

Bioenergetic trajectories underlying partial migration in Patuxent River (Chesapeake Bay) white perch (*Morone americana*)

Lisa A. Kerr and David H. Secor

Abstract: Partial migration, the coexistence of resident and migratory individuals within the same population, may be common in fish populations. A proposed mechanism underlying partial migration is differing dispersive responses to early growth conditions, but few studies have explicitly tested this. During their first year of life, white perch (*Morone americana*) in the Patuxent River (Maryland, USA) exhibit either residency in freshwater natal habitats (resident contingent) or disperse down-estuary into brackish habitats (dispersive contingent). We tested whether white perch juveniles exhibited differing growth and metabolic trajectories based on contingent membership or in response to salinity. A randomized factorial experiment with two contingent types and two salinity treatments (1 and 8) was conducted over a 30-day period. The experiments supported a contingent effect, with the dispersive contingent exhibiting higher consumption rates and a higher scope for growth. In addition, we identified a weak salinity effect with evidence of increased consumption and routine metabolism in mesohaline conditions. Juvenile growth rates calculated from individuals in the field supported laboratory results, with dispersive contingent members exhibiting higher growth rates. We conclude that contingent membership and the related phenomenon of partial migration in this population is associated with varying energetic tactics that significantly influence the scope for growth.

Résumé : La migration partielle, la coexistence d'individus résidents et migrants au sein d'une même population, peut être répandue chez les populations de poissons. Un mécanisme sous-jacent proposé pour expliquer la migration partielle est la présence de réactions différentes de dispersion aux conditions du début de la croissance; peu d'études l'ont cependant testé de façon explicite. Durant leur première année d'existence, les jeunes barettes (*Morone americana*) de la rivière Patuxent (Maryland, É.-U.) ou bien demeurent dans leurs habitats natals d'eau douce (contingent résident) ou se dispersent en aval dans l'estuaire dans des habitats saumâtres (contingent dispersé). Nous testons si les jeunes barettes ont des trajectoires différentes de croissance et de métabolisme selon leur appartenance à l'un ou l'autre contingent et d'après leur réaction à la salinité. Une expérience factorielle aléatoire présentant deux types de contingent et deux conditions de salinité (1 et 8) a été menée pendant 30 jours. Les résultats confirment l'existence d'un effet du contingent; le contingent dispersé possède des taux de consommation plus élevés et des perspectives de croissance plus grandes. Nous identifions, en plus, un faible effet de la salinité avec une consommation et un métabolisme de base accrus dans les conditions mésohalines. Les taux de croissance juvéniles obtenus chez des jeunes en nature confirment les résultats de laboratoire, car les membres du contingent dispersé possèdent des taux de croissance plus élevés. Nous concluons que l'appartenance à un contingent et le phénomène relié de migration partielle dans cette population sont associés à des tactiques énergétiques différentes qui influencent de manière significative les perspectives de croissance.

[Traduit par la Rédaction]

Introduction

Partial migration, or the presence of resident and migratory forms within a population, has been identified in several diadromous (Secor et al. 2001; Tsukamoto and Arai 2001; Kraus and Secor 2004) and marine (Able et al. 2003; Fromentin and Powers 2005; Elsdon and Gillanders 2006) fish populations. The coexistence of resident and migratory individuals within a single population is hypothesized to be related to differences in the behavioral response of individu-

als to trade-offs associated with migration versus residence (Jonsson and Jonsson 1993). Benefits of migration have been documented in many anadromous populations, with migrants typically having increased growth potential and achieving a larger size than resident fish because of increased feeding opportunities and osmoregulatory benefits associated with higher salinity waters (Gross 1987; Metcalfe and Thorpe 1990; Jonsson and Jonsson 1993). Increased predation risk and disease are among the costs of migration,

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contributing to higher mortality rates of migratory individuals (Jonsson and Jonsson 1993).

Although the ultimate cause of movement out of a habitat is likely related to food availability and predation risk (Werner and Gilliam 1984), the proximate cause of this behavior continues to be debated. Despite some evidence that contingents can occur as reproductively isolated subpopulations (e.g., Verspoor and Cole 1989), the preponderance of evidence supports partial migration as an expression of a conditional strategy leading to polyphenic responses within populations. In a single genetic population, the adoption of resident or migratory tactics relates to an individual's condition relative to a threshold, most likely related to growth (Lundberg 1988; Gross and Repka 1998a, 1998b). Differences in growth between residents and migrants are hypothesized to be established early in life and have been attributed to factors such as timing of spawning, social status, feeding hierarchies, density, and sex-specific differences (Jonsson and Jonsson 1993; Secor 1999). Investigations of growth thresholds as a cue to initiate migration (or reinforce retention) have documented migrants within a population to be either faster growing (Jonsson 1985; Forseth et al. 1999; Thériault and Dodson 2003) or slower growing than residents at the time of dispersal (Bujold et al. 2004; Kraus and Secor 2004). In some populations, slow growers benefit more from migration out of an environment that does not meet their energetic needs to a new habitat with potential higher food availability, whereas in others, migration may be limited to larger- or faster-growing fish that have the energy reserves necessary to migrate (Jonsson and Jonsson 1993; Thériault and Dodson 2003). Thus, migration within a population is condition-dependent in relation to habitat-specific predation risk and potential growth rate benefits, with individual habitat use reflecting the tactic that achieves maximum individual fitness (Jonsson and Jonsson 1993; Brodersen et al. 2008). Understanding the bioenergetic differences associated with resident and migratory life history strategies can enhance our understanding of partial migration within fish populations.

During their first year of life, estuarine-dependent white perch (*Morone americana*) in the Patuxent River estuary (Maryland) either persist as juveniles in freshwater natal habitats (resident contingent) or disperse down-estuary into brackish water habitats (dispersive contingent). Otolith microchemical analysis indicates that these two behaviors are discrete (Kraus and Secor 2004), with patterns of divergent habitat use initiated shortly after the larval–juvenile transition (Kraus and Secor 2004) and predominantly persisting into adulthood (Kerr et al. 2009). Thus, this population can be characterized as exhibiting partial migration. Adult growth rates were higher for migratory fish than for residents in the Patuxent River estuary (Kraus and Secor 2004). Similarly, juveniles that dispersed from natal habitats were larger at the end of their summer growth season than those that were resident, despite beginning their juvenile period at a smaller size. This led Kraus and Secor (2004) to speculate that postdispersal growth or size-dependent mortality must be higher in the dispersive contingent. We hypothesized that juveniles in brackish water habitats might achieve higher growth rates due to salinity condi-

tions, underlying energetic differences between contingents, or the interaction of these two factors.

Habitat-related differences in salinity are known to influence fish energetics by affecting scope for growth and metabolism (Fry 1971; Boeuf and Payan 2001; Kestemont and Baras 2001). Metabolic influences of salinity on fish are attributable to the cost of osmoregulation, changes in ion transport, and the impact of salinity stress (Morgan and Iwama 1991; Kirschner 1995). A commonly observed phenomenon is that of higher growth rates in mesohaline salinities (salinities of 5–18), which are often attributed to decreased osmoregulatory costs associated with isotonic (salinities of 9–12) environments (Morgan and Iwama 1991; Boeuf and Payan 2001). In addition, food intake is influenced by salinity, with consumption inhibited at both high and low salinities and maximized at optimal salinities (Kestemont and Baras 2001; Niklitschek and Secor 2005).

Higher growth rate and (or) growth efficiency have been associated with mesohaline salinities for several juvenile fishes that utilize estuaries, including two congeners of white perch, striped bass (*Morone saxatilis*; Otwell and Merriner 1975; Secor et al. 2000) and white bass (*Morone chrysops*; Heyward et al. 1995). Secor et al. (2000) documented a significant effect of salinity on growth of young-of-the-year (YOY) striped bass, where growth rates were highest at an intermediate salinity of 7 compared with freshwater and a salinity of 15. Similarly, growth of white bass was highest in intermediate salinity treatments (4 and 8) compared with freshwater and higher salinities (12, 16, and 20) (Heyward et al. 1995). Thus, one alternative hypothesis is that lower routine metabolism and higher food intake in mesohaline waters could lead to increased scope for growth in juvenile white perch (Jobling 1995; Boeuf and Payan 2001). The second alternative hypothesis is that intrinsic energetic differences may exist between resident and dispersive contingents.

There has been limited evaluation of the proximate cause of life cycle diversity from an energetic perspective, with most investigations focused on salmonid populations (e.g., Forseth et al. 1999; Cutts et al. 2002; Morinville and Rasmussen 2003). In this study, we investigate energy intake and allocation by resident and migratory forms of the estuarine-dependent white perch. We tested if differences in energy intake and allocation between contingents are intrinsic (i.e., related to the proximate causes of contingent behavior) or extrinsically driven by habitat differences in salinity. We used laboratory studies to compare ecophysiological responses, including growth, consumption, and routine metabolism, between juvenile contingents and salinity levels. Additionally, we examined larval and juvenile growth rates of field-collected individuals from both contingents. We specifically tested the hypotheses that (i) contingent membership is associated with specific energetic tactics, with the dispersive contingent exhibiting higher consumption, growth, and routine metabolism relative to the resident contingent, and (ii) regardless of contingent membership, fish reared in mesohaline conditions exhibit higher consumption and growth and lower routine metabolism relative to fish reared in freshwater conditions.

Materials and methods

Laboratory experiment

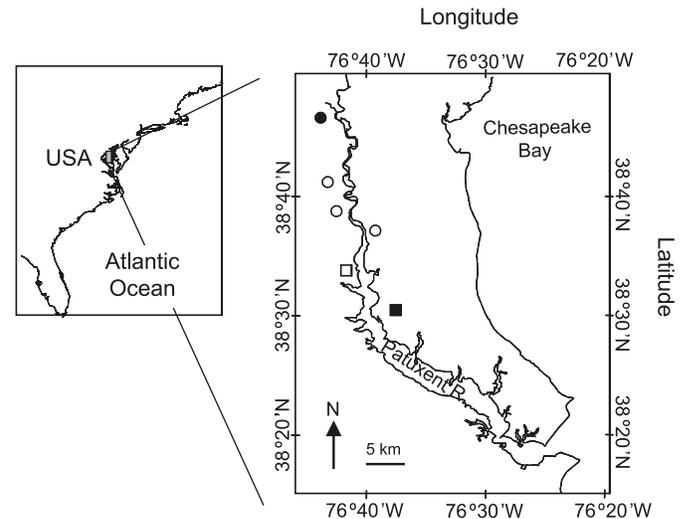
Fish collection and acclimation

Juvenile white perch were collected in the Patuxent River estuary on 25 July 2005 using a 30.5 m × 1.24 m bagless beach seine (mesh size 6.4 mm) set from shore. Samples of the resident contingent were collected from a tidal freshwater site (river km 72), and samples of the dispersive contingent were collected from a brackish water site (river km 25; Fig. 1). Juvenile fish were transported in ambient water equipped with aeration pumps to a holding tank at the Chesapeake Biological Laboratory (Solomons, Maryland). Fish were maintained in water conditions similar to those at capture for 5 days to acclimate them to laboratory conditions. During this period, well water was mixed with ambient seawater (Patuxent River estuary) to maintain the resident contingent at a salinity of 1 and the dispersive contingent at a salinity of 8. Although they can survive in freshwater in the field, resident fish were held at a salinity of 1 in the laboratory experiment because of low survival in 100% well water in the laboratory due to very low hardness levels. Both contingents were maintained at a temperature of ~25 °C, which was representative of summer water temperatures in the Patuxent River estuary. Fish were treated with antibiotics (Kanamycin sulfate), and an antibacterial (Melafix; Aquarium Pharmaceuticals, Mars Fishcare Inc., Chalfont, Pa.) and antifungal (Pimafix; Aquarium Pharmaceuticals) bath was administered for 7 days to reduce infections and possible associated mortality. Juvenile white perch were fed chironomid larvae (San Francisco Bay Brand frozen bloodworms) ad libitum twice daily during the acclimation period. The feeding regime was selected based on results indicating that ad libitum feeding of YOY striped bass, a congener of white perch, in the laboratory was not significantly different from when fish were fed 2–4 times daily (Hartman and Brandt 1995). Prior to the start of the experiment, fish underwent acclimation to experimental conditions over the course of 10 days, with salinity being maintained at the same level or being changed at a rate of 1-day⁻¹ until the desired salinity treatment level was reached.

Experimental design and methods

The experimental design was a randomized factorial design with salinity treatments 1 and 8, two contingent types (resident and dispersive), four replicate tanks per treatment, and five fish per tank. Replicate tank was the experimental unit of study. Treatments ($n = 4$) included all possible crosses between contingent and salinity levels. Prior to initiation of the experiment, fish were weighed in water and transferred to experimental tanks. Fish were reared in 60 L tanks held within a recirculating heated water bath to maintain the temperature at 25 °C. Salinity treatments were static with a 50% water change every 2 days. Water was tempered and aerated in heated baths for 24 h before water changes. Photoperiod was identical for all treatments and timed to mirror ambient daylight cycles in August (13 h light – 11 h dark). Fish were fed chironomid larvae to satiation twice daily throughout the experiments. Water quality data (water temperature, salinity, dissolved oxygen, conductivity, and pH) were recorded daily for each tank using a YSI-85 probe (YSI Inc., Yellow Springs, Ohio).

Fig. 1. Map of the Patuxent River estuary, a subestuary of the Chesapeake Bay (Maryland) (Kraus and Secor 2004). The map illustrates locations of collection of resident (river km 72; solid circle) and dispersive contingent (river km 25; solid square) white perch (*Morone americana*) used in laboratory study and locations of collection of resident (river km 50, 53, 64, and 72; open and solid circles) and dispersive contingent (river km 16 and 45; open squares) used in field growth rate analysis.



Growth rate was measured in a 20-day experiment. Initial wet weight of fish was measured after fish had fasted for 24 h (Hartman and Brandt 1995). Final wet weight of fish was measured on day 20 after a 24-h period of fasting. Six fish from each treatment were freeze-dried at the end of the experiment and a conversion of wet to dry weight (g) was calculated using linear regression. Daily specific growth rate (SGR; % body weight-day⁻¹) was calculated as

$$(1) \quad \text{SGR} = \frac{\ln(W_f) - \ln(W_i)}{t} \times 100$$

where W_f is final weight (g, dry weight basis) of each replicate tank, W_i is initial weight (g, dry weight basis), and t is time (days).

Consumption was measured twice daily during the last 7-day period of the growth experiment. Wet weight of chironomid larvae was determined prior to feeding, and food not consumed 1 h after introduction was removed from the tank, drained of excess water, and weighed wet. Dry weight of the recovered food was determined after drying in an oven (60 °C) for 24 h. A conversion of wet to dry weight was calculated for chironomid larvae using linear regression.

Daily specific feeding rate (SFR; % body weight-day⁻¹) was calculated based on a 7-day experimental duration:

$$(2) \quad \text{SFR} = \left(\sum_{t=0}^{t=7} C_t W_t^{-1} \right) 7^{-1} \times 100$$

where C_t is the total weight of food consumed on day t (g, dry weight basis) and W_t is the total weight of fish per replicate tank on day t (g, dry weight basis). Daily weight of fish in each tank was estimated assuming exponential growth:

$$(3) \quad W_t = W_0 e^{Gt}$$

where W_0 is the initial weight of fish in the tank (g), t is time (days), and G is the instantaneous growth coefficient:

$$(4) \quad G = \frac{\ln(W_t) - \ln(W_i)}{t}$$

Gross growth efficiency (%) was calculated over the same 7-day period as feeding rate:

$$(5) \quad K_1 = FI^{-1} \times 100$$

where F is the total fish growth (g, dry weight basis) per replicate tank and I is the total consumption (g, dry weight basis) over the 7-day period.

Routine metabolism measures were conducted on fish from each treatment after growth and consumption experiments were completed. Routine metabolic rates of two juvenile white perch from each replicate of each of the four experimental treatments were estimated based on oxygen consumption rates measured over a 24-h period in a computer-controlled, closed-circuit microrespirometer (Micro-Oxymax; Columbus Instruments, Columbus, Ohio). Individual fish were placed in 1 L experimental Fernback flasks containing water from their corresponding treatment. Flasks were housed in a controlled temperature unit maintained at 25 °C. The microrespirometer measured oxygen depletion over time at 1.5-h intervals from the flasks' headspace. Fish were starved for 24 h prior to the respiration measurement to minimize the impact of feeding metabolism on the measure of routine metabolism. In addition to experimental flasks, a flask without fish was run as a control and a flask containing a medical battery with a known oxygen depletion level was run to evaluate the accuracy of the Oxymax sensors. Oxygen consumption was reported on a per replicate tank basis as mean $\text{mg O}_2 \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ (dry weight basis).

Energy budgets (Winberg 1956) were constructed for each treatment to compare relative differences in energy allocation. The energy budget included experimentally measured values for total energy consumed, energy devoted to growth calculated over the same 7-day period, and energy devoted to routine metabolism. In addition, values of specific dynamic action (SDA) and energy of feces and excretory products were modeled and included in the energy budget. Scope for growth of white perch was calculated for each treatment as the difference between energy consumed and the energy devoted to egestion, excretion, SDA, and routine metabolism.

Energy density was determined for chironomid prey and six fish per treatment on a per gram dry weight basis through bomb calorimetry. Fish and chironomid larvae were freeze-dried and ground to a powder. Powdered samples were submitted for bomb calorimetry analysis to the Central Analytical Lab at the Center of Excellence for Poultry Science at the University of Arkansas. Growth, consumption, and routine metabolism measures were converted to kilojoules (kJ) per day. Mean energy density of fish in each treatment was used to convert grams fish growth to kJ. Mean energy density of chironomid larvae ($9.7 \text{ kJ} \cdot \text{g}^{-1}$, standard deviation (SD) = 1.5) was used to convert grams of food consumed to kJ, and an oxycaloric conversion factor

($0.014 \text{ kJ} \cdot (\text{mg O}_2 \text{ consumed})^{-1}$) was used to convert oxygen consumed to kJ (Schmidt-Nielsen 1990).

Energy devoted to egestion, excretion, and specific dynamic action was not directly measured in this study but was estimated as the proportion of energy consumed or assimilated based on values determined for YOY striped bass (Hartman and Brandt 1995). It is important to note that the use of bioenergetic values of a congener cannot be taken as absolute values for white perch. This approach assumed that the proportion of energy allocated to these functions did not differ between contingents or salinity treatments. Specific dynamic action and excretion were modeled as constant proportions of assimilated energy (0.172 and 0.068, respectively); egestion was a constant proportion of energy consumed (0.104; Hartman and Brandt 1995). Energy not accounted for by measured and modeled parameters relative to the total amount of energy consumed was classified as "other" and most likely represents energy attributable to the active metabolism of the fish.

Statistical analyses

All calculations, unless otherwise specified, are reported in terms of dry weight. This measure was taken as a means of standardization because of the high water content of chironomid larvae relative to fish and the difficulty in blotting food dry in a consistent manner for accurate measurement of wet weight. Two-way analysis of variance was employed to test the significance of the effects of contingent membership and salinity on each response variable. Diagnostics were employed to test for univariate normality, equal variance, and influential observations. Statistical analyses were conducted with SAS (version 8.2; SAS Institute Inc., Cary, North Carolina); $\alpha = 0.05$ was used as a critical level of significance.

Field data

Fish collection

Juvenile white perch were collected in the Patuxent River estuary at monthly intervals from June to August in 2005 by beach seine (same specifications as described above). The seine survey included freshwater sites (river km 50, 53, 64, and 72) and brackish water sites (river km 16 and 45) in close proximity to the sites at which experimental fish were collected (Fig. 1). Total lengths of white perch (mm) were measured at the time of collection.

Age estimation methods

A random subsample ($n = 55$) of juveniles collected on 21 and 28 June 2005 from each habitat (freshwater ($n = 28$) vs. brackish water ($n = 27$)) were selected for age estimation at a daily time step. Sagittal otoliths were extracted, rinsed, cleaned of adhering tissue, and dried for at least 24 h. One otolith from the pair was embedded in Stuers epoxy and transversely sectioned using a low-speed saw equipped with two diamond blades separated by a 0.3 mm spacer. Otoliths were polished on both sides until the primordium (core) was clearly visible using a grinding wheel with a slurry of $25 \mu\text{m}$ aluminum oxide and a felt, metallographic cloth covered with a slurry of $0.3 \mu\text{m}$ alumina powder to achieve a final polish. Otolith microstructure was examined under a compound microscope ($200\times$ – $600\times$ magnification), and

daily age was estimated by one reader (three independent reads). Daily increment formation in juvenile white perch was previously verified in a laboratory study (Kraus and Secor 2004). Otolith radius was measured along the ventral side of the sulcal ridge from the primordium to growth increments at specific time intervals (days 20, 45, and 60).

Growth rate analysis

Larval growth rates were back-calculated using the biological intercept method. This method assumes a linear relationship between fish length and otolith radius and uses a biological intercept that is determined from the mean size of the fish and the otolith at the smallest larval stage (Campana 1990). Fish length was calculated as

$$(6) \quad L_a = L_c + (O_a - O_c)(L_c - L_0)(O_c - O_0)^{-1}$$

where L_a is length of fish at some previous age a , L_c is fish length at capture, O_a is otolith radius at age a , O_c is otolith radius at capture, L_0 is fish length at biological intercept, and O_0 is otolith radius at biological intercept. The biological intercept of 3.2 μm at 3 mm TL was used (Kraus and Secor 2004). Back-calculated larval growth rates were compared between contingents across growth stanzas during early life history (0–20 days, 20–45 days, and 45–60 days) using t tests to analyze growth rate data from 0–20 days and 45–60 days and a Kolmogorov–Smirnov test to analyze growth rate data from 20–45 days because of unequal variance and non-normality of these data.

Median length (mm) of juvenile white perch from the resident (river km 72) and dispersive contingent (river km 45) was determined on each date of collection (28 June, 7 July, and 18 August). Mean salinity was 0.1 at the location of resident fish collections (mean temperature = 28 °C) and 8.4 at the collection location of the dispersive contingent (mean temperature = 29 °C). Because the trend in YOY white perch growth over this time period was a linear function of time, juvenile white perch growth rate was calculated as the mean daily linear growth rate (GR):

$$(7) \quad \text{GR} = \frac{L_2 - L_1}{t}$$

where L_2 is median length (mm) at the second time step, L_1 is median length at the initial time step, and t is time (days). Assuming independence of samples at each collection date, contingent differences in median length at each collection date were examined using Wilcoxon rank-sum tests.

Results

Laboratory experiment

Young-of-the-year white perch collected in July 2005 ranged in wet weight from 1.41 g to 3.38 g at the initiation of the laboratory experiments. Total fish weight per treatment did not differ significantly at the inception of the experiment ($F_{[3,12]} = 0.2$, $p = 0.87$). Mean wet weight of resident contingent fish (2.10 ± 0.45 g) was similar to that of dispersive contingent fish (2.09 ± 0.39 g; $t = -0.1$, $df = 78$, $p = 0.90$). The conversion of wet to dry weight for white perch was described by the linear regression equation $y = 0.29x - 0.12$ ($r^2 = 0.99$), where y represents dry weight and x represents wet weight. Similarly, a conversion of wet to

dry weight was calculated for chironomid larvae: days 1–5, $y = 0.07x + 5 \times 10^{-5}$ ($r^2 = 0.89$); days 6–7, $y = 0.12x + 0.004$ ($r^2 = 0.84$). Two regression equations were calculated because of differences in the size and wet–dry weight relationship of chironomid larvae from two commercially purchased batches from the same manufacturer.

Fish energy density (kilojoules per gram) was not significantly different between contingent ($F_{[1,20]} = 0.7$, $p = 0.43$) or salinity ($F_{[1,20]} = 0.4$, $p = 0.51$) treatments, but the interaction of the terms was significant ($F_{[1,20]} = 13.0$, $p < 0.01$). Mean fish energy density was highest for dispersive fish reared in freshwater and resident fish reared in brackish water (resident–freshwater = 18.4 $\text{kJ}\cdot\text{g}^{-1}$ (SD = 0.6); resident–brackish = 19.8 $\text{kJ}\cdot\text{g}^{-1}$ (SD = 0.8); dispersive–freshwater = 19.9 $\text{kJ}\cdot\text{g}^{-1}$ (SD = 0.8); dispersive–brackish = 18.9 $\text{kJ}\cdot\text{g}^{-1}$ (SD = 1.1)), although these differences were less than 10% within contingent treatments.

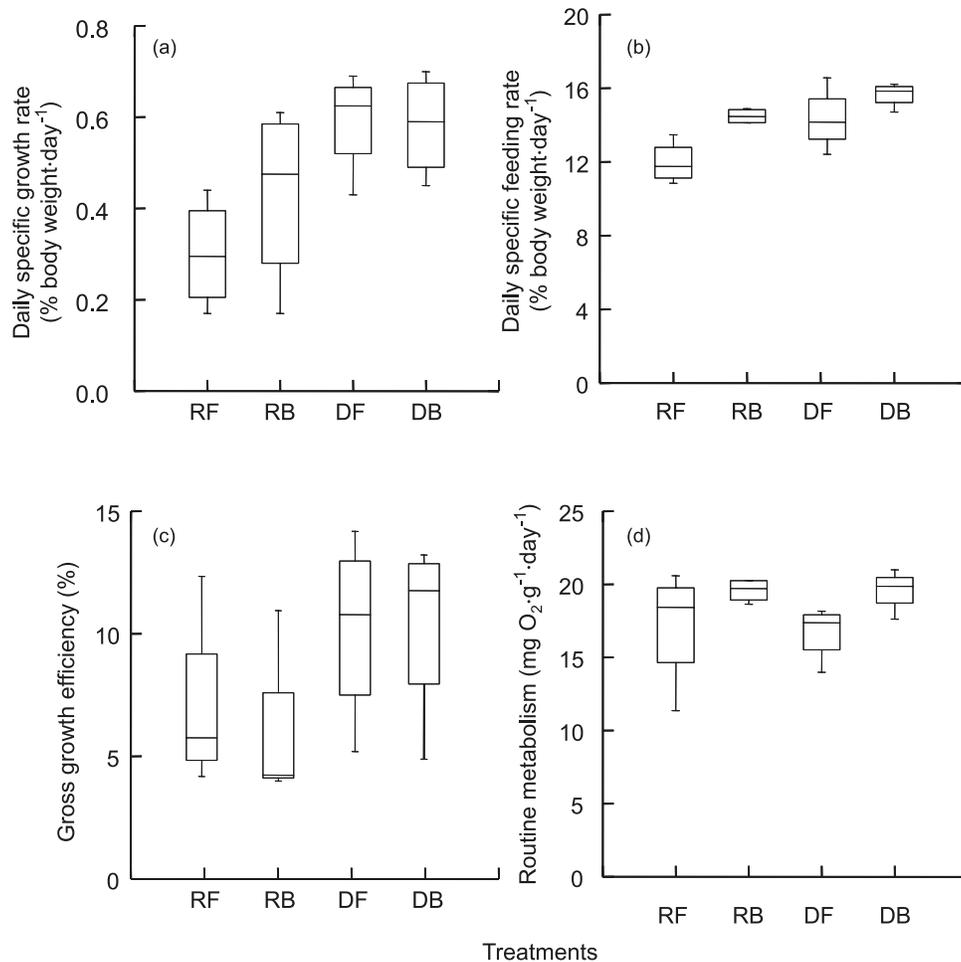
Overall, mean specific growth rate was 60% higher for dispersive contingent treatments compared with resident contingent treatments (Fig. 2a). This was reflected in the mean specific growth rate, reported in terms of dry weight (resident–freshwater = 0.30% body weight-day⁻¹ (SD = 0.12); resident–brackish = 0.43% body weight-day⁻¹ (SD = 0.20); dispersive–freshwater = 0.59% body weight-day⁻¹ (SD = 0.11); dispersive–brackish = 0.58% body weight-day⁻¹ (SD = 0.11)) (Fig. 2a). Two-way analysis of variance indicated a significant effect of contingent ($F_{[1,12]} = 9.7$, $p < 0.01$) on daily specific growth rate, but no significant effect of salinity ($F_{[1,12]} = 0.8$, $p = 0.39$) or the interaction of the terms ($F_{[1,12]} = 1.0$, $p = 0.34$).

Overall, specific feeding rate was 13% higher in dispersive contingent treatments compared with resident contingent and 8% higher in brackish water treatments compared with freshwater treatments (Fig. 2b). The effect of both contingent and salinity is evident in mean specific feeding rates, reported in terms of dry weight (resident–freshwater = 11.7% body weight-day⁻¹ (SD = 1.1); resident–brackish = 14.5% body weight-day⁻¹ (SD = 0.4); dispersive–freshwater = 14.3% body weight-day⁻¹ (SD = 1.7); dispersive–brackish = 15.7% body weight-day⁻¹ (SD = 0.7)) (Fig. 2b). Two-way analysis of variance indicated a significant effect of contingent ($F_{[1,12]} = 10.4$, $p < 0.01$) and salinity ($F_{[1,12]} = 12.3$, $p < 0.01$), but no significant effect of the interaction of the two terms ($F_{[1,12]} = 1.2$, $p = 0.30$) on specific feeding rate.

There was no evidence of changed growth efficiency due to contingent-specific attributes or alternate salinity conditions. Gross growth efficiency ranged from 6.8% to 15.9% for the resident contingent and from 7.2% to 15.2% for the dispersive contingent (Fig. 2c). Gross growth efficiency was not significantly different based on contingent ($F_{[1,11]} = 1.6$, $p = 0.23$), salinity ($F_{[1,11]} = 0.2$, $p = 0.71$), or the interaction of the two terms ($F_{[1,11]} = 0.2$, $p = 0.65$).

Contrary to our expectations that less energy would be required for fish maintained in mesohaline conditions, mean routine metabolism was higher for both contingents reared in brackish water than in freshwater (Fig. 2d). The range of daily oxygen consumption rate was 11.4 to 20.6 $\text{mg O}_2\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ for resident contingent treatments and 14.0 to 21.0 $\text{mg O}_2\cdot\text{g}^{-1}\cdot\text{day}^{-1}$ for dispersive contingent treatments (Fig. 2d). Two-way analysis of variance indicated a

Fig. 2. (a) Daily specific growth rate (% body weight·day⁻¹), (b) daily specific feeding rate (% body weight·day⁻¹), (c) gross growth efficiency (%), and (d) routine metabolism (mg O₂·g⁻¹·day⁻¹) of juvenile white perch (*Morone americana*) across experimental treatments. Treatments include resident fish reared in freshwater (RF), resident fish reared in brackish water (RB), dispersive fish reared in freshwater (DF), and dispersive fish reared in brackish water (DB). In box-and-whisker plots, the center vertical line marks the median, and the length of each box shows the range within which the central 50% of the values fall, with the box edges at the first and third quartiles.



significant effect of salinity ($F_{[1,12]} = 4.9$, $p = 0.05$) but no significant effect of contingent ($F_{[1,12]} = 0.04$, $p = 0.84$) or the interaction of the two terms ($F_{[1,12]} = 0.04$, $p = 0.84$) on routine metabolism. Based on studentized residual values, one outlier was identified in the data set (resident contingent individual in freshwater: 11.4 mg O₂·g⁻¹·day⁻¹). Removal of this outlying value did not, however, significantly alter the outcome of the two-way analysis of variance and thus it was not removed from the final analysis.

Two-way analysis of variance indicated a significant effect of contingent ($F_{[1,12]} = 10.0$, $p < 0.01$) on scope for growth but no significant effect of salinity ($F_{[1,12]} = 1.6$, $p = 0.23$) or the interaction of the terms ($F_{[1,12]} = 4.1$, $p = 0.07$). Overall, the mean scope for growth was 29% higher for the dispersive contingent treatments compared with the resident contingent (dispersive contingent, 3.0 kJ·day⁻¹ (SD = 0.4); resident contingent, 2.3 kJ·day⁻¹ (SD = 0.6)) (Fig. 3a). This was reflected in the measured differences in growth between contingents, with the dispersive contingent allocating, on average, 63% more energy to growth (1.4 kJ·day⁻¹, SD = 0.4) compared with the resident contingent (0.8 kJ·day⁻¹, SD = 0.3) (Fig. 3a). There was no significant difference in

percent allocation of energy to growth or routine metabolism between contingents, salinity treatments, or the interaction of the terms ($p > 0.5$ for all terms; Fig. 3b).

Field data

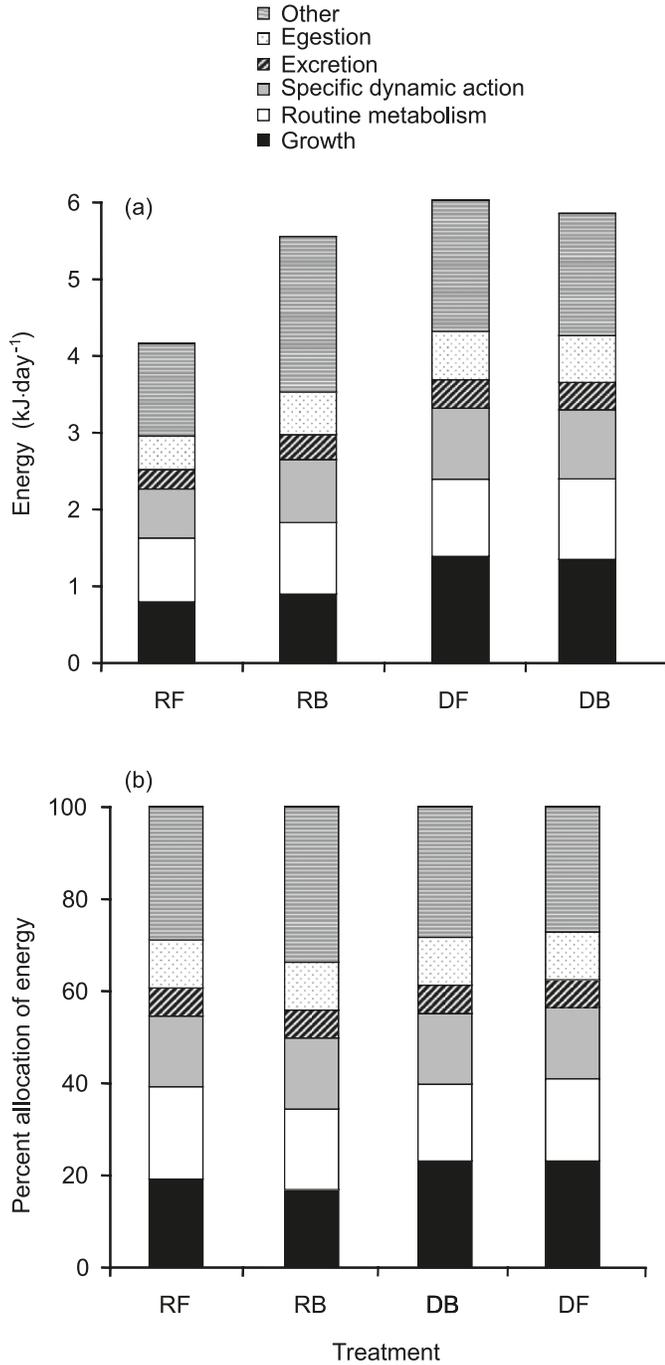
Larval growth rate

Back-calculated larval growth rates of juvenile resident fish were consistently higher across growth stanzas compared with dispersive contingent fish (Fig. 4a). Significantly higher growth rates were observed in resident contingent fish from day 45 to day 60 ($t_{35} = -2.38$, $p = 0.02$). Growth rates were not significantly different in earlier growth stanzas (0–20 days, $t_{53} = -1.96$, $p = 0.06$; 20–45 days, $KS_{52} = 0.2$, $p = 0.70$). It is important to note, however, that back-calculated growth rates are calculated from fish that survived to the juvenile stage and thus may give a biased representation of larval growth.

Juvenile growth rate

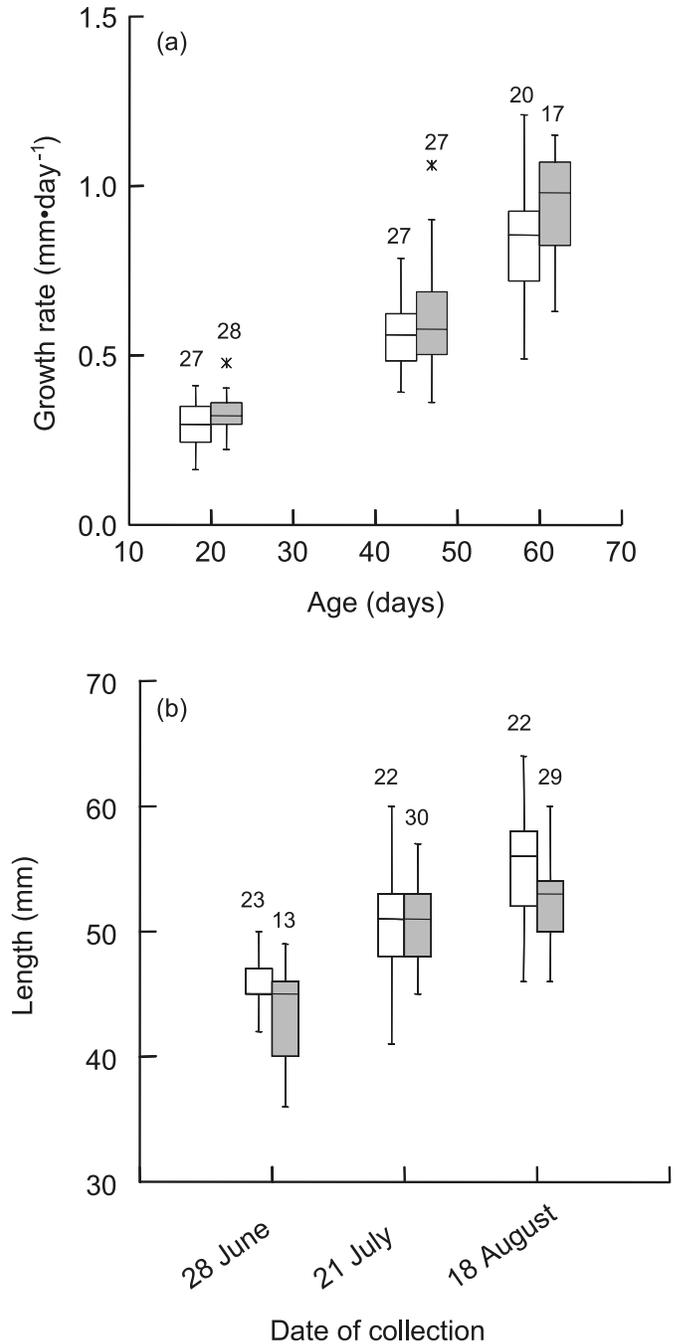
Length of fish from both resident and dispersive contingents increased linearly over the summer collection period

Fig. 3. (a) Energy budget (kilojoules (kJ)·day⁻¹) and (b) percent allocation of energy (%) for resident fish reared in freshwater (RF), resident fish reared in brackish water (RB), dispersive fish reared in freshwater (DF), and dispersive fish reared in brackish water (DB).



(Fig. 4b). Juvenile growth rate was higher for dispersive contingent individuals (0.20 mm·day⁻¹) compared with the resident contingent (0.16 mm·day⁻¹). Median length at time of collection was not significantly different between contingents for June (Wilcoxon rank-sum test, $Z = 1.59$, $p = 0.11$) and July ($Z = -0.04$, $p = 0.97$) collection dates. Median length was significantly different in August ($Z = -2.18$, $p = 0.03$), when the dispersive contingent was 5% larger than the resident contingent (Fig. 4b).

Fig. 4. (a) Back-calculated larval growth rates (mm·day⁻¹) of white perch (*Morone americana*) from dispersive fish (open bars) and resident contingents (shaded bars) across growth stanzas during early life history (0–20 days, 20–45 days, and 45–60 days). (b) Median lengths (mm) of juvenile white perch from dispersive fish (open bars) and resident contingents (shaded bars) during the summer months (June, July, and August) of 2005 in the Patuxent River estuary. Numbers above each box indicate sample size. In box-and-whisker plots, the center vertical line marks the median, and the length of each box shows the range within which the central 50% of the values fall, with the box edges at the first and third quartiles.



Discussion

Contingent effect

Laboratory experiments revealed a significant effect of contingent membership and, to a lesser degree, an effect of salinity on juvenile white perch energetics. The higher daily specific feeding rate of dispersive contingent members, regardless of the salinity environment, resulted in a higher energy budget and higher growth compared with resident contingent fish. Field-collected data reflected the trend in growth rate observed in the laboratory, with dispersive contingent fish exhibiting higher juvenile growth rates compared with resident contingent fish. Laboratory results support the idea that apparent growth differences between resident and dispersive contingents identified in the field are not solely the result of differences in size-dependent mortality. In addition, despite ample food availability within the laboratory setting, resident contingent fish did not consume as much as dispersive contingent fish, indicating food limitation is not the cause of lower juvenile growth rates of resident contingent individuals.

This study provides evidence that partial migration in this white perch population has an underlying bioenergetic basis. Larval and juvenile growth rates determined from juveniles collected in the wild indicated that migratory individuals exhibited accelerated growth during the juvenile stage relative to the slow growth exhibited during the larval period. In 2005, growth of dispersive fish remained slower than that of resident fish through a mean age of 60 days. Following dispersal, accelerated growth of dispersive fish was evident based on equal median length between contingents collected on 28 June and significantly higher median length of dispersive fish collected on 18 August. Kraus and Secor (2004) identified similar patterns in growth rate in white perch collected in 2001. In 2001, back-calculated growth rates of dispersive individuals remained lower than those of resident fish through age 45 days, whereas subsequent to dispersal, dispersive contingent fish were larger on average than resident fish. Slow growth of white perch during early life history appears to be linked to expression of migratory behavior during the juvenile stage. We speculate that the timing of dispersal, and thus the reversal in the growth trajectory, could shift from year to year in relation to environmental conditions.

The reversal of growth trajectory for the dispersive contingent from relatively slow growth during the larval period to relatively fast growth during the early juvenile period may indicate compensatory growth (Metcalf and Monaghan 2001). Compensatory growth typically involves increased consumption rates, documented here for white perch, as a means of accelerating growth rate. Thus, although factors such as environmental conditions that influence larval growth rate may be the proximate cause of contingent structure, the energetic needs of the individual are likely the ultimate cause of dispersal from the natal freshwater habitat. Here, freshwater habitats do not meet the energetic needs of the dispersive contingent. Their dispersal and the subsequent accelerated growth suggests that their energetic needs are met in the brackish water environment.

Habitat transition of dispersive contingent fish appears to occur in early summer when fish first transition to the juvenile stage. Temporal trends in macrozooplankton (copepods, adult copepods, and *Bosmina* cladocerans) abundance in the Patuxent River estuary typically peak in early to mid-May and subsequently decline through the summer and fall months (Herman et al. 1968; Campfield 2004; L. Kerr, unpublished data). Decreased abundance of forage macrozooplankton in late spring, such as *Eurytemora* and *Acartia* calanoid copepods (St. Hilaire et al. 2002; Campfield 2004), may serve as the trigger that initiates migration in individuals that are growing below their optimum level. Within the Patuxent River estuary, an increasing trend in the biomass of adult copepods with salinity was documented in average streamflow years (Reaugh et al. 2007). Thus, it appears that temporal and spatial trends in productivity within the Patuxent River estuary are consistent with the idea that the brackish water habitat presents greater feeding opportunities to white perch than the freshwater habitat.

Evidence of higher consumption and growth rates for dispersive contingent members prompts the question of what favors the persistence of the resident life history tactic. Life history trade-offs, such as the costs of compensatory growth to the dispersive contingent, likely play a role in the maintenance of resident behavior. Ultimately, the long-term trade-off of accelerated growth in individuals is lower fitness and, consequently, lower survival (Mangel and Stamps 2001; Munch and Conover 2003). Specific costs associated with compensatory growth in fish include adverse effects on physical processes (bone ossification rate, growth rate, age at sexual maturation, muscle lesions; Metcalfe et al. 2002) that have consequences to swimming performance, feeding ability, and defense against predators (Arendt and Wilson 2000; Billerbeck et al. 2001). In addition, decreased abundance of piscivore predators with decreasing salinity or depth has been documented within estuaries (Miller et al. 1985; Miltner et al. 1995; Paterson and Whitfield 2000). Although trends in predator abundance have not been studied directly within the Patuxent River estuary, we speculate that this phenomenon could contribute to increased direct mortality with movement into higher salinity waters.

An alternative cause of energetic differences between contingents identified in the laboratory is underlying genetic structure. Temporal or spatial isolation of contingent spawning (assortive mating) would be required for genetic separation of contingents. Examination of variation in mitochondrial DNA of white perch from eight subestuaries in Chesapeake Bay identified three genetically distinct populations of white perch, with the Patuxent River grouped into a population that included the Upper Bay, Choptank, and Nanticoke rivers (Mulligan and Chapman 1989). Although hypothesis testing of genetic differences between contingents was not the objective of that study, genetic dimorphism was not evident within the Patuxent River estuary. Additionally, the collection of gravid adult white perch from both contingents in the freshwater region of the Patuxent River, as determined by retrospective analysis of habitat use based on otolith chemistry (Kraus and Secor 2004), suggests significant mixing between contingents during the springtime spawning period. These observations do not support the idea of assortive mating.

Salinity effect

Overall, the influence of salinity on juvenile white perch physiology was less than that of contingent membership. Evidence for an effect of salinity on white perch physiology included higher consumption rate and routine metabolism of individuals reared in brackish water. There was no significant effect of salinity on scope for growth, measured growth, or gross growth efficiency. Thus, despite higher consumption rates in brackish water, this energy was not converted to somatic growth.

Higher consumption rate of white perch in brackish water compared with freshwater was expected, and a similar response has been reported in other species, including coho salmon (*Oncorhynchus kisutch*; Otto 1971; Kestemont and Baras 2001). Contrary to expectations based on studies of white perch congeners, we documented higher routine metabolism of fish reared in brackish water compared with freshwater treatments. Across species, the relationship between fish metabolism and salinity appears to be inconsistent, with the impact on osmoregulatory costs (10% to >50% of total energy budget; Kirschner 1993; Morgan and Iwama 1991; Boeuf and Payan 2001) associated with rearing fish in isotonic conditions compared with freshwater ranging widely. Oxygen consumption has been documented to both increase (~+14% (*Salmo gairdneri*), ~+5% (*Oncorhynchus mykiss*), and ~+10% (*Oncorhynchus tshawytscha*); Morgan and Iwama 1991) and decrease (-16% (*Salmo gairdneri*; Rao 1968); -31% (*Mugil curema*; Fanta-Feofiloff et al. 1986); -39% (*Centropomus undecimalis*; Pérez-Pinzón and Lutz 1991) with movement from freshwater to isotonic conditions. In a literature review, Morgan and Iwama (1991) identified several fish for which there was no change in metabolic rate over a wide range of salinities and classified this response as typical of euryhaline fish. Thus, the influence of increased salinity on osmoregulatory costs of the euryhaline white perch may have been minimal (i.e., too small to be detected against individual variation). We speculate that interacting effects of salinity on other processes, such as feeding rate (i.e., routine metabolism increased in fish feeding at higher rates; Madenjian and O'Connor 1999), may have contributed to the higher routine metabolism in brackish water treatments.

There were no significant interactions of contingent and salinity effects identified except with respect to fish energy density. Dispersive and resident fish had higher energy content when reared in transposed salinities rather than in their respective salinities. This interaction defies easy explanation based on expectations for the effects of growth and salinity on energy density. Still, relatively small differences in energy content (5%–7% between contingent and 5%–8% between salinity) were observed, particularly relative to the magnitude of energetic responses (e.g., growth rate, feeding rate, and routine metabolism) to the main effects of salinity and contingent, indicating that the changes in energy density among crossed treatments did not confound overall results of contingent and salinity effects on metabolism and growth trajectories.

Partial migration

In this study, we moved beyond describing patterns in fish life history to gain an understanding of the ecophysiological

basis underlying the behavior. We concluded that contingent membership and the related phenomenon of partial migration in this white perch population is associated with varying energetic tactics that significantly influence the scope for growth. Similar to populations of brown trout (*Salmo trutta*; Forseth et al. 1999) and Atlantic salmon (*Salmo salar*; Metcalfe et al. 1995; Metcalfe 1998; Bujold et al. 2004), growth performance of white perch during early life appears to determine contingent behavior. Identification of growth differences between resident and migratory individuals has improved our understanding of the mechanisms governing partial migration and the potential consequences of partial migration to population productivity. The concept of partial migration has been adopted from the avian literature to describe diversity in life history tactics in salmonid populations (Jonsson and Jonsson 1993) but may be widely applicable to fish populations in general. We hypothesize that similar to avian populations, partial migration may be a fundamental behavior pattern in fish populations and associated theory could form the basis of a comprehensive theory of fish migration.

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