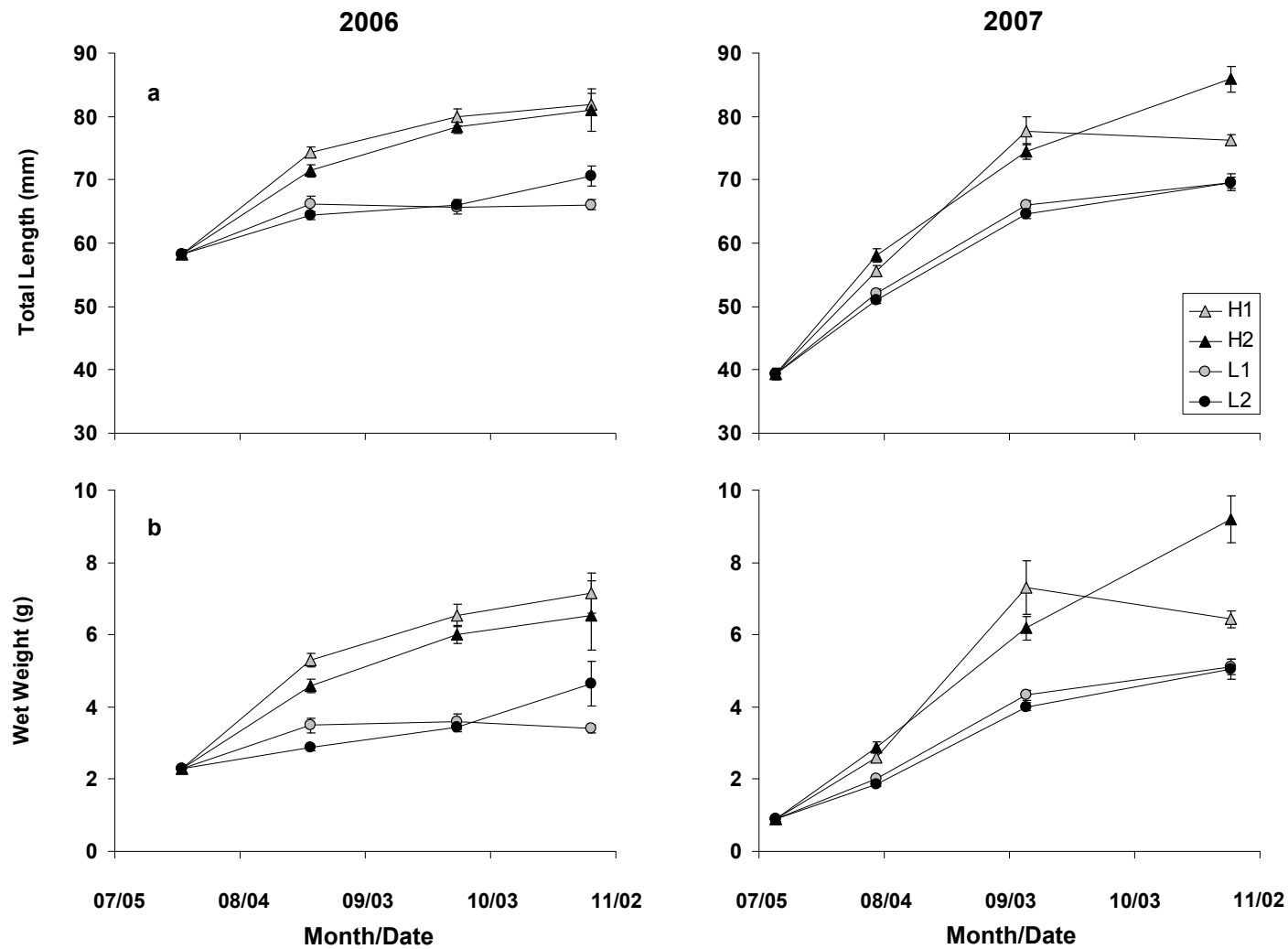


Figure 5) Means (\pm standard error) for a) length (mm), and b) wet weight (g) by raceway for each date measured in outdoor raceway experiments for 2006 and 2007. Triangles indicate samples from high-ration raceways; circles indicate samples from low-ration raceways.

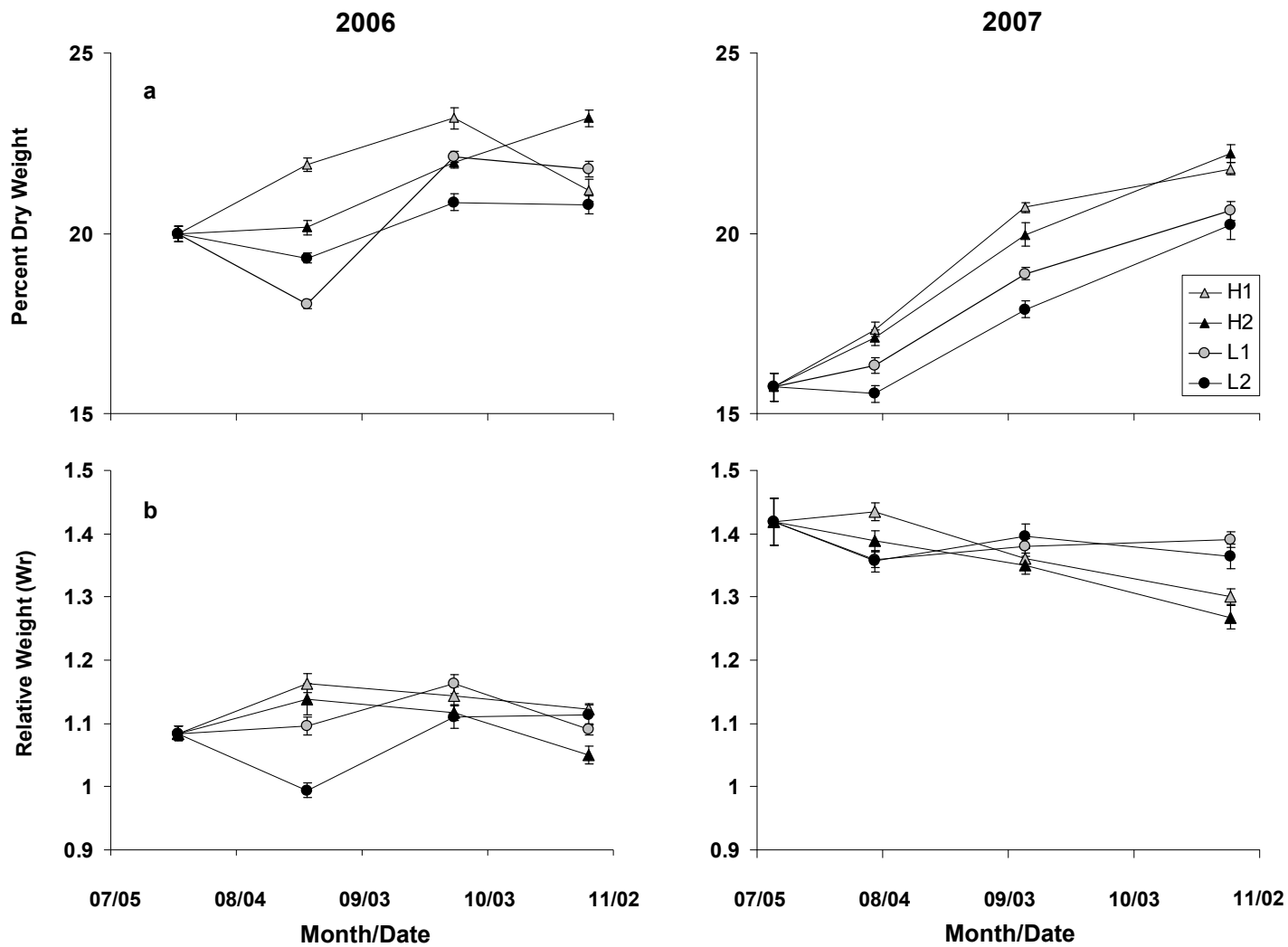


Figure 6) Means (\pm standard error) for a) relative weight (W_r) and b) Percent dry weight by raceway for each date measured in outdoor raceway experiments for 2006 and 2007. Triangles indicate samples from high-ration raceways; circles indicate samples from low-ration raceways.

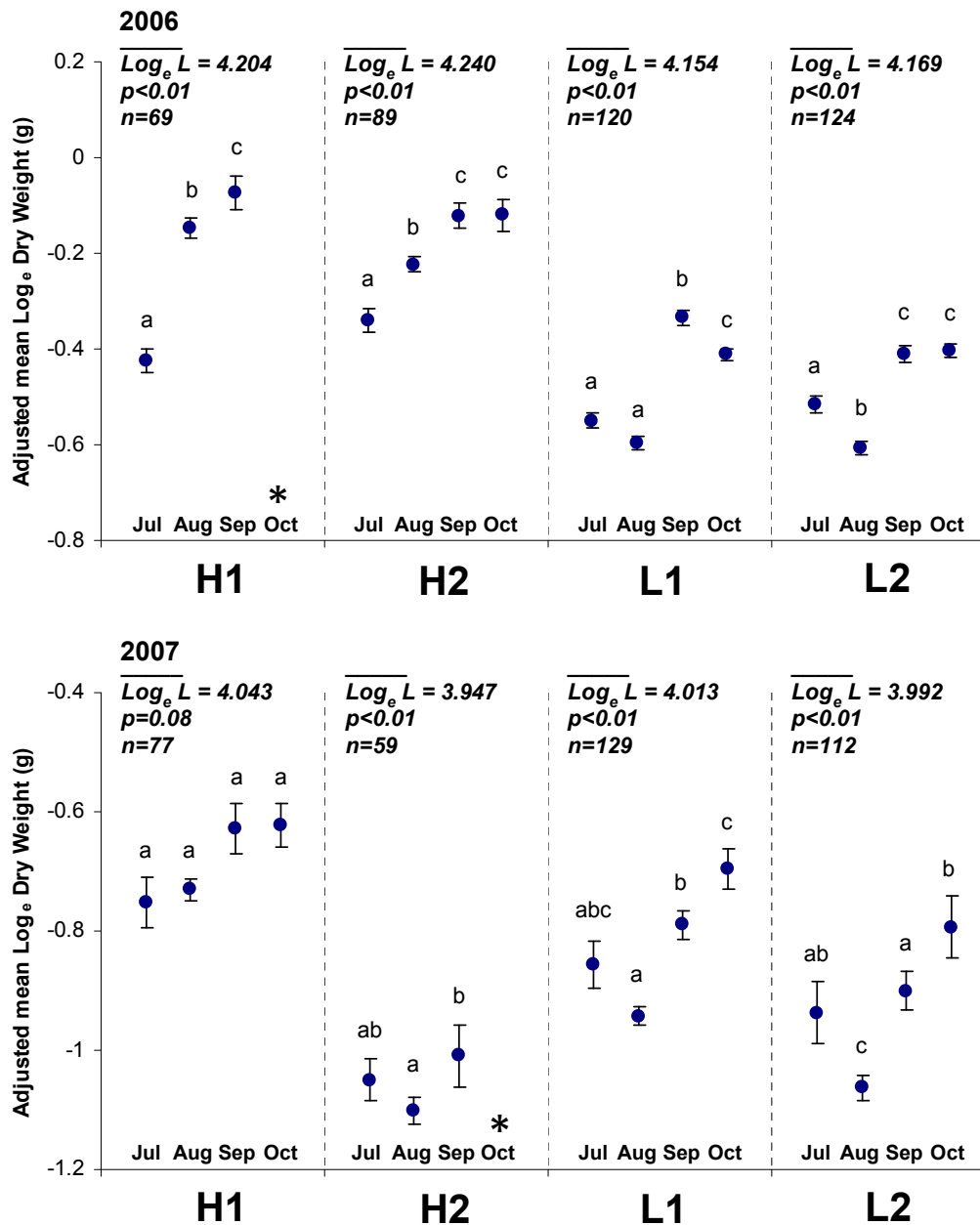


Figure 7) Seasonal differences in energy allocation pattern using results from analysis of covariance for length-adjusted \log_e dry weight of young-of-year largemouth bass from raceway experiments in 2006 and 2007. Values are mean (\pm standard error) \log_e length-adjusted \log_e dry weights. ANCOVA were conducted separately by raceway (divided by vertical dotted lines) across all sampling dates. Log_e lengths to which \log_e dry weights were adjusted and resulting p-values from each ANCOVA are reported in italics. Letters denote Tukey homogenous subsets within raceways. $\text{Log}_e L$ represents the grand mean length to which dry weights were adjusted in each ANCOVA.

* Months with a significantly different slope for \log_e length vs. \log_e dry weight

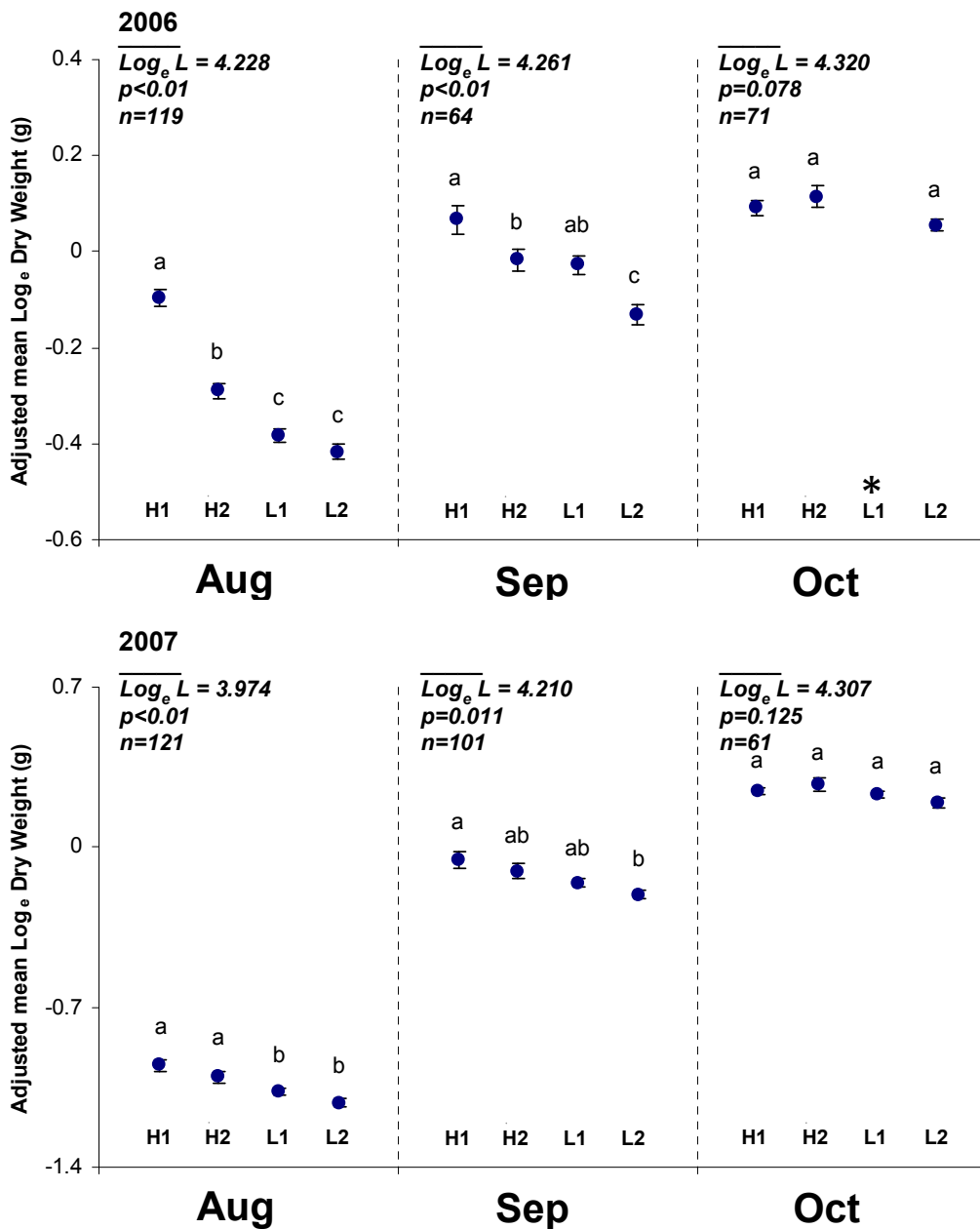


Figure 8) Ration-mediated changes in energy allocation pattern using results from analysis of covariance for length-adjusted \log_e dry weight of young-of-year largemouth bass from raceway experiments in 2006 and 2007. Values are mean (\pm standard error) \log_e length adjusted \log_e dry weights. ANCOVA were conducted by sampling month separately (divided by vertical dotted lines) across treatments. \log_e lengths to which \log_e dry weights were adjusted and resulting p-values from each ANCOVA are reported in italics. Letters denote Tukey homogenous subsets within sampling months. $\log_e L$ represents the grand mean length to which dry weights were adjusted in each ANCOVA.

* Raceways with significantly different slopes for \log_e length vs. \log_e dry weight