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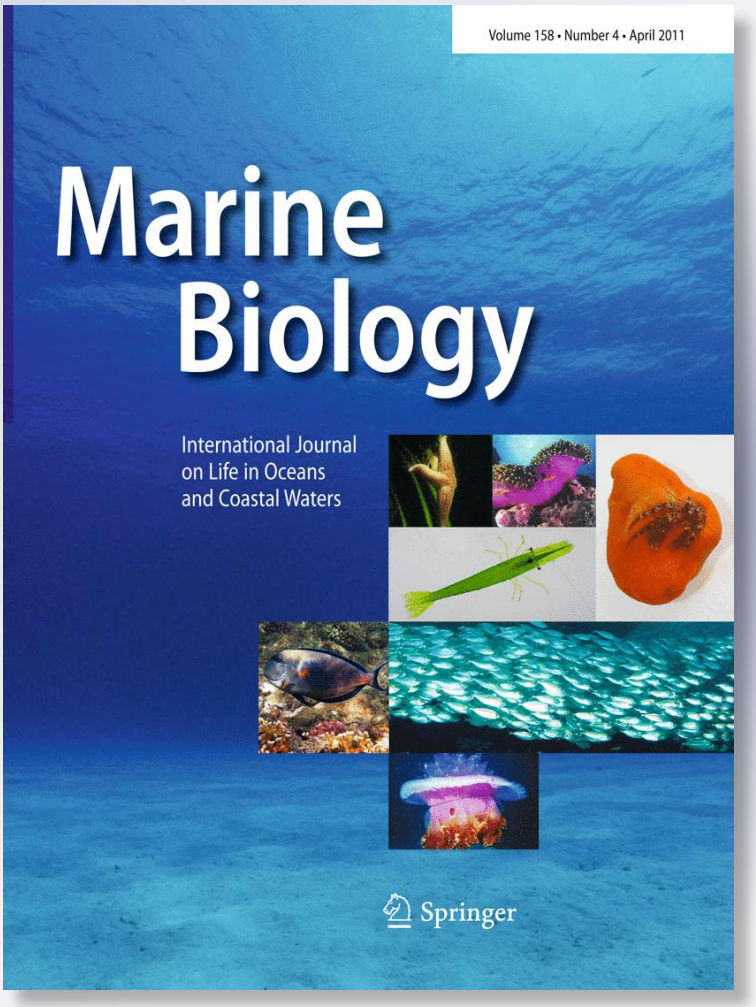

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ORIGINAL PAPER

Bioenergetic responses of Chesapeake Bay white perch (*Morone americana*) to nursery conditions of temperature, dissolved oxygen, and salinity

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Abstract Changes in the physical and chemical structure of estuaries control the aerobic scope for activity of coastal fishes and thereby influence the quality and extent of nursery habitats. We evaluated the effects of temperature, dissolved oxygen, and salinity on the ecophysiology of a species that completes its life cycle in estuaries: white perch (*Morone americana*), which were reared at treatment levels that emulated nursery conditions in the Chesapeake Bay. Salinity influenced only consumption rate and energy density, which were diminished at the highest salinity level (16). In hypoxic environments (≤40% saturation), routine metabolic rates increased as much as fourfold while growth rate decreased threefold and consumption rate decreased twofold. Experimental growth rates were within the range of growth rates observed in the field. Results indicate that hypoxia substantially reduces potential nursery production for a dominant estuarine species, through its influence on diminished aerobic capacity for growth and activity.

Introduction

Temperate estuaries are dynamic yet productive systems, exhibiting large ranges in thermal, oxygen, and osmotic conditions and functioning as nurseries for many coastal fishes (Beck et al. 2001). The freshwater and saltwater interchange that defines estuaries together with variable bathymetry, result in substantial spatial and temporal heterogeneity in salinity, temperature, dissolved oxygen, and turbidity (Tyler and Seliger 1989). These dynamic habitat variables in turn affect fish production directly through their influence on physiology and indirectly through their influence on predators and prey. Consumption, growth, metabolism, and the aerobic scope for activity (Lankford et al. 2001; Pörtner 2010) represent particularly relevant responses in evaluating the role of estuaries as juvenile habitats (Neill et al. 1994; Manderson et al. 2002; Eby et al. 2005; Harrison and Whitfield 2006). These responses define the spatio-temporal domain of potential habitats within which estuarine fishes select habitats based upon other functions such as forage availability and predation refuge (Gilliam and Fraser 1987; Metcalfe et al. 1988; Miltner et al. 1995).

A critical feature in many estuaries is cultural eutrophication, which can lead to increased prevalence of hypoxia (dissolved oxygen [DO] at levels deemed harmful for growth and survival, stipulated variously at 2–4 mg l^{-1} depending on fish species and temperature; Boesch 2002; US EPA 2003; Diaz and Rosenberg 2008). In the Chesapeake Bay, hypoxia is a prevalent feature during summer months, despite large government investments to limit nutrient inputs. Long-term warming of surface waters (~0.2°C per decade; Najjar et al. 2010) will further exacerbate the influence of persistent hypoxia (Breitburg et al. 2009). Particularly during summer, warm temperature can interact with DO or salinity distributions resulting in a curtailment known as a "habitat squeeze" (Coutant and Benson 1990; Niklitschek and Secor 2005). Temperature also influences aerobic capacity and performance of fishes and thereby amplifies hypoxic stress (Guderley and Pörtner 2010).

We investigated how temperature and DO as dynamic estuarine habitat variables influence consumption, growth,

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and basal metabolism of juvenile white perch. Despite the strong potential for temperature and DO to interact in their effects on juvenile fish production in estuaries, relatively few experimental studies have tested their simultaneous influence. Here, we exposed a species that completes its life cycle in estuaries, white perch *Morone americana*, to levels of temperature, DO, and salinity that are representative of the first summer and fall growth seasons in the Chesapeake Bay. Based upon previous studies for other estuarine species (Claireaux and Lagardere 1999; McNatt and Rice 2004; Wuenschel et al. 2004; Stierhoff et al. 2006; Niklitschek and Secor 2009a, b), we predicted that these principal physiological responses would show non-linear relationships with temperature, DO, and salinity in accordance with controlling (dome-shaped), limiting (saturating), and masking (U-shaped) effects on the aerobic scope (Fry 1971; Kellogg and Gift 1983; Niklitschek and Secor 2009b). Further, we predicted strong interactive effects between temperature and DO with elevated basal metabolism at higher temperatures limiting the scope for growth, particularly in treatment levels where DO was limiting (Guderley and Pörtner 2010). Finally, we expected nil or small main effects of salinity on metabolic responses (Buckel et al. 1995; Niklitschek and Secor 2009a).

White perch is a member of the temperate sea bass family Moronidae (maximum size ~40 cm) found in West Atlantic estuaries from Nova Scotia to South Carolina with largest populations (those that currently or historically supported commercial fisheries) in the Hudson River, Delaware River, and Chesapeake Bay (Setzler-Hamilton 1991). A dominant demersal fish in lower salinity regions of the Chesapeake Bay (Jung and Houde 2003), they are an important forage species for piscivores (Gartland et al. 2006; Heimbuch 2008). Adults migrate to tidal freshwater each spring to spawn, some returning to brackish water to over-winter (Mansueti 1961; Setzler-Hamilton 1991; Kerr et al. 2009). Demersal eggs hatch in a 2–3 d period; larvae occur throughout the water column and show retention above the salt front, often associated with the estuarine turbidity maximum (North and Houde 2001). Young-of-the-year (YOY) white perch occupy shallow habitats (<3 m depth) in both freshwater (natal) and brackish water regions. Chesapeake Bay populations exhibit partial migration, with both resident (freshwater) and migratory (brackish water) contingents persisting throughout the adult period (Kerr et al. 2009). Although adults can occur in coastal waters, very rarely are they captured at salinity >15 (Setzler-Hamilton 1991). During summer and fall months (June–October), shallow open-water nursery habitats fluctuate between 16 and 32°C and <10% to >100% DO saturation (DO_{sat}) depending on season tide and salinity (Lippson et al. 1979; Tyler et al. 2009).

Methods

Collection and maintenance of experimental fish

During August and September 2006–2007, YOY white perch (0.5–7.0 g) were collected from freshwater tidal regions of the Potomac and Patuxent Rivers of Chesapeake Bay (Fig. 1), using a 30 m × 1.2 m bagged beach seine with 6 mm mesh. Temperatures ranged 24–29°C. Fish were transported to Chesapeake Biological Laboratory (Solomons, Maryland) in coolers equipped with air stones and filled with ambient river water. They were then allowed to recover in 60 l holding tanks with water similar (±3°C, ±2 salinity) to field conditions for 7–14 days. During this time, fish were fed thawed Chironomid larvae ad libitum and treated with natural botanical antibiotics (Pimafix® and Melafix® each at 125 ppm) to reduce infections and associated mortality.

An incomplete factorial design emphasized temperature and DO main effects and interactions and salinity main effects. The design contained 10 combinations of factor levels 6, 12, 20, and 28°C; 20, 40, and ≥70% DO_{sat}; and 1, 4, and 16 salinity (Table 1). These levels were selected to represent ranges experienced during the YOY growth phase (summer and fall), but also provided contrast by including lower temperatures (6, 12°C) and a higher salinity (16). The center treatment (20°C, ≥70% DO_{sat} and salinity 4), received nine replicates; the remaining treatments received three replicates. Each replicate tank was treated as a single experimental unit. This design allowed

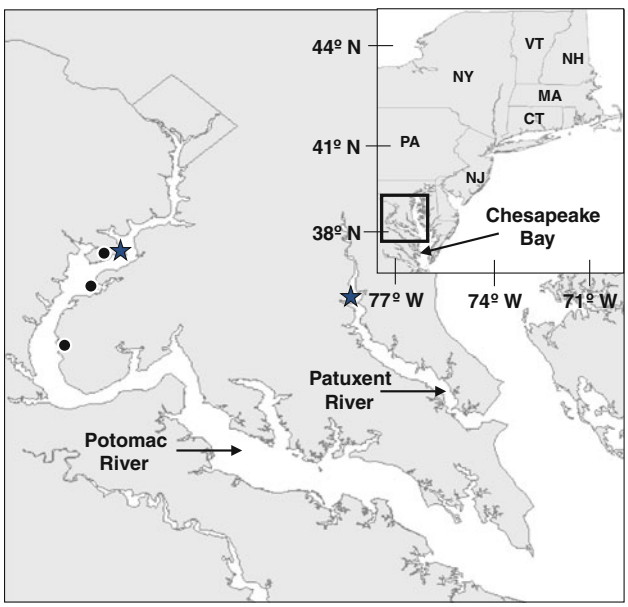

Fig. 1 Map of sites of collection for Chesapeake Bay white perch. *Stars* indicate collection site for experimental fish. *Circles* indicate sites where historical monitoring supported analysis of growth for wild white perch juveniles

Table 1 Experimental treatment levels, replicate number, and principal metabolic responses (mean ± SE) by young-of-the-year white perch

Temp (°C)	DO (%)	Sal	*R*	Growth rate (g d^{-1})	Consumption rate (g g^{-1} fish wt)	Routine metabolism (mg O^2 g $fish^{-1}$ d^{-1})	Density (KJ g^{-1})
6	70	4	3	0.000 ± 0.001	0.03 ± 0.002	26.3 ± 1.0	23.0 ± 0.33
12	70	4	3	−0.001 ± 0.001	0.055 ± 0.003	16.2 ± 1.5	22.9 ± 0.42
20	70	1	3	0.021 ± 0.008	0.14 ± 0.008	21.2 ± 2.6	23.0 ± 0.40
20	70	16	3	0.012 ± 0.001	0.11 ± 0.006	21.3 ± 1.4	22.0 ± 0.48
20	20	4	3	0.006 ± 0.001	0.11 ± 0.002	36.2 ± 2.3	22.2 ± 0.32
20	40	4	3	0.010 ± 0.001	0.11 ± 0.002	33.9 ± 2.8	22.5 ± 0.22
20	70	4	9	0.019 ± 0.002	0.11 ± 0.006	23.6 ± 2.0	23.6 ± 0.35
28	20	4	3	0.020 ± 0.003	0.11 ± 0.008	37.1 ± 3.1	21.8 ± 0.34
28	40	4	3	0.032 ± 0.002	0.15 ± 0.009	49.1 ± 4.7	23.0 ± 0.86
28	70	4	3	0.032 ± 0.002	0.17 ± 0.011	18.8 ± 2.3	23.7 ± 0.46

Temp temperature, *DO* dissolved oxygen saturation, *Sal* salinity, *R* replicate number

evaluation of functional responses to main temperature effects (DO_{sat} = 70%; salinity = 4), and salinity effects (temperature = 20°C; DO_{sat} = 70%), as well as first order interactions for temperature and DO_{sat} (20, 40, 70%) at 20 and 28°C (salinity = 4).

Experiments were conducted in temperature-controlled rooms, where fish in 60 l opaque tanks were acclimated to experimental conditions at the rate of salinity = 1, 1°C, and 5% DO_{sat} per day. Conditions in tanks were maintained with a 50% water change every other day with water previously tempered to experimental levels. Salinity levels were maintained by mixing freshwater with filtered (5 μm), ambient brackish water (salinity 13–18) from the local estuary. DO_{sat} was maintained within 10% of targeted levels by mixing nitrogen gas with ambient air and monitoring levels every 2 h during the daytime hours (when feeding occurred). Photoperiod was a 12:12 h light:dark cycle.

Each tank contained five to eight fish, the number adjusted to maintain similar biomass among tanks. As white perch are shoaling fish, individuals were reared in groups to maintain normal feeding behavior (Secor et al. 2000). Fish were fasted 12 h and weighed before and after each 10 d experiment. During the experiments, Chironomid larvae were provided ad libitum twice a day. Non-consumed food was removed 1 h after feeding, weighed, and dried at 60°C for 48 h.

Instantaneous daily growth rate (G), consumption rate (CR) and gross growth efficiency (K_1) were calculated for each 10 d experiment:

$$G = \frac{\ln(W_f) - \ln(W_i)}{t = 10}$$

$$CR = \left(\sum_{t=0}^{t=10} C_t W_t^{-1}\right) 10^{-1}$$

$$K_1 = AI^{-1} \times 100$$

where W_i is the initial dry weight (grams); W_f is the final dry weight; and W_t is the dry weight at time t assuming exponential growth: $W_t = W_t e^{G_t}$. C_t is the total weight of food consumed on day t; $A = W_t - W_i$, and I is the total consumption. To provide more consistent measures of mass between fish and their diet, wet weights were converted to dry weights. The fish and Chironomid larvae were freeze-dried, and a dry/wet conversion was calculated using linear regression on subsamples of fish and diet (fish dry weight = 0.29 wet weight −0.07, $r^2 = 0.99$, $N = 24$; Chironomid dry weight = 0.12 wet weight +0.02, $r^2 = 0.96$, $N = 27$).

To test the effect of individual fish mass on maximum daily consumption rate (C_{max}), we provided excess food twice daily in 10 d experiments on four size classes (3, 5, 6, 9 g; three replicates each; 5 fish per replicate) at the central treatment condition. Each tank served as an experimental unit.

Respirometry experiment

Routine metabolism (RM) respirometry experiments were conducted immediately after the growth-consumption experiments. Because fish could not be immobilized, routine metabolism (rate of metabolism at low routine activity) was measured as a proxy for basal metabolism (Niklitschek and Secor 2009a). Oxygen consumption was measured using a computer-controlled, closed-circuit respirometer (Micro Oxymax©, Columbus Instruments). Five fish from each treatment, following 12 h fasting, were placed in individual 1 l experimental Fernback flasks containing water from their corresponding treatment. Additionally, one flask without fish was run as a control, and one flask containing a medical battery with known oxygen depletion

was run to evaluate the accuracy of the Oxymax sensors. During the next 24 h, oxygen was recorded every 2.6 h. The mean was a less biased estimate of RM, as determined by a one-way ANOVA to test for skewness between treatments (Rowe 2003). Consumed oxygen was converted to energy equivalents using the oxycalorific coefficient of 0.014 kJ mg^{-1} O_2 (Schmidt-Nielsen 1990).

Calorimetry

Energy content of white perch was measured using a bomb calorimeter (Parr 6200, Calorimeter, Moline, IL). Five fish from each treatment level were sacrificed after experiments using an overdose of tricaine methanesulfonate (MS222), freeze-dried for 24 h, and ground into a homogenized sample. This sample was then formed into a pellet ($\sim$0.05–0.11 g) and incinerated in an oxygen rich bomb. Two subsamples of each fish were combusted, and the mean average was used as an estimate of energy content. If the percent difference between two subsamples was greater than 10%, a third subsample was measured. The closest two of the three samples were then averaged to obtain the mean energy content.

Field corroboration

Experimental growth rates were corroborated against growth rates estimated from lengths of YOY juveniles collected as part of a state monitoring program (E.Q. Durell, personal communication, Maryland Department of Natural Resources, Fisheries Service) (Fig. 1). Juveniles were collected using a 30 m $\times$ 1.2 m bagless beach seine during the months of July, August, and September. Potomac River sampling sites with recorded salinity 0–3 were selected, corresponding to 3 sites and 10 years of data. From the recorded minimum and maximum lengths for each seine haul, a mean was estimated and converted to weight using a length-weight relationship (Kerr and Secor 2009). Instantaneous growth rate was estimated as above but here W_f was the weight at the last sampling month (September), W_i was the weight at the first sampling month (July), and t was the number of days between the first and the last sampling month. Mean surface water temperature was estimated from July to September observations from the same monitoring program.

Statistical analyses

All statistical analyses were conducted using SAS Version 9.0 (SAS Institute 1999, Cary, NC) or SYSTAT Version 12.0 (SYSTAT Software, Inc., 2007, Richmond, CA) with a significance level of $\alpha = 0.05$. Two principal analyses were performed: (1) univariate analyses on temperature (salinity held constant at 4, DO_{sat} held constant at 70%) and salinity (temperature = 20°C, DO_{sat} held constant at 70%) effects on growth, consumption, RM, and energy density; and (2) a two-way analysis of variance using crossed levels of 20 and 28°C, and 20, 40, and 70% DO_{sat}. Diagnostics to test for univariate normality, equal variance, and influential observations were performed. For conversion efficiency, it was necessary to remove two negative values attributable to negative growth to achieve normality. Levene's test detected heterogeneity in conversion efficiency responses to temperature ($p = 0.005$) and dissolved oxygen ($p = 0.02$), which could not be ameliorated through transformation (e.g., arcsine transformation); all other responses showed homogenous variance among treatment levels. Therefore, tests for crossed effects of temperature and DO_{sat} were performed for growth, consumption and RM only.

Results

Temperature and salinity effects

Growth and consumption were similarly responsive to temperature levels (ANOVA; DF 3,14; $p < 0.001$), exhibiting a positive curvilinear response (Fig. 2). Instantaneous growth and consumption rates ranged, respectively from -3.8×10^{-4} to 3.6×10^{-2} g d^{-1} and 0.027 to 0.19 g g^{-1} fish weight (all mass units are measured as dry weight). Rates at 6 and 12°C were significantly lower than at 20°C, which in turn was lower than at 28°C. Conversion efficiency (range -5 to 20%) showed a similar, albeit less ordered response to temperature ($p = 0.001$; Fig. 2). Interestingly, RM responses (range 10.9–37.1 mg O_2 g $fish^{-1}$ d^{-1}) were ordered differently (ANOVA; DF = 3,31; $p = 0.03$), with highest respiration at the lowest temperature; all other RM estimates were similar among temperature levels. Salinity significantly affected only consumption rate (ANOVA; 20°C; 70% DO_{sat}: DF = 2,12; $p = 0.001$), with lower consumption at salinity 16 than at 4 or 1 (Tukey's test: $p < 0.05$) (Fig. 3). There was a similar nonsignificant trend for low growth rate at the highest salinity.

Crossed temperature and DO effects

At temperatures 20 and 28°C, significant DO_{sat} effects were detected for growth, consumption and RM. Lower DO_{sat} levels depressed growth (ANOVA: DF 1,2,2,18; $p = 0.002$) and consumption rates ($p = 0.02$), but increased RM (ANOVA: DF = 1,2,2,40; $p = 0.001$) (Fig. 4). Temperature, as expected, increased growth ($p = 0.001$) and consumption rates ($p = 0.001$) but did not significantly influence RM ($p = 0.14$). No significant

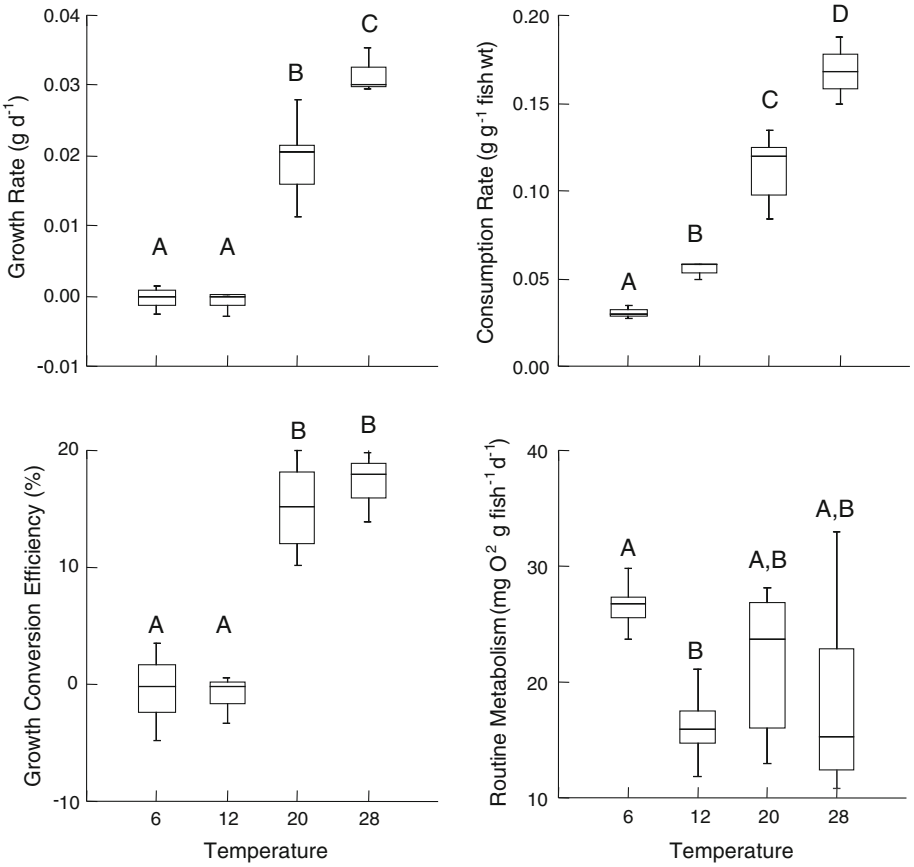

Fig. 2 Temperature main effects on growth rate, consumption rate, gross growth conversion efficiency, and routine metabolism of juvenile white perch. *Boxes* show the median (*horizontal line*), the first and third quartiles (*box edges*) and ±1.5 times the inner quartile range (*whiskers*). Within each plot, treatment levels that differ (Tukey's test) are indicated by differing letters

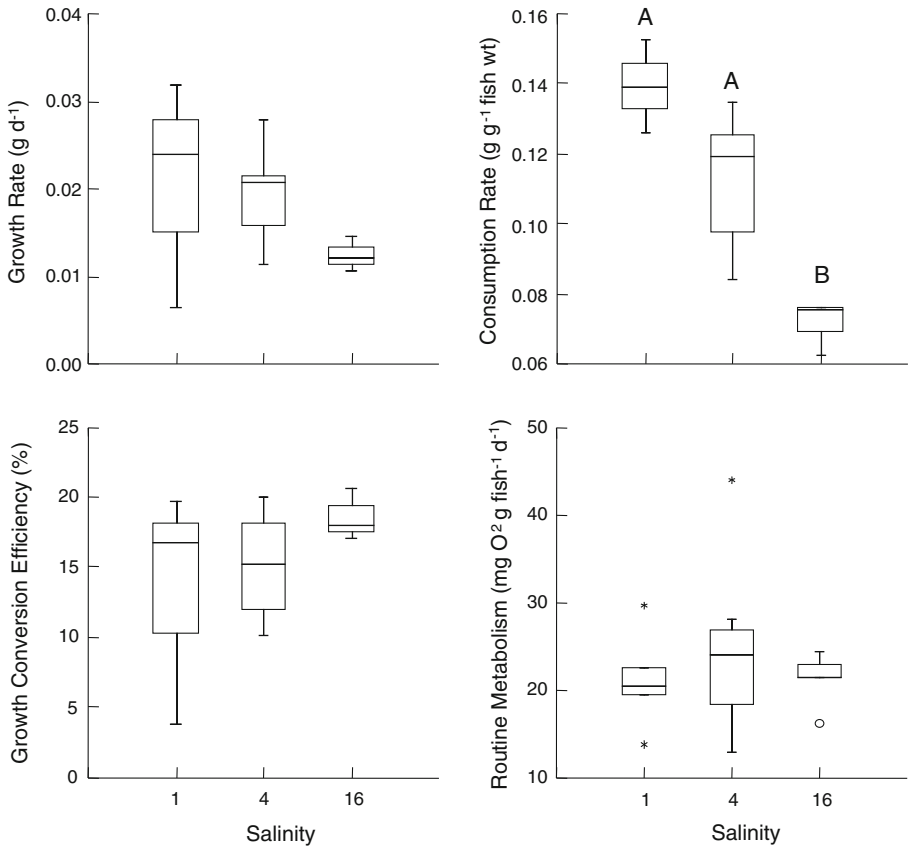

Fig. 3 Salinity main effects on growth rate, consumption rate, gross growth conversion efficiency, and routine metabolism of juvenile white perch. See Fig. 2 legend for description of box-whisker plots

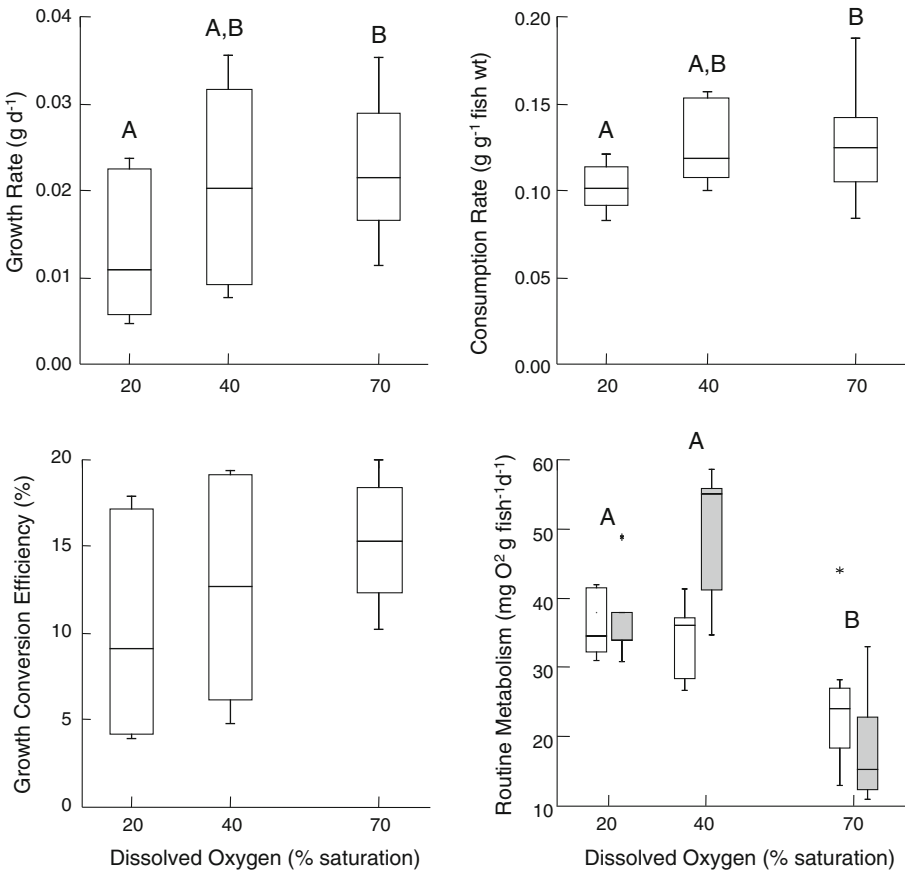

Fig. 4 Dissolved oxygen main effects on growth rate, consumption rate, and gross growth conversion efficiency; effect of combined temperature and DO levels on routine metabolism. For routine metabolism plot, *open* and *shaded boxes* represent 20 and 28°C. See Fig. 2 legend for description of box-whisker plots

crossed effects between temperature and DO_{sat} were detected for growth and consumption rates, but were observed for RM ($p = 0.005$). The interaction was due to increased RM at 28°C to 40% DO_{sat} in comparison to other DO levels (Fig. 4). Paired comparisons of responses to DO were similarly ordered between growth and consumption rates, and the pattern of change suggested a threshold-like response with depressed rates occurring below 40% $DO_{sat.}$ Similar to growth and consumption rates, gross growth efficiency was greater at higher DO_{sat} levels.

Consumption as a function of mass

Among YOY white perch between 3 and 9 g, maximum daily consumption ranged from 0.04 to 0.15 g g^{-1} fish wt. An analysis of covariance found that maximum consumption was not influenced by size class, nor was maximum consumption significantly affected by predicted daily weight during the experiments (ANCOVA, DF = 3,1,3, 14; $p = 0.53$). Additionally, a linear regression analysis failed to detect a significant relationship between weight and maximum consumption rate ($N = 40$; $p = 0.4$). As a result, data was not adjusted for differences in fish weight among experimental units.

Energy density

In general, energy density increased with increasing DO_{sat} levels (Fig. 5). Mean energy densities ranged from 21.6 to 23.9 kJ g^{-1} dry weight across temperature and DO_{sat} treatments with highest values at high DO saturations (ANOVA: 20, 28°C; salinity = 4: DF = 2,31; $p = 0.004$). Paired comparisons detected significant differences between 20 and 70% DO_{sat} (Tukey's test: $p < 0.05$). Temperature did not significantly influence energy density (ANOVA: DO_{sat} = 70%; salinity = 4: DF = 3,20; $p = 0.34$) but salinity did (ANOVA: 20°C; 70% DO_{sat}: DF = 2,16; $p = 0.02$). Interestingly, higher energy density was observed at lower salinities, but only salinity 4 was significantly greater than salinity 16 (Tukey's test: $p < 0.05$). At temperatures 20 and 28°C, energy density showed positive correlations with growth ($r = 0.61$) and consumption ($r = 0.75$), but neither were significant ($p > 0.15$).

Field corroboration

Wild juvenile growth rates were lower, ranging 0.011–0.024 g d^{-1}, than experimental growth rates at 20 or 28°C (70% DO_{sat}), which ranged from 0.006 to 0.036 g d^{-1} (Table 1; Fig. 6). Mean growth rates for the Potomac River

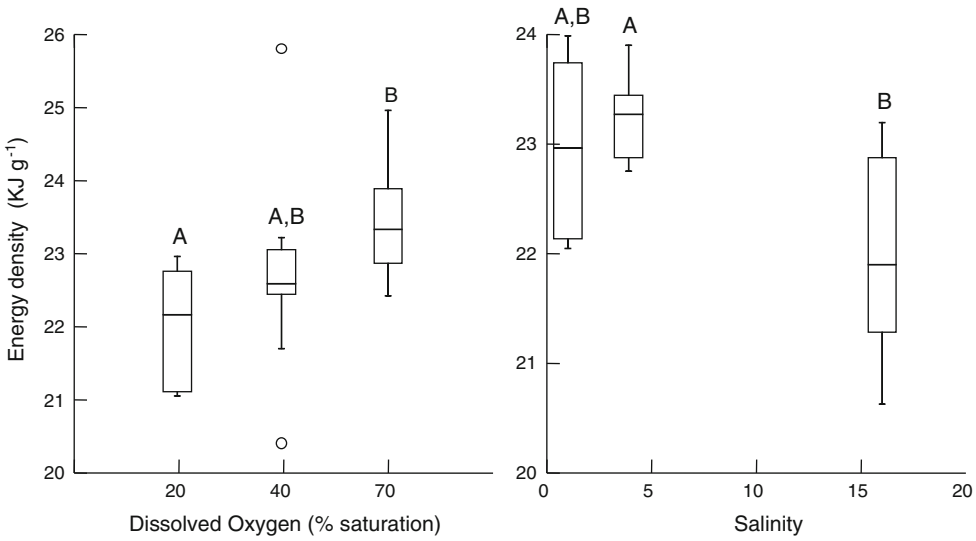

Fig. 5 Effects of dissolved oxygen and salinity on energy density of juvenile white perch. See Fig. 2 legend for description of box-whisker plots

(0.016 g d^{-1}) were more similar to experimental growth rates at 20°C (0.018 g d^{-1}) than experimental growth rates at 28°C (0.032 g d^{-1}) (Fig. 6). Because field temperatures were closer to 28 than 20°C, we compared field growth rates against the 28°C experimental data; these growth rates significantly differed (ANOVA; DF = 1, 25; $p < 0.001$).

Discussion

Aerobic scope

In general, laboratory-reared white perch juveniles responded to nursery habitat variables according to Fry's predictions: (1) a nonlinear increasing production response to temperature; (2) threshold responses to DO; and (3) some indication of depressed feeding and growth rates as salinity was elevated beyond their normal habitat range. Routine metabolism as a proxy for basal metabolism was substantially elevated in low DO treatments: consistent with the view that oxyregulation incurs nontrivial energetic costs. Thus, results suggested that estuarine gradients in temperature and DO but not salinity should have strong influences on habitat suitability for white perch as measured by their aerobic scope.

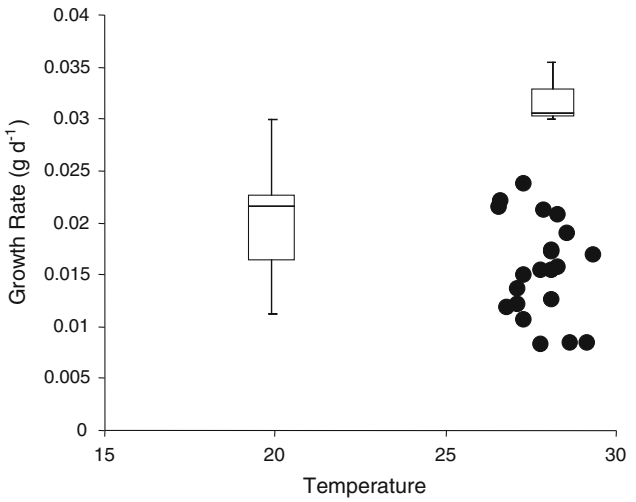

Fig. 6 Comparison of growth rate between experimental fish (salinity = 4; DO = 70%) and field-collected juvenile white perch. *Filled symbols* represent sites-specific growth rates, plotted against mean summer temperature. Experimental fish are represented by *box whisker* plots (see Fig. 2 legend)

Change in the aerobic scope for growth and activity is depicted as energetic allocations for the crossed temperature-DO experiments (Fig. 7). Here, energy allocations are derived from experimental data on total energy (consumption rate) and RM supplemented with experimental measures of egestion (Hanks 2009) and excretion (for congeneric striped bass *Morone saxatilis*; Hartman and Brandt 1995). The aerobic scope; indexed as the difference between total consumed energy and that which was egested, excreted, or used for routine metabolism; markedly expanded with increasing DO, increasing 223% at 20°C and 292% at 28°C (Fig. 7). These changes are the direct result of increased metabolic costs associated with oxyregulation at lower DO levels. Because the aerobic scope includes energy allocations towards growth, feeding (aka specific dynamic action), and activity many facets of habitat suitability are potentially impacted by hypoxia.

Temperature and salinity effects

Over a fairly broad temperature range, 6–28°C, relevant to the range that a Chesapeake Bay white perch will experience during its first year of life, mean growth rates increased from slightly negative growth rates to

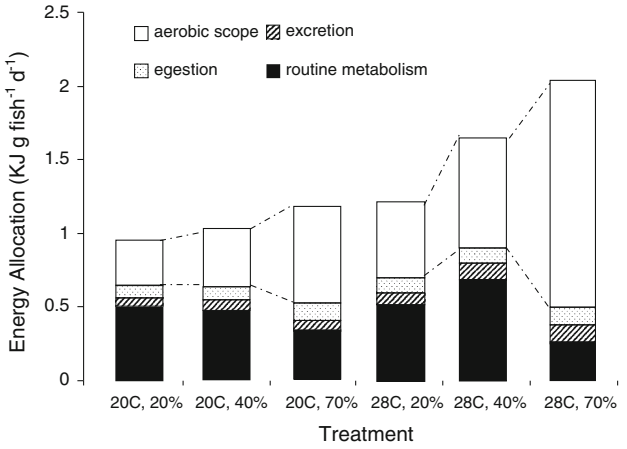

Fig. 7 Juvenile white perch energy allocation patterns for combinations of temperature and dissolved oxygen. The aerobic scope is indexed as the difference between total consumed energy and that which was egested, excreted, or used for routine metabolism. *Dashed lines* connect the aerobic scope for growth and activity

0.032 g d^{-1} (Table 1). Higher growth rates were due to higher consumption, which increased over fourfold from 0.03 to 0.17 g g^{-1} fish wt, but also due to an increase in conversion efficiency, which increased from 0 to 17% over the same temperature range. Routine metabolism was relatively insensitive to temperature, except at 6°C, which may well have been due to lack of acclimation as other experimenters have shown that cold-temperature acclimation should occur over months rather than the several week period used in this study (Hurst et al. 2000; Lankford and Targett 2001). Still, at higher temperatures, similar RM values suggested that the aerobic scope for activity could vary at least fourfold during the first year of life.

Super-optimal responses were not detected for the highest temperature level tested (28°C), and without evidence of declining growth at higher temperatures, maximum growth rates could not be predicted. In a separate rearing study on white perch YOY juveniles, Kellogg and Gift (1983) estimated maximum growth rate at 27–29°C, where after growth rapidly declined to nil at 35°C. These results could suggest that white perch are well adapted to thermal conditions in the Chesapeake Bay, where summer water temperatures rarely exceed 30°C (Wingate and Secor 2008). At the other extreme, the lower limit for positive growth for YOY white perch was estimated to be approximately 12°C (5.8×10^{-4} g d^{-1}). Temperatures persist below 12°C from November through March each year (Lippson et al. 1979), indicating a fairly long period of low to nil winter growth if experimental results are valid.

Previous studies on Moronidae indicated that white perch and striped bass juveniles grew better at intermediate salinities (4–8) than in freshwater or higher salinities (Secor et al. 2000; Kerr and Secor 2009), albeit the differences were small. Here, we only detected diminished consumption rate and energy density at the highest salinity (16). Acclimation is an important issue because growth performance is influenced by whether individuals were sampled in fresh- or brackish water (Kerr and Secor 2009). Further, the nearly twofold decline in consumption rate from salinity 0–16 would indicate that had the experiment continued, a growth effect should have been observed. Depressed energy density supports the view that fish exposed to this treatment may have been relying on energy stores. White perch are known to transit salinities greater than 15 (Nemerson and Able 2004), but rarely are they captured in these salinities (Setzler-Hamilton 1991), consistent with the idea that these are sub-optimal growth habitats.

Oxygen limitation

Here we provided strong evidence for oxygen limitation of growth and the aerobic scope for activity in a dominant estuarine species. For white perch, a threshold effect level likely occurs between 20 and 40% DO_{sat} at warmer temperatures and between 40 and 70% at cooler temperatures. Similar to white perch, low DO_{sat} has been shown to significantly depress growth in other estuarine species (Niklitschek and Secor 2009a). However species show large differences in their tolerance to low DO. Atlantic sturgeon *Acipenser oxyrinchus* experienced a decrease in growth with DO_{sat} levels at $\leq$70% (Secor and Gunderson 1998; Niklitschek and Secor 2009a) while species such as spot *Leiostomus xanthurus*, menhaden *Brevoortia tyrannus*, and mummichog *Fundulus heteroclitus* exhibited growth effects at about 10–15% DO_{sat} (Buentello et al. 2000; Stierhoff et al. 2003; McNatt and Rice 2004).

Depressed growth in white perch was likely due to changes in aerobic scope because growth and consumption rate responses mirrored each other. Reduced consumption rate in response to hypoxia has been reported in several studies (Stierhoff et al. 2006; Niklitschek and Secor 2009a) and could indicate an ecophysiological strategy for shunting energy towards oxyregulation by reducing energy required to convert consumed energy. For instance, Niklitschek and Secor (2009b) observed that juvenile Atlantic sturgeon allocated less energy towards feeding metabolism and more towards basal metabolism during hypoxic exposures. Although not observed directly, increased RM under hypoxia could be due to increased ventilation, heart rate, and other costs related to oxyregulation (Randall 1982). Interestingly, energy density also declined at low DO levels. Speculating, this could indicate that tissue energy stores were recruited during hypoxia.

Strong interactive effects between temperature and oxygen may only occur when temperatures and DO levels

are jointly stressful (Pörtner 2010). The failure to detect strong interactions between temperature and DO may be due to experimental design limitations, where provided temperatures (20 and 28°C) were close to optimum for this species. Had we crossed lower or higher temperatures, we might have observed a similar three dimensional expression of both DO (saturating curve) and temperature (dome shaped curve) as reported by Niklitschek and Secor (2009b) for juvenile Atlantic sturgeon. Here the threshold of responsiveness to hypoxic conditions shifts to higher DO levels under thermal stress (i.e., temperatures that depart from optimal conditions). Similar results were described by Claireaux and Lagardere (1999) for European sea bass *Morone labrax* and Pörtner and Knust (2007) for eelpout *Zoarces viviparus*.

Oxygen limitation and estuarine nursery habitats

Hypoxia-induced depression in consumption and activity is an effective survival strategy (Dalla Via et al. 1994), but ultimately leads to reduced growth, condition, and increase the possibility of predation. A threefold decrease in growth rate, for instance, as seen between the 70 and 20% DO_{sat} treatments could affect recruitment by keeping small juveniles vulnerable to predation for much longer. Further, decreased aerobic scope due to higher basal metabolism under hypoxia will reduce available energy for evasion and escape from predators (Lankford et al. 2001). Therefore, hypoxia not only reduces habitat quality for juvenile growth but also has consequences to survival and recruitment through indirect effects.

The combined effect of low DO and warm temperature is a loss of habitat available to an organism creating, as Coutant (1985) described, a "temperature-oxygen squeeze". Studies have shown that estuarine organisms such as weakfish *Cynoscion regalis*, spot, pinfish *Lagodon rhomboides*, Atlantic croaker *Micropogonias undulatus*, menhaden, white mullet *Mugil curema*, Atlantic sturgeon, and brown shrimp *Farfantepenaeus aztecus* will choose to avoid hypoxic areas and move into more energetically favorable habitats (Wannamaker and Rice 2000; Tyler and Targett 2007; Niklitschek and Secor 2010). However, avoidance of areas of poor water quality could lead to overcrowding, increased competition, and increased interactions with predators (Breitburg et al. 1997). In comparison to other estuarine fishes, one might expect that YOY white perch would be less affected by the temperature-oxygen squeeze due to their high thermal tolerance (Kellogg and Gift 1983) and their occurrence in shoal waters that tend to be well mixed (Coutant 1985; Breitburg et al. 2003). However, studies in the Chesapeake Bay show that even shallow, littoral habitats can exhibit large, diurnal fluctuations in DO (Breitburg 1990) similar to that noted in other mid-Atlantic estuaries (Tyler et al. 2009). Thus the littoral zones that serve as principal nurseries are vulnerable to hypoxia and negative interactions with temperatures that curtail growth and feeding.

Clearly, the aerobic scope for white perch is sensitive to low DO conditions, especially during the summer. This is a critical period of production given the long winter periods during which little or no juvenile growth occurs. With warming in the Chesapeake Bay and other temperate estuaries longer growth seasons are likely for white perch and other overwintering species, but these will be offset by thermal stress during summer due to warmer temperatures in concert with pervasive hypoxia.

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