

ABSTRACT

Title of Document: BIOENERGETIC RESPONSES OF
 CHESAPEAKE BAY WHITE PERCH TO
 NURSERY CONDITIONS OF
 TEMPERATURE, SALINITY, AND
 DISSOLVED OXYGEN.

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 Marine, Estuarine, and Environmental Science.

Changes in the physical and chemical structure of estuaries affect the habitat availability for anadromous species. White perch, an estuarine species, are among the most abundant and important fishes in the Chesapeake Bay. Here, I evaluate nursery quality for juvenile white perch by measuring metabolic and growth responses over a range of environmental conditions such as salinity, temperature, and dissolved oxygen. Rearing white perch in 10-d trials varying in temperature, salinity and dissolved oxygen conditions, I estimated growth rates, feeding rates, gross growth efficiency, and routine metabolism. Juveniles experienced higher feeding and growth rates in warmer, more oxygenated waters. In hypoxic environments (<40% saturation), metabolic rates increased as much as 4-fold while growth decreased 3-fold and feeding decreased 2-fold. My results indicate that while white perch are well suited to the saline and thermal conditions present in the Bay, nursery habitat value can be substantially curtailed by hypoxia.

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OXYGEN.

By

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Dedication

To my parents Galen and Eileen McQuarrie: You taught me to value and love learning. Thank you.

To my siblings Kevin, Nadine, and Marguerite: You have given me financial, intellectual, and emotional support. Thank you.

To my husband Ryan: Without your timely intervention, I would be both homeless and penniless while finishing this thesis. Thank you.

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Table of Contents

Dedication.....	ii
Acknowledgements.....	iii
Table of Contents.....	iv
List of Tables.....	v
List of Figures.....	vi
Introduction.....	1
Goals and Hypotheses.....	15
Methods.....	17
Food Consumption and Growth Experiments.....	17
Collection and Maintenance.....	17
Experimental Design and Methods.....	17
Salinity Effects.....	21
Respirometry Experiment.....	23
Egestion Experiment.....	24
Calorimetry.....	25
Energy Budgets.....	25
Statistical Analyses.....	26
Parameter Validation.....	27
Results.....	30
Food Consumption and Growth Experiments.....	30
Growth.....	30
Consumption.....	33
Consumption as a Function of Mass.....	36
Gross Growth Efficiency.....	37
Routine Metabolism.....	39
Egestion.....	44
Energy Budgets.....	45
Parameter Validation.....	47
Discussion.....	49
Salinity Effects.....	49
Temperature Effects.....	51
Dissolved Oxygen Effects.....	53
Temperature and Dissolved Oxygen Interaction.....	55
Limitations and validation.....	58
White perch in Chesapeake Bay.....	59
Appendices.....	62

List of Tables

Table 1: Examination of the effect of abiotic environmental factors on the bioenergetic parameters of growth, consumption and routine metabolism for estuarine fish.....	8
Table 2: YOY white perch growth and consumption treatments separated by year accomplished.....	19

List of Figures

- Figure 1. Incomplete factorial experimental design for YOY white perch growth and consumption experiments. Circles represent treatment and number within circles indicates the replicate number. 18
- Figure 2. Instantaneous growth rates of YOY white perch at temperatures 20 and 28°C and salinities of 1, 4, 8, and 12. Boxes indicate the median (horizontal line), the first and third quartiles (box edges), and ± 1.5 times the inner quartile range (whiskers)..... 22
- Figure 3. Mean daily feeding rates of YOY white perch at temperatures 20 and 28°C and salinities of 1, 4, 8, and 12. Boxes indicate the median (horizontal line), the first and third quartiles (box edges), and ± 1.5 times the inner quartile range (whiskers). 23
- Figure 4. A diagram of Chesapeake Bay with labeled sub-estuaries. Marked sites are fixed seine sites for the MD DNR juvenile striped bass survey. (Durell, E.Q., and Weedon, C. 2007. Striped Bass Seine Survey Juvenile Index Web Page. <http://www.dnr.state.md.us/fisheries/juvindex/index.html>. Maryland Department of Natural Resources, Fisheries Service.) 28
- Figure 5. Instantaneous growth rates for YOY white perch at temperatures 6, 12, 20, and 28°C and percent dissolved oxygen saturation combinations of 20, 40, and $\geq 70\%$. Data points were offset slightly to aid presentation. 30
- Figure 6. Instantaneous growth rates for YOY white perch at temperatures 20 and 28°C and percent dissolved oxygen saturations of 20% (black hatched boxes), 40% (grey filled boxes), and $\geq 70\%$ (unfilled boxes). 31
- Figure 7. Instantaneous growth rate of YOY white perch as a function of temperature and dissolved oxygen. Surface contours are calculated from the equation given in the text..... 33
- Figure 8. Mean daily feeding rates by YOY white perch at temperatures 6, 12, 20, and 28°C and percent dissolved oxygen saturation combinations of 20, 40, and $\geq 70\%$. Data points were offset slightly to aid presentation. 34
- Figure 9. Mean daily feeding rates of YOY white perch at temperatures 20 and 28°C and percent dissolved oxygen saturations of 20% (black hatched boxes), 40% (grey filled boxes), and $\geq 70\%$ (unfilled boxes). Boxes indicate the median (horizontal line), the first and third quartiles (box edges), and ± 1.5 times the inner quartile range (whiskers)..... 35

Figure 10. Mean daily feeding rate as a function of temperature and dissolved oxygen. Surface contours are calculated from the equation given in the text.	36
Figure 11. Mean daily fish weight versus maximum consumption relationship for YOY white perch. Four weight classes were looked at 3, 5, 6, 9 g reported here in dry weight units.....	37
Figure 12. Gross growth efficiencies of YOY white perch at temperatures 6, 12, 20, and 28°C and percent dissolved oxygen saturation combinations of 20, 40, and ≥70%. Data points were offset slightly to aid presentation.....	38
Figure 13. Gross growth efficiencies of YOY white perch at temperatures 20 and 28°C and percent dissolved oxygen saturations of 20% (black hatched boxes), 40% (grey filled boxes), and ≥70% (unfilled boxes). Boxes indicate the median (horizontal line), the first and third quartiles (box edges), and ± 1.5 times the inner quartile range (whiskers).....	39
Figure 14. Oxygen consumption of YOY white perch at temperatures 6, 12, 20, and 28°C and percent dissolved oxygen saturation combinations of 20, 40, and ≥70%. Data points were offset slightly to aid presentation.....	40
Figure 15. Oxygen consumption for summertime treatments 20 and 28°C and percent dissolved oxygen saturations of 20% (black hatched boxes), 40% (grey filled boxes), and ≥70% (unfilled boxes). Boxes indicate the median (horizontal line), the first and third quartiles (box edges), and ± 1.5 times the inner quartile range (whiskers).....	41
Figure 16. Mean oxygen consumption as a function of temperature and dissolved oxygen. Surface contours are calculated from the equation given in the text.	42
Figure 17. Energy density of YOY white perch at temperatures 6, 12, 20, and 28°C and percent dissolved oxygen saturation combinations of 20, 40, and ≥70%. Data points were offset slightly to aid presentation.	43
Figure 18. Energy Densities of juvenile white perch for summertime treatments 20 and 28°C and percent dissolved oxygen saturations of 20% (black hatched boxes), 40% (grey filled boxes), and ≥70% (unfilled boxes). Boxes indicate the median (horizontal line), the first and third quartiles (box edges), and ± 1.5 times the inner quartile range (whiskers).....	44
Figure 19. Egestion rates for YOY white perch at 40% dissolved oxygen levels (shaded bars) and ≥70% dissolved oxygen levels (open bars) across three different temperatures (12, 20, and 28°C). Boxes indicate the median (horizontal line), the first and third quartiles (box edges), and ± 1.5 times the inner quartile range (whiskers).	45
Figure 20. YOY white perch energy budgets for eight different treatments. Top graph shows total energy allocation in KJ g fish ⁻¹ day ⁻¹ . Bottom graph is percent of	

total energy allocation. Temperatures are 12, 20 and 28°C and percent dissolved oxygen levels are 20, 40, and $\geq 70\%$ 47

Figure 21. Experimentally and field derived instantaneous growth rates of YOY white perch. Field growth rates were measure from two sub-estuaries of the Chesapeake Bay: the Potomac and the Patuxent. Experimental Data looked at temperatures treatments 20 and 28 °C and dissolved oxygen treatments 40 and $\geq 70\%$ 48

Introduction

Marine fish nurseries, as defined by Beck et al. (2001), are specific subsets of all juvenile habitats that disproportionately contribute on a per-unit-area basis to recruitment to the adult population. Small changes (e.g. a 10% deviation) in early mortality and growth rates can significantly influence recruitment to the adult population (Houde 1987). Nursery habitats therefore, will maximize growth and survival while minimizing predation, starvation, and environmental stress. Because estuaries support high abundances of juveniles that later recruit to both estuarine and coastal fisheries (Haedrich and Hall 1976; Juanes et al. 1996; Ross 2003), scientists have considered them as critical nurseries.

Estuaries can constitute predation refugia for juveniles through their physical characteristics such as extensive shallow habitat, turbid waters, and structurally complex shelters (Able and Fahay 1998). Estuaries also experience high primary and secondary production, which provide a broad food base for juvenile fishes, which in turn act as secondary consumers in marine food webs (Beck et al. 2001). For certain species, warmer water temperatures and lower salinity that occur in estuaries can also favor juvenile production rates (Attrill and Power 2002; Ross 2003).

However, in comparison to coastal ocean environments, estuaries are more variable in abiotic conditions (Ketchum 1983). Estuaries are by definition “a semi-enclosed body of water, which has a free connection with the open sea and within which sea water is measurably diluted with freshwater derived from land drainage.” (Pritchard 1967). This freshwater and saltwater interchange influences hydrology and hydrography resulting in substantial spatial and temporal heterogeneity in salinity,

temperature, dissolved oxygen, and turbidity, which can change abruptly across meters to km scales and over tidal, daily, seasonal, and interannual cycles (Tyler and Seliger 1989). These factors affect fish production indirectly through their influence on the food distribution and abundance (Jung and Houde 2003). Environmental factors and their interactions can also directly alter fish production by influencing physiological responses such as growth and metabolism (Eby et al. 2005) and may represent a stronger influence on habitat suitability than either predation refugia and food availability (Manderson et al. 2002; Harrison and Whitfield 2006). Habitat suitability will in turn affect habitat selection as juveniles will reside or change habitats based upon their physiological status (Werner et al. 1983; Gilliam and Fraser 1987; Metcalfe et al. 1988). Here, I evaluate the physiological responses of metabolic and growth rates to a range of estuarine environmental conditions as a means to evaluate nursery habitats.

Although variable, estuaries have been found to be energetically favorable, with some species achieving greater growth in estuarine versus marine nursery habitats (Lenanton and Potter 1987; Yamashita et al. 2003). Still, juveniles of other species, which occur in both estuaries and nearshore habitats, show equivalent or higher growth in marine environments (Able et al. 2003; Callihan 2005). Facultative use of estuaries is common, and a growing body of research is examining the broad question of nursery values in estuarine versus coastal habitats (Able 2005; Able et al. 2006). One approach then to understand how estuaries function as nurseries is to focus on species that are not facultative users. Here, I focus on subsets of habitats

within estuaries (defined by water quality conditions) for a species that completes its life cycle in estuaries: white perch *Morone americana*.

In the Chesapeake Bay and other temperate estuaries, juvenile fish must contend with variable temperature and salinity conditions. White perch are found primarily in salinities ranging from 0 to 13 (Setzler-Hamilton 1991), although they have also been caught in salinities as high as 17 (*personal communication* E. Q. Durell, Maryland Department of Natural Resources, Fisheries Service.). Many estuarine juveniles show euryhaline and eurythermal adaptations to survive and grow under variable conditions (Haedrich and Hall 1976). For most marine teleost fish, the outer estuary is an osmoregulatory refuge because lower salinities here require reduced hypo-osmoregulation (Jobling 1995). However, further penetration into the middle estuary by a marine fish would require reversal in the direction of salt transport, favoring physiological mechanisms of salt retention. Thus, a completely estuarine dependent species requires rapid adaptation to hyper- and hypo-osmotic conditions, and it should not be surprising that the number of estuarine resident species is low (Haedrich 1983; Bulger et al. 1993; Wagner 1999). For systems such as the Chesapeake Bay that have tidal influences, large, acute fluctuations in temperature can occur particularly in shallow habitats (Schulte 2007). Chesapeake Bay is a shallow estuary and therefore has a reduced capacity for storing heat. Yearly temperatures range from 1 to 29 °C (The Chesapeake Bay Program [http://www.chesapeakebay.net/status_weather.aspx? menuitem=19787](http://www.chesapeakebay.net/status_weather.aspx?menuitem=19787)). Resident estuarine fish within the bay therefore must show eurythermal adaptations by tolerating a wide range of temperatures.

A critical feature in many estuaries is cultural eutrophication, which is one of the leading causes of coastal ecosystem degradation (Boesch 2002; Diaz and Rosenberg 2008). An important consequence of eutrophication is low levels dissolved oxygen (DO) or hypoxia, which is increasingly prevalent in estuaries, even for those that are considered well-mixed (Verity et al. 2006). Hypoxia, defined by the Ecological Society of America as waters in which dissolved oxygen concentration falls below 2-3 mg l⁻¹ (Ecological Society of America. "Hypoxia fact sheet" 1 Dec. 2008 <<http://www.esa.org/education/edupdfs/hypoxia.pdf>>), can reduce juvenile fish growth rates, modify distributions and behaviors, and lead to mortality. These repercussions can affect food web dynamics through changes in predator-prey interactions which include encounter, attack, and capture rates (Breitburg 2002). As early as the 18th century, the Chesapeake Bay showed signs of human disturbance (Brush 2001). However, evidence from dated sediment cores show recurring deep-water hypoxia starting in the 1950's (Kemp et al. 2005). The trend since then has been one of increasing volume and rate. Hagy et al. (2004) estimated anoxic volume (DO < 0.2 mg l⁻¹) to have increased from 0 in 1950 to 3.6 x 10⁹ m³ in 2001 while severe hypoxia (DO < 1.0 mg l⁻¹) increased from 1.6 x 10⁹ to 6.5 x 10⁹ m³ and mild hypoxia (DO < 2.0 mg l⁻¹) increased from 3.4 x 10⁹ to 9.2 x 10⁹ m³ during the same time period. Incidence of hypoxia has also increased in duration, now typically beginning in May and extending into September (Officer et al. 1984). Hypoxia is also a problem within the tributaries of Chesapeake Bay. The Potomac and the Patuxent estuaries are the first and second most hypoxic of all the sub-estuaries of the

Bay. During June-August, 63% of the bottom (sub-pycnocline) water of the Patuxent is hypoxic (Fisher et al. 2006).

Eutrophication and resulting hypoxia can alter food web structure through the loss of demersal fish habitat and production, which in turns leads to a more pelagic dominated food web (Caddy 2000). This trend has been seen in the Chesapeake with an increase in the pelagic to demersal fish species ratio from 1.90 in the 1960's to 2.66 in the 1990's and an increase prevalence of fish lesions and HAB-induced fish kills (Kemp et al. 2005). Demersal species that were once prominent in the bay, such as the Atlantic sturgeon have experienced severely depressed nursery habitat volume due to the increased prevalence of bottom water hypoxia (Niklitschek and Secor 2005).

Climate change is an additional stressor to estuaries that is predicted to result in an increase in temperature and river flow (Pyke et al. 2008). Najjar (1999) modeled a $24\% \pm 13\%$ increase in Susquehanna River flow with a doubling of CO₂ using conservative predictions of precipitation and temperature. These effects could further alter fish distributions, habitat suitability, and habitat availability (Perry et al. 2005). Greater freshwater flow can lead to increased stratification and in turn hypoxia incidence during summer months (Hagy et al. 2004). Warming during summer months could lead to super-optimal temperatures curtailing nursery habitat and exacerbating the effects of bottom water hypoxia. In tandem, reduced thermal habitat and reduced oxygenated habitat can result in a "habitat squeeze" where organisms are forced to areas of greater densities, competition, and predation (Coutant 1985; Coutant and Benson 1990). Hence, a central challenge in evaluating

estuarine nursery habitats is an integrative framework to quantitatively evaluate the effects of numerous stressors due to eutrophication, climate change, and other environmental and anthropogenic influences on living resources.

Bioenergetic models are a principal approach used to identify current nursery habitat as well as to forecast changes in habitat suitability (Luo et al. 2001; Niklitschek and Secor 2005). Bioenergetic models use mass balance equations that equates energy consumed to energy expended in growth (somatic and reproductive), metabolism, and waste (Winberg 1956). The models can predict either growth or consumption if one or the other is known. As discussed previously, growth serves as an important measure of physiological status and habitat suitability (Werner et al. 1983; Niklitschek and Secor 2005). Bioenergetic models can predict growth by integrating the effects of environmental factors on the physiological responses of consumption, assimilation, and respiration and thereby provide a quantitative and predictive framework for assessing habitat suitability across a range of environmental stressors. Bioenergetic models depend upon series of experiments relating environmental conditions or forage to consumption, growth, and other metabolic responses. In this study, I evaluate temperature, salinity, and dissolved oxygen as they play large roles in energetics and survival.

Fry (1971) developed a framework that categorized interactive and nonlinear physiological effects of temperature, DO, and salinity. These categories include controlling, masking, and limiting factors. Controlling factors, such as temperature, affect molecular activity and are characterized by steep dome-shaped curves. Metabolism increases with increases in temperature, but at some high temperature,

thermal conditions become physiological stressful and metabolic activity drops. Salinity is a masking factor and is illustrated by a shallow upward concave shaped curve. High and low salinities incur increased metabolic costs while mid-range salinities result in reduced osmoregulatory costs. Finally, limiting factors such as DO are represented by saturating curves. Metabolic activities, such as growth and respiration, will increase with an increase in the limiting factor until receptors and processing rates reach saturation (a “threshold”) at which point activity remains constant. An important difference in this model compared to most bioenergetic models developed to date is that DO replaces foraging as the main limiting factor. Therefore, while temperature will drive physiological rates, the rates will ultimately be limited by the amount of oxygen available to sustain the aerobic metabolism (Niklitschek and Secor in press).

Many studies have examined the effects of one or two abiotic factors on physiological processes in isolation, but few have attempted to combine and integrate the effects of multiple abiotic factors in a bioenergetics framework (Table 1). Only two of the studies listed in Table 1 looked at the interactive effects of DO, salinity, and temperature. Claireaux and Lagardere (1999) examined ambient DO level under imposed treatments temperature and salinity for European sea bass while Niklitschek and Secor’s (in press) experiments on Atlantic sturgeon evaluated multiple levels of DO, temperature, and salinity in an incomplete factorial design.

Table 1: Examination of the effect of abiotic environmental factors on the bioenergetic parameters of growth, consumption and routine metabolism for estuarine fish.

Authors	Species/System	Energetic parameters	Environmental Parameters	Results of Study
Lankford and Targett 1994	juvenile weakfish (<i>Cynoscion regalis</i>)/Delaware Bay, Delaware, USA	Growth	Temperature	significant
			Salinity	significant
		Consumption	Temperature x Salinity	significant
			Temperature	significant
		Gross growth efficiency	Salinity	significant
			Temperature x Salinity	not significant
Buckel et al. 1995	juvenile bluefish (<i>Pomatomus saltatrix</i>), Great South Bay, New York, USA	Growth	Temperature	significant
			Salinity	not significant
		Consumption	Temperature	significant
			Salinity	not significant
Secor and Gunderson 1997	juvenile Atlantic sturgeon (<i>Acipenser oxyrinchus</i>)/Chesapeake Bay, Maryland, USA	Growth	Temperature	not significant
			DO	significant
		Routine metabolism	Temperature	significant
			DO	not significant
			Temperature x DO	significant

Table 1 Continued.

Authors	Species/System	Energetic parameters	Environmental Parameters	Results of Study
Claireaux and Lagardere 1999	European sea bass (<i>Dicentrarchus labrax</i>)/L'Houmeau, France**	Routine metabolism	Temperature	significant
			Salinity	significant
Secor et al. 2000	juvenile striped Bass (<i>Morone saxatilis</i>)/Maryland and South Carolina, USA**	Growth	DO	significant
			Temperature x Salinity	significant
			Temperature x DO	significant
			Salinity x DO	not significant
			Temperature	significant
		Consumption	Salinity	not significant
			Temperature x Salinity	not significant
			Temperature	significant
			Salinity	not significant
			Temperature x Salinity	not significant
Altinok and Grizzle 2001	juvenile channel catfish (<i>Ictalurus punctatus</i>)/Alabama, USA***	Growth	Temperature	not significant
			Salinity	not significant
			Temperature x Salinity	not significant
	juvenile goldfish (<i>Carassius auratus</i>)/Alabama, USA***	Growth	Salinity	significant
			Salinity	significant
			Salinity	significant
		Gross growth efficiency	Salinity	significant
			Salinity	significant
			Salinity	significant

Table 1 Continued

Authors	Species/System	Energetic parameters	Environmental Parameters	Results of Study
	juvenile rainbow trout (<i>Oncorhynchus mykiss</i>)/Alabama, USA***	Growth	Salinity	significant
		Gross growth efficiency	Salinity	significant
	juvenile striped bass (<i>Morone saxatilis</i>)/Alabama, USA***	Growth	Salinity	significant
		Gross growth efficiency	Salinity	significant
	juvenile Gulf sturgeon (<i>Acipenser oxyrinchus desotoi</i>)/Alabama, USA***	Growth	Salinity	significant
		Gross growth efficiency	Salinity	significant
	juvenile brown trout (<i>Salmo trutta</i>)/Alabama, USA***	Growth	Salinity	significant
		Gross growth efficiency	Salinity	significant
Imsland et al. 2001	juvenile turbot (<i>Scophthalmus maximus</i>)/Bergen, Norway	Growth	Temperature	significant
			Salinity	significant
			Temperature x Salinity	significant
Stierhoff et al. 2003	mummichog (<i>Fundulus heteroclitus</i>)/Canary Creek, Lewes, Delaware, USA	Growth	DO	significant
		Consumption	DO	not significant

Table 1 Continued

Authors	Species/System	Energetic parameters	Environmental Parameters	Results of Study
McNatt and Rice 2004	juvenile spot (<i>Leiostomus xanthurus</i>)/Beaufort, North Carolina, USA	Growth	Temperature	significant
			DO Temperature x DO	significant not significant
Wuenschel et al. 2004a	juvenile Atlantic menhaden (<i>Brevoortia tyrannus</i>)/Beaufort, North Carolina, USA	Growth	Temperature	significant
			DO Temperature x DO	significant significant
Wuenschel et al. 2004a	juvenile grey snapper (<i>Lutjanus griseus</i>)/Beaufort, North Carolina, USA	Growth	Temperature	significant
			Salinity Temperature x Salinity	not significant significant*
		Consumption	Temperature	significant*
			Salinity Temperature x Salinity	significant significant*
Wuenschel et al. 2004b	juvenile spotted seatrout (<i>Cynoscion nebulosus</i>)/Corpus Christi, Texas, USA**	Gross growth efficiency	Temperature	significant
			Salinity Temperature x Salinity	significant* not significant
		Routine metabolism	Temperature	significant
Rocha et al. 2005	juvenile fat snook (<i>Centropomus parallelus</i>)/Cananéia estuary, Sao Paulo, Brazil	Growth	Salinity Temperature x Salinity	significant significant
		Routine metabolism	Salinity	significant

Table 1 Continued

Authors	Species/System	Energetic parameters	Environmental Parameters	Results of Study
Lee and Johnson 2005	round goby (<i>Neogobius melanostomus</i>)/Lake Erie and Lake St. Claire, Ontario, Canada	Consumption	Temperature	significant
Wuenschel et al. 2005	juvenile grey snapper (<i>Lutjanus griseus</i>)/Beaufort, North Carolina, USA	Routine metabolism Routine metabolism	Temperature Temperature	significant significant
Stierhoff et al. 2006	juvenile summer flounder (<i>Paralichthys dentatus</i>)/Delaware Bay, Delaware, USA	Growth	Salinity Temperature x Salinity Temperature x DO	significant significant significant
	juvenile winter flounder (<i>Pseudopleuronectes americanus</i>)/Delaware Bay, Delaware, USA	Consumption Growth Consumption Growth	DO Salinity x DO DO Temperature x DO	significant significant significant significant
Allen and Cech 2007	juvenile green sturgeon (<i>Acipenser medirostris</i>)/Klamath River, Davis, CA, USA**	Consumption Routine metabolism	DO Salinity	significant not significant
		Growth	Salinity	significant

Table 1 Continued

Authors	Species/System	Energetic parameters	Environmental Parameters	Results of Study	
Niklitschek and Secor in press	juvenile Atlantic sturgeon (<i>Acipenser oxyrinchus</i>)/Hudson River, New York, USA**	Growth	DO	significant	
			Consumption	Temperature	significant
				Salinity	significant
		Temperature x Salinity		not significant	
		Temperature x DO		significant	
		Salinity x DO		not significant	
		DO		significant	
		Temperature		significant	
		Salinity		significant	
		Temperature x Salinity		not significant	
		Temperature x DO	not significant		
		Salinity x DO	not significant		
		Routine metabolism	DO	significant	
			Temperature	significant	
			Salinity	significant	
		Temperature x Salinity	not significant		
		Temperature x DO	significant		
		Salinity x DO	not significant		

*significance varied

**aquaculture brood stock

***Fish obtained from various sources

To build upon this limited literature, I parameterized and modeled the major effects and first order interactions of temperature, DO, and salinity on juvenile white perch metabolism, consumption and growth.

White perch is an ideal experimental species as they are truly estuarine within the Chesapeake Bay. White perch are found along the Atlantic coast 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). Females migrate from lower estuaries to tidal fresh water each spring to spawn, returning to brackish water to over-winter (Mansueti 1961; Setzler-Hamilton 1991). Young-of-the-year (YOY) white perch occupy shallow freshwater and brackish tidal creeks, typically up to salinities of 15. White perch play an important role in the species composition of the Chesapeake Bay, supporting the second highest abundance and third highest fish biomass during the years 1995-2000 (Jung and Houde 2003). The species has economic significance, supporting important commercial and recreational fisheries in Maryland and Virginia. During 2000-2007, commercial value for white perch in the Chesapeake Bay ranged from 0.4 to 1 million dollars (NOAA Annual Landings: http://www.st.nmfs.gov/st1/commercial/landings/annual_landings.html). In 2007, U.S. recreational fishery landings of white perch were 1.5 million pounds (<http://www.st.nmfs.noaa.gov/st1/recreational/queries/index.html>).

Goals and Hypotheses

The goal of this thesis was to assess the physiological responses of YOY white perch to salinity, temperature, and DO within the ranges observed during the summer and fall in Chesapeake Bay by conducting laboratory rearing experiments in an incomplete factorial design. I used the energy budget framework developed by Winberg (1956): $G=C-(RM+ACT+SDA)-(F+U)$, where G=growth, C=consumption, RM=routine metabolism, ACT=activity cost, SDA=post-prandial metabolism, F=egestion, and U=excretion. I then combined these responses in a multiple-linear response surface analysis, which can be used in a predictive framework.

I hypothesized that growth and feeding rates would increase with increasing temperature and DO. Secor et al. (2000) observed that striped bass, a congener of white perch, increased consumption at warmer temperatures, which led to increased growth rates. I also expected greatest growth and feeding at oligohaline salinities (0.5-5.0) compared to freshwater (salinity 0-0.5) or mesohaline salinities (salinity 5-18) based on the same study on striped bass by Secor et al. (2000). Similarly, I proposed that routine metabolism (respiration) would increase with warmer temperatures as observed in previous work performed on spotted seatrout and striped bass (Klyashtorin and Yarzhombek 1975; Wuenschel et al. 2004b).

Low DO has been shown to negatively affect metabolic processes (Stierhoff et al. 2006; Niklitschek and Secor in press). For this reason, I expected DO levels at $\leq 40\%$ saturation to affect consumption, assimilation, and respiration. Levels $\leq 20\%$ saturation were thought to result in stressed or lethal responses. Because fish extract oxygen using a pressure gradient rather than a concentration gradient, and partial

pressure of DO increases with temperature and salinity, we chose to use percent DO in our analyses rather than concentration in mg l^{-1} (EPA 2003). This allowed us to keep the same biologically relevant DO levels between treatments regardless of the temperature and salinity of the treatments.

Among first order interactions, I hypothesized that temperature would interact significantly with DO with respect to growth, feeding, and metabolism. At higher temperatures, I expected the effect of hypoxia to be more pronounced. Temperature could interact with salinity to affect metabolic processes as observed by Wuenschel et al. (2004b), but others have observed no significant interactions with salinity, DO, and temperature (Buckel et al. 1995; Niklitschek and Secor in press). I did not expect to detect significant interactions between salinity and DO.

Methods

Food Consumption and Growth Experiments

Collection and Maintenance

During August and September 2006-2007, YOY white perch (0.5 to 7.0 g) were collected from freshwater tidal regions of the Potomac River (2006) and the Patuxent River (2007) using a 30 m x 1.2 m bagged beach seine with 6 mm mesh. The collected fish were transported back to Chesapeake Biological Laboratory (Solomons, Maryland) in coolers equipped with air stones and filled with ambient river water. I maintained fish in 60 liter holding tanks with water conditions similar to those in the field for 7 to 14 days with approximately 15 fish per tank to ensure complete recovery from handling and transportation-incurred stress. During this time, fish were treated with natural botanical antibiotics Pimafix® (1 tsp per 40L), an antibacterial solution, and Melafix® (1 tsp per 40L), an antifungal solution, to reduce infections and associated mortality. YOY white perch were fed thawed Chironomid larvae *ad libitum* twice a day during this period. We used Chironomid larvae because they are commercially available, and although they are a freshwater species, they represent a natural prey for white perch juveniles residing in lakes and rivers.

Experimental Design and Methods

I used an incomplete factorial design to test temperature, salinity, and dissolved oxygen effects on food consumption and growth rates. The design contained 13 combinations of factor levels 6, 12, 20, and 28°C; 20, 40, and $\geq 70\%$

DO_{sat}; and 1, 4, 8, and 16 salinity (Figure 1). The factor levels were chosen to represent ranges white perch experience during their YOY growth phase (summer and fall). The center treatment (20°C, ≥70% DO_{sat} and salinity 4), designed to represent the expected optimum environmental conditions for growth and consumption, received nine replicates; the remaining treatments received three replicates, with each replicate tank as the experimental unit. This design allowed evaluation of functional responses to main effects as well as first order interactions.

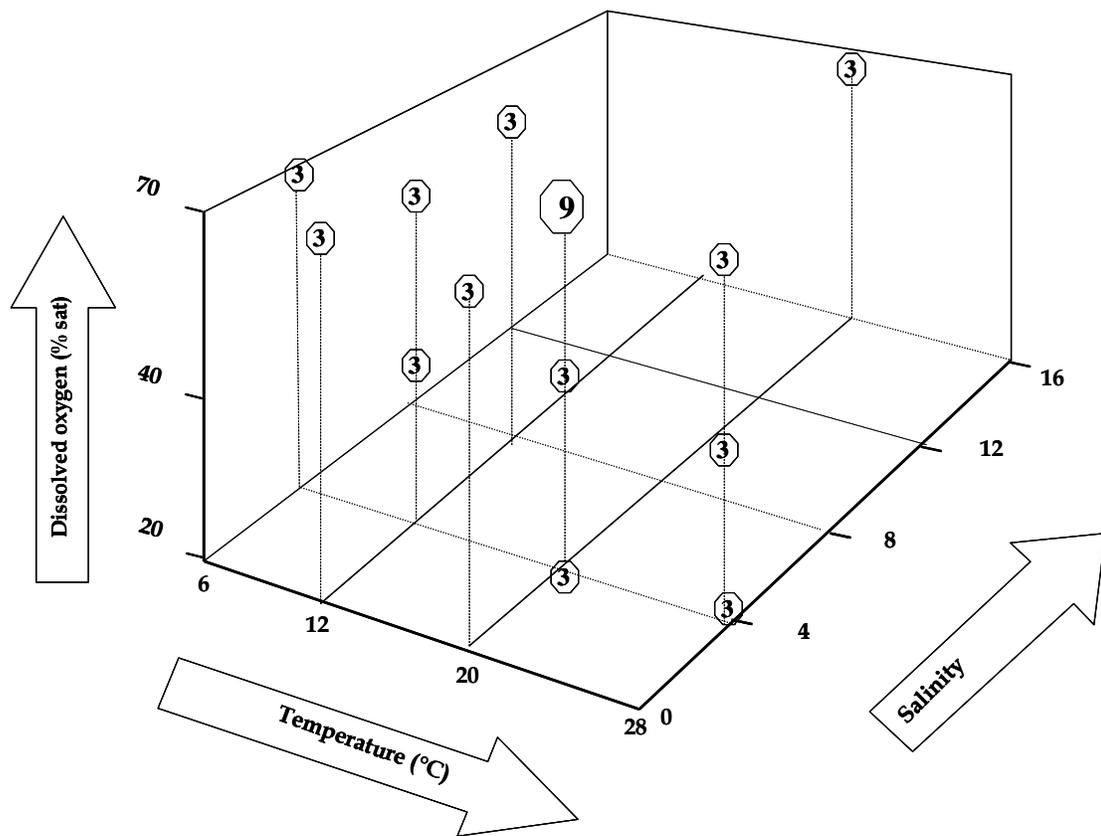


Figure 1. Incomplete factorial experimental design for YOY white perch growth and consumption experiments. Circles represent treatment and number within circles indicates the replicate number.

A large number of treatments and replicates required two experimental seasons (2006 and 2007; Table 2). Because the center treatment was replicated across years, a one-way ANOVA was performed to test for a year effect on growth and consumption. This was found to be non-significant (Growth: $p = 0.29$; Consumption: $p = 0.21$)

Table 2: YOY white perch growth and consumption treatments separated by year accomplished.

Temperatre	Dissolved Oxygen	Salinity	Replicate Number
2006			
6°C	70%	4	3
12°C	40%	4	3
12°C	70%	1	3
12°C	70%	4	3
12°C	70%	8	3
20°C	20%	4	3
20°C	40%	4	3
20°C	70%	4	3
20°C	70%	16	3
2007			
20°C	70%	4	6
20°C	70%	1	3
28°C	20%	4	3
28°C	40%	4	3
28°C	70%	4	3

Experiments were conducted in temperature-controlled rooms containing circular, 60 liter, opaque containers. Fish were acclimated to experimental conditions at the rate of salinity=1, 1°C and 5% DO_{sat} per day. Conditions in tanks were held static with a 50% water change every other day, and water was tempered and aerated 24 hours before each water change. Salinity levels were maintained by combining local well water with filtered, ambient brackish water (salinity 13-18) from the Patuxent River. DO was within 10% of targeted levels by mixing nitrogen gas with

ambient air, monitoring the levels every two hours during the daytime hours (when feeding occurred). Photoperiod was a 12h:12h light:dark cycle. Each tank contained five to eight fish, with the number of fish per tank being adjusted to maintain similar biomass among tanks. As white perch are a shoaling fish, experimental fish were reared in groups to simulate normal feeding behavior. Previous experimental consumption studies have found that fish will not feed when placed individually in tanks (Secor et al. 2000). Each fish was fasted 12 hours and weighed before and after each 10-d experiment. During the experiments Chironomid larvae were provided *ad libitum* twice a day at approximately 9 AM and 3 PM. I removed the non-consumed food one hour after feeding and weighed and dried it at 60°C for 48 hours. For each tank, water quality data (water temperature, salinity, dissolved oxygen, and conductivity) were collected daily using a YSI-85 probe.

I calculated instantaneous daily growth rate (G), feeding rate (FR) and gross growth efficiency (K₁) using the following equations and based on the 10-day experimental duration:

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

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

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

where W_i is the initial weight; W_f is the final weight; and W_t is weight at time t assuming exponential growth : W_t = W_ie^{Gt}. C_t is the total weight of food consumed on day t; A = W_f-W_i; and i is the total consumption. The fish were freeze dried, and a

dry/wet conversion was calculated using linear regression (dry weight = 0.29 wet weight - 0.07, $R^2 = 0.99$, $df = 24$). A dry/wet conversion was also calculated for Chironomid larvae using linear regression (dry weight = 0.12wet weight + 0.02, $R^2 = 0.96$, $N = 27$).

To test the effect of fish mass on maximum daily consumption rate (C_{max}), I performed similar 10 day experiments on four size classes (3, 5, 6, 9 g) at the central treatment condition of 20°C, salinity=4, and $\geq 70\%$ DO_{sat} . Each size class was replicated three times. All experiments were conducted simultaneously.

Salinity Effects

Salinity did not significantly affect consumption or growth in 10-day experiments conducted in 2005. A 2-way ANOVA with four different salinities (1, 4, 8, 12) and two temperatures (20°C and 28°C) showed only a significant influence of temperature on energetic responses (growth: $F = 4.54$, $DF = 1,22$, $p = 0.04$; consumption: $F = 69.25$, $DF = 1,22$, $p = <0.001$). Neither salinity main effects nor interaction terms were significant for growth (salinity: $p = 0.8$, interaction: $p = 0.7$; Figure 2) or consumption (salinity: $p = 0.4$, interaction: $p = 0.3$; Figure 3). For this reason, only temperature and DO treatments were applied to 2006 and 2007 experiments.

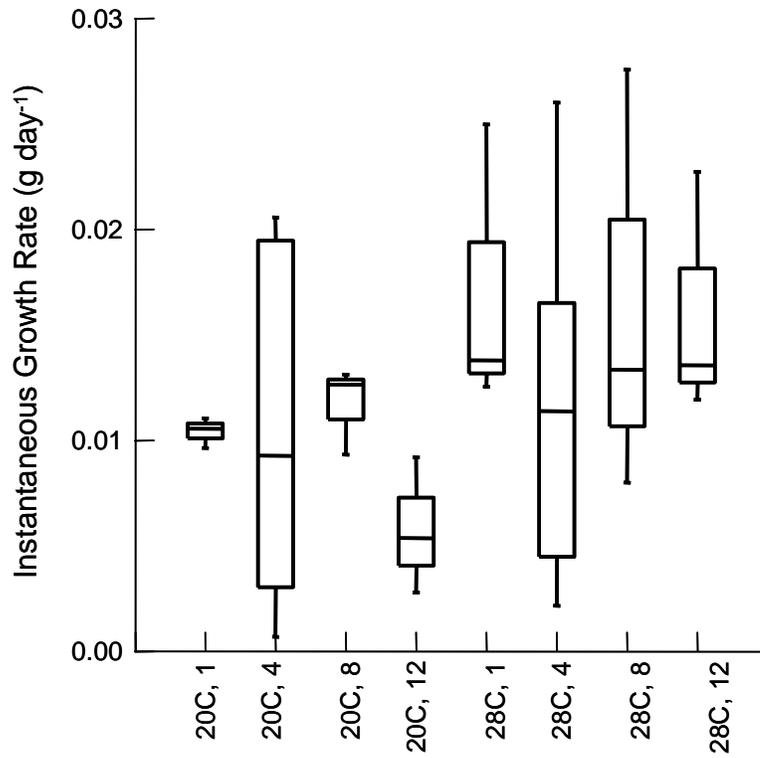


Figure 2. Instantaneous growth rates of YOY white perch at temperatures 20 and 28°C and salinities of 1, 4, 8, and 12. Boxes indicate the median (horizontal line), the first and third quartiles (box edges), and ± 1.5 times the inner quartile range (whiskers).

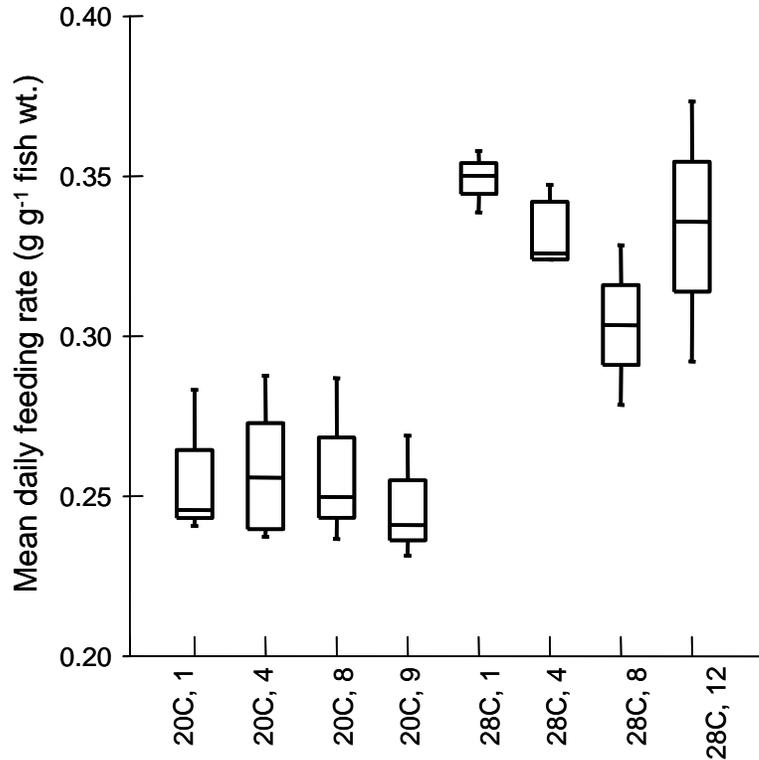


Figure 3. Mean daily feeding rates of YOY white perch at temperatures 20 and 28°C and salinities of 1, 4, 8, and 12. Boxes indicate the median (horizontal line), the first and third quartiles (box edges), and ± 1.5 times the inner quartile range (whiskers).

Respirometry Experiment

I performed routine metabolism respirometry experiments on individual fish directly after the growth-consumption experiments and the mass effects experiments. As fish rarely remain still enough during metabolic measurements to determine resting metabolism, routine metabolism was measured instead. This value represents the fish's metabolic rate at low routine activity. Oxygen consumption was measured on individual fish using a computer-controlled, closed-circuit respirometer (Micro OxyMax ©, Columbus Instruments). Five fish from each treatment 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. The experiments lasted 24 hours with nine oxygen readings measured every 2.6 hours. Respirometer mortality occurred for fish held at 28°C and 70% DO_{sat}. It was thought that fish at this treatment were depleting the oxygen more rapidly than fish in other treatments. In order to prevent mortality, I set the respirometer to refresh the oxygen more frequently. This change, however, should not affect the respirometry data. To determine whether the median or the mean was a less biased estimate of routine metabolism, I conducted a one-way ANOVA to test for skewness between treatments (Rowe 2003). I converted consumed oxygen to consumed energy using the oxycalorific coefficient of 0.014 kJ·mg⁻¹ O₂ (Schmidt-Nielsen 1990).

Egestion Experiment

For the egestion experiment, I used a 2 x 3 factorial design replicated three times with two different dissolved oxygen saturation levels (40 and 100%) and three temperatures: 12, 20, and 28°C. Salinity was maintained at 4 across all treatments. Prior to the experiment, fish were fasted for 48 h. Afterwards, they were weighed and transferred to clean 60-L tanks with filtered salinity=4 water. Three replicates with three fish each were used for all treatments. I fed the fish *ad libitum* twice a day at approximately 9 AM and 3 PM. Non-consumed food was siphoned after 30 minutes to a screen and dried for 48 hours at 60°C. Fecal samples were then removed from the screen and weighed.

Calorimetry

I determined energy content of white perch from the consumption and growth experiments using a bomb calorimeter (Parr 6200, Calorimeter, Moline IL). Five fish from each treatment were sacrificed after experiments using an overdose of MS222, freeze-dried for 24 hours, and ground up into a homogenized sample using a mortar and pestle. I formed the homogenized sample into pellets (~0.05-0.11g) and incinerated them in an oxygen rich bomb. Two subsamples of each fish were combusted and the average was used as the energy content. If the percent difference between two subsamples was greater than 10%, a third subsampled was measured. The closest two of the three samples were then averaged to obtain the mean energy content.

Energy content was estimated for one egestion treatment representing my center treatment (20°C, salinity=4, and $\geq 70\%$ DO_{sat}). Dried fecal samples were homogenized using a mortar and pestle. Due to insufficient sample volumes, the treatment replicates were combined. Two subsamples of circa 0.05g were analyzed and averaged to obtain a mean energy content. To assess the effects of temperature and percent dissolved oxygen on egestion as a proportion of consumption, I conducted a two-way analysis of variance.

Energy Budgets

I developed energy budgets for temperatures 12, 20, and 28°C and at 20, 40, and $\geq 70\%$ DO_{sat} (except for 12°C which was only crossed with 40 and $\geq 70\%$ DO_{sat}) in order to compare energy allocations between treatments. Experimentally derived values included total energy consumed, energy attributed to growth, and that

attributed to routine metabolism. Using the energy content obtained from bomb calorimetry on the center treatment (20°C, salinity=4, and $\geq 70\%$ DO_{sat}), I converted feces weight to energy values. In addition, excretion was modeled as a proportion of assimilated energy using the value of 0.068 which was estimated by Hartman and Brandt (1995a) for striped bass, a congener of white perch. As specific dynamic action (SDA; post-prandial metabolism) is poorly modeled, I combined SDA and active metabolism into a category labeled “other,” which was energy not accounted for by measured and modeled parameters.

Statistical Analyses

All statistical analyses, unless otherwise stated, were conducted using SAS Version 9.0 (SAS Institute 1999, Cary, NC) with a significance level of $\alpha = 0.05$. Statistical analyses were performed on dry weight unless otherwise stated. In order to test the significance of temperature and DO on growth, consumption and routine metabolism, I performed multiple linear regression analyses. Data was log-transformed ($\log(\text{variable} + 0.033)$) to meet the assumptions of linearity and homogeneity of variances. Diagnostics to test for normality were also performed. To test for the effects of DO and temperature and their interactions on growth, consumption, and routine metabolism, I performed a two-way analysis of variance using only those temperature treatments that were crossed with all levels of DO. These were the warmest temperatures (20 and 28 °C) and represent summer time conditions in Chesapeake Bay. A review of the treatment variances for growth and routine metabolism indicated heterogeneity, with the center treatment showing greater variance than the other treatments. A Levene’s heterogeneity test showed that the

differences were significant (growth: $p = 0.004$, routine metabolism: $p = 0.006$).

Separate variances were calculated for the center treatment to satisfy the homogeneity of variances assumption. Akaike's information criterion (AIC) confirmed that separate variances in the model constituted a better fit.

Finally, to integrate and visualize the effects of temperature and DO and to model optima of response parameters, I performed a quadratic response surface analysis estimated by least-squares regression using the general model:

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1^2 + \beta_4 x_2^2 + \beta_5 x_1 x_2 + \varepsilon$$

where y is growth, consumption or routine metabolism, x_1 is temperature in °C, and x_2 is percent DO_{sat} . A lack-of-fit test was conducted to determine the adequacy of the model in explaining the data.

To assess the effects of temperature and DO on egestion as a proportion of consumption, I performed a two-way analysis of variance.

Parameter Validation

I used data from the Maryland Department of Natural Resources (*personal communication* E. Q. Durell, Maryland Department of Natural Resources, Fisheries Service) to compare my experimental growth rates to white perch field growth rates. MD DNR has conducted a fixed-site juvenile striped bass survey since 1954 (Figure 4).

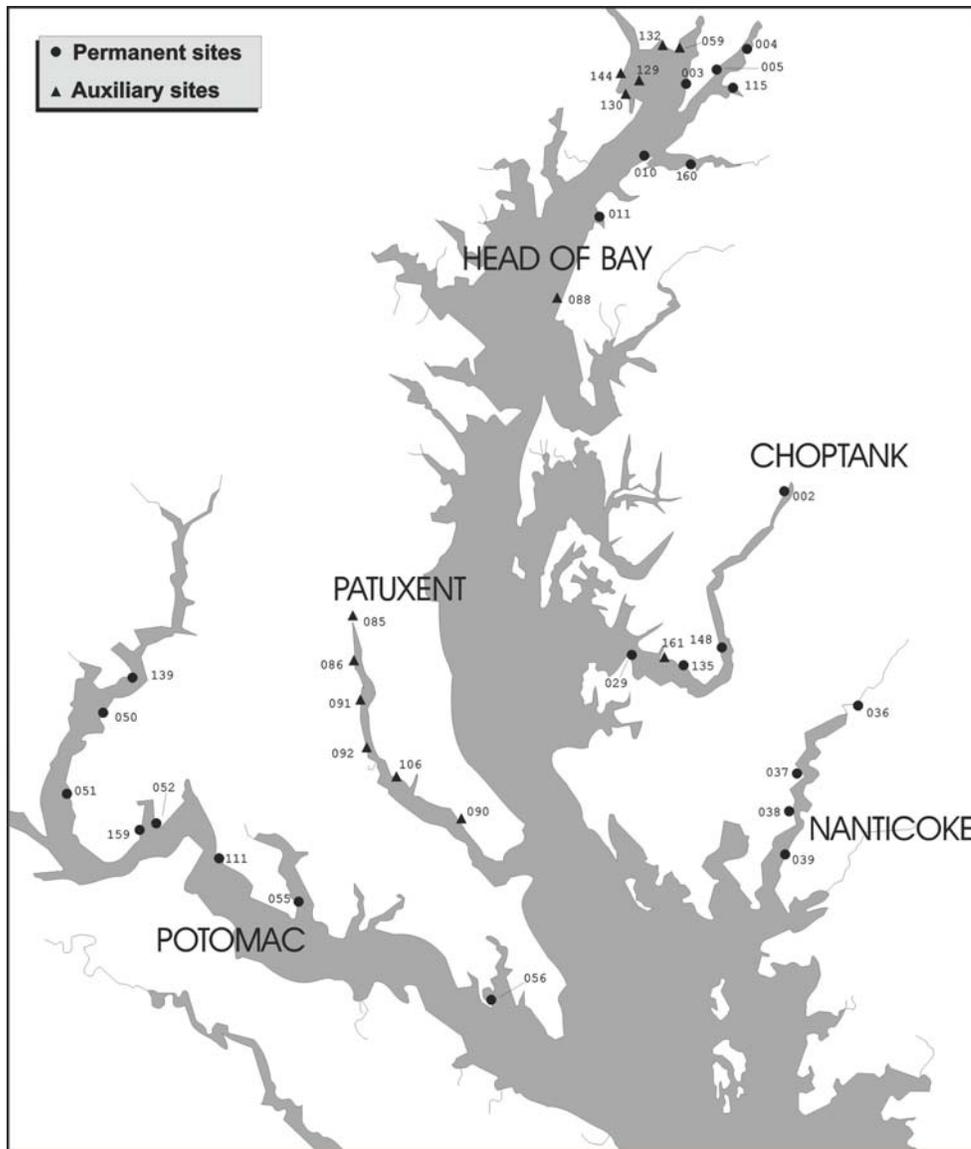


Figure 4. A diagram of Chesapeake Bay with labeled sub-estuaries. Marked sites are fixed seine sites for the MD DNR juvenile striped bass survey. (Durell, E.Q., and Weedon, C. 2007. Striped Bass Seine Survey Juvenile Index Web Page. <http://www.dnr.state.md.us/fisheries/juvindex/index.html>. Maryland Department of Natural Resources, Fisheries Service.)

Young-of-the-year juveniles were collected using a 30.5-m x 1.24-m bagless beach seine during the months of July, August, and September. Once caught, fish were separated into 0 (YOY) and 1+ year age groupings using length thresholds that were verified through scale-based ageing (Durell, E.Q., and Weedon, C. 2007. Striped Bass

Seine Survey Juvenile Index Web Page. <http://www.dnr.state.md.us/fisheries/juvindex/index.html>. Maryland Department of Natural Resources, Fisheries Service). Minimum and maximum lengths were recorded along with surface water temperature (°C), tide stage, surface salinity, bottom substrates, and submerged aquatic vegetation. Dissolved oxygen, pH, conductivity, and turbidity have been measured since 1997.

Because experimental fish were collected from freshwater regions of the Potomac and the Patuxent sub-estuaries, I used only sites with recorded salinity 0 to 3 from the Patuxent and Potomac Rivers. From the minimum and maximum lengths for age-0 white perch, I took an average and converted this mean length to weight (g) using a length-weight relationship developed for YOY white perch in the Patuxent (L. Kerr, Chesapeake Biological Laboratory, unpublished). I then averaged these station-specific weights for each month. To calculate an instantaneous growth rate, I used the equation: $G = \frac{\ln(W_f) - \ln(W_i)}{t}$ where W_f is the weight at the last sampling month (September) and W_i is the weight at the first sampling month (July); t is the number of days between the first and the last sampling month. For a temperature comparison, I averaged the surface water temperature during the three months. Growth rates were \log_e transformed to meet the assumptions of linearity.

Results

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Growth

Instantaneous growth rates ranged from -3.8×10^{-4} to 2.8×10^{-2} g day⁻¹. A multiple linear regression analysis supported my hypothesis that growth rate increased with increasing temperature and DO. Temperature was a significant variable in predicting growth and explained 80% of the variance ($F = 56.22$; $DF = 3$; $R^2 = 0.80$, $p < 0.0001$). There was no significant effect of DO ($p = 0.91$) nor was there a significant interaction between temperature and DO ($p = 0.36$; Figure 5).

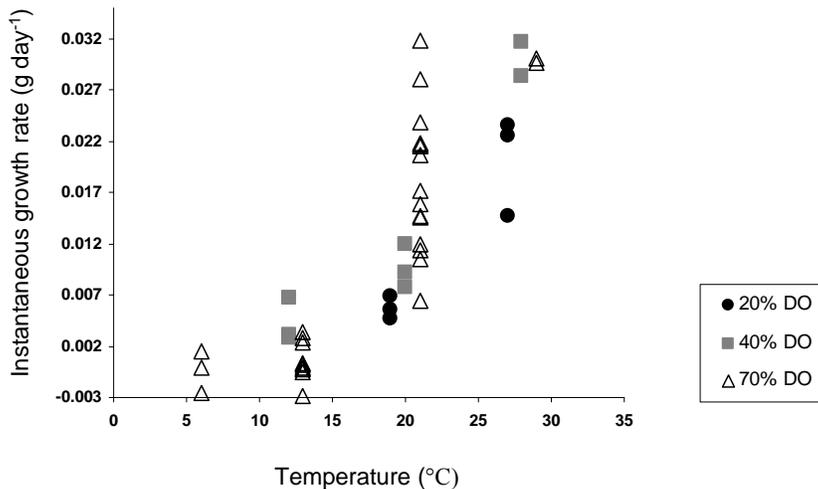


Figure 5. Instantaneous growth rates for YOY white perch at temperatures 6, 12, 20, and 28°C and percent dissolved oxygen saturation combinations of 20, 40, and $\geq 70\%$. Data points were offset slightly to aid presentation.

In analyses curtailed to summertime temperatures, 20°C and 28°C, both temperature ($F = 122.53$; $DF = 1, 13.7$; $p < 0.001$) and DO ($F = 21.14$; $DF = 2, 12.8$; $p < 0.001$) significantly affected growth rates but here again, the interaction between

temperature and DO was not significant ($p = 0.07$). Within each temperature treatment, lowest growth occurred at 20% DO_{sat} treatments followed by the 40% and then the $\geq 70\%$ DO levels, however, at 28°C there was no difference in growth between 40% and $\geq 70\%$ DO. Although the interaction was not significant, the difference between DO treatments was more pronounced at 28°C than at 20°C (Figure 6).

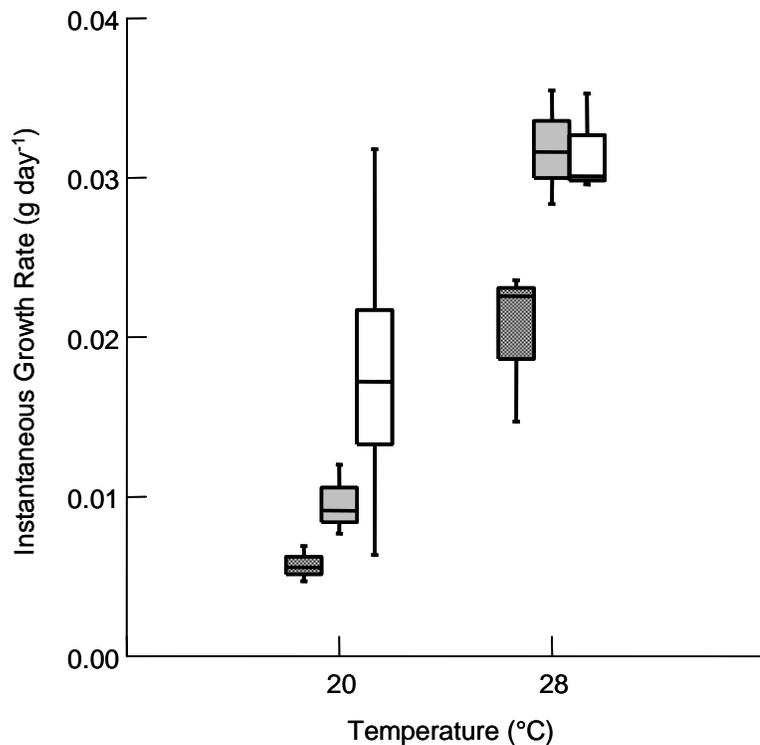


Figure 6. Instantaneous growth rates for YOY white perch at temperatures 20 and 28°C and percent dissolved oxygen saturations of 20% (black hatched boxes), 40% (grey filled boxes), and $\geq 70\%$ (unfilled boxes). Boxes indicate the median (horizontal line), the first and third quartiles (box edges), and ± 1.5 times the inner quartile range (whiskers).

The best fitted surface response equation for growth rate (GR) as a function of temperature (T) and DO was: $GR = -4.5 \times 10^{-4} * T + 4.4 \times 10^{-5} * T^2 + 5.4 \times 10^{-4} * DO -$

$5.8 \times 10^{-6} \cdot \text{DO}^2 + 9.7 \times 10^{-6} \cdot \text{T} \cdot \text{DO} - 1.5 \times 10^{-2}$. In general, growth rate was positively associated with temperature and DO, with highest growth rates (0.035 g day^{-1}) occurring at the warmest temperatures ($28 \text{ }^\circ\text{C}$) and highest DO levels ($\geq 70\%$ DO; Figure 7). The total model was significant ($F = 35.47$; $DF = 5$; $p < 0.001$) as were linear and quadratic functions ($F = 84.19$; $DF = 2$; $p \leq 0.001$ and $F = 3.97$; $DF = 2$; $p = 0.03$, respectively). Still, the lack of fit test was also significant ($F = 3.33$; $DF = 3$; $p = 0.03$), which may have been due to low degrees of freedom among treatment levels or fewer DO levels at low temperatures ($12 \text{ }^\circ\text{C}$) than at higher temperatures. Growth also appears to be more sensitive to changes in DO at higher temperatures than at lower temperatures. For instance, at $28 \text{ }^\circ\text{C}$, growth increased from 0.015 to 0.035 g day^{-1} between 20 and $\geq 70\%$ DO, but at $12 \text{ }^\circ\text{C}$ increased from 0.00 to 0.01 g day^{-1} across those same DO levels.

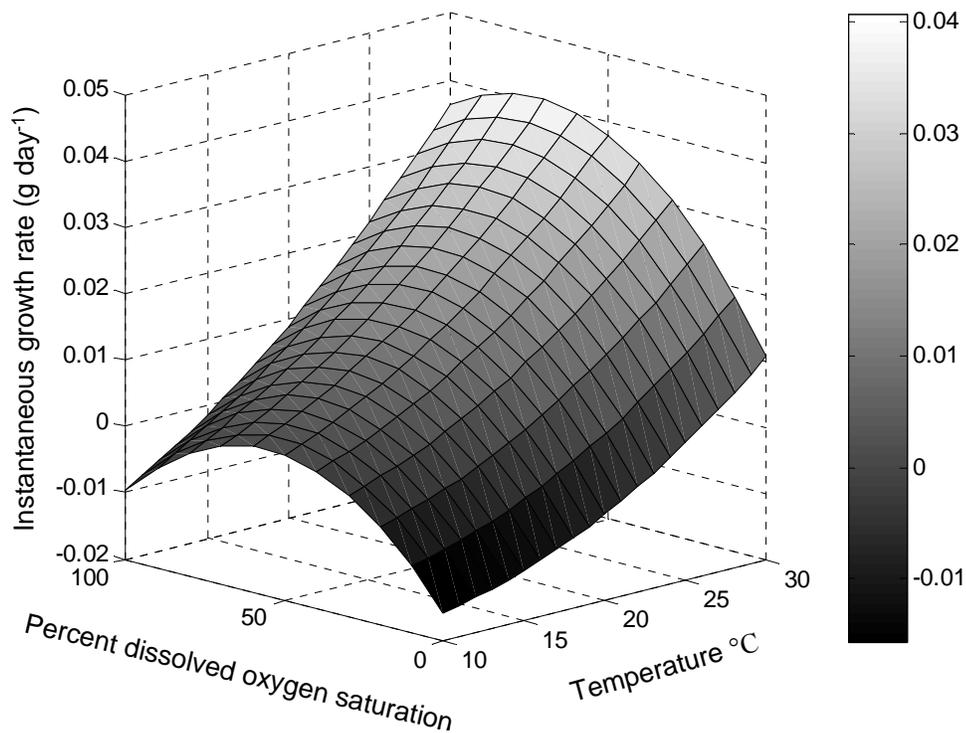


Figure 7. Instantaneous growth rate of YOY white perch as a function of temperature and dissolved oxygen. Surface contours are calculated from the equation given in the text.

Consumption

Consumption was significantly associated with temperature, DO and their interaction. Mean daily feeding rates ranged between 0.03 and 0.19 g g⁻¹ fish wt. The multiple linear regression model was significant ($F = 71.04$; $DF = 3$; $p < 0.001$) with a significant interactive effect ($F = 5.33$; $DF = 1$; $p < 0.05$). The model explained 84% of the variance and indicated that at higher temperatures, increased differences in feeding rate occurred among DO levels (Figure 8).

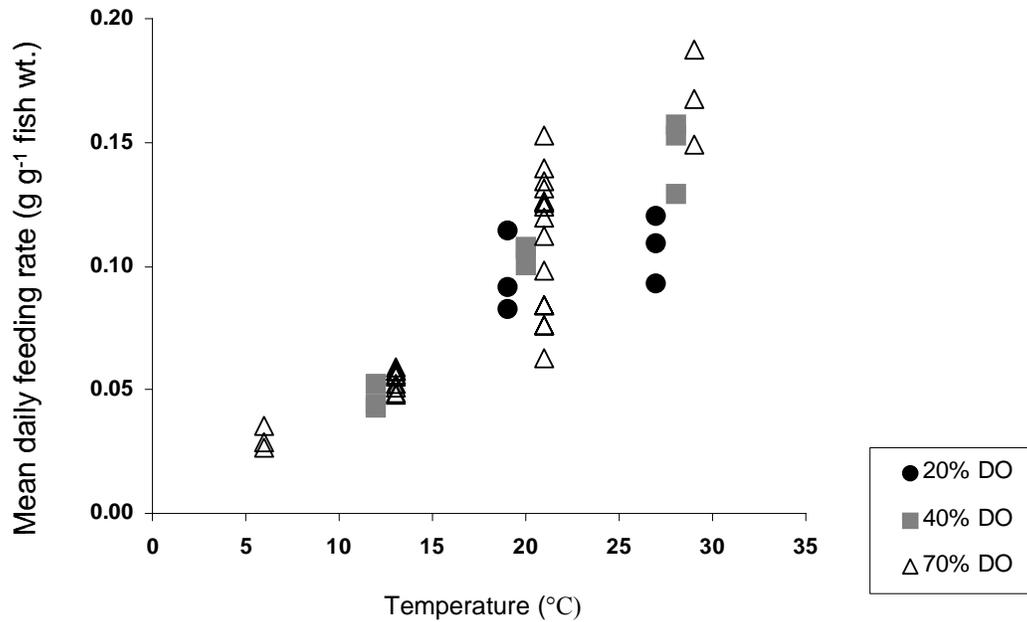


Figure 8. Mean daily feeding rates by YOY white perch at temperatures 6, 12, 20, and 28°C and percent dissolved oxygen saturation combinations of 20, 40, and $\geq 70\%$. Data points were offset slightly to aid presentation.

At summer temperatures (20 and 28°C), the significant main (T: $F = 30.38$; $DF = 1$, 12.8 ; $p < 0.001$; DO: $F = 10.54$; $DF = 2$, 12.4 ; $p = 0.002$) and interaction effects ($F = 4.22$; $DF = 2$, 12.4 ; $p = 0.04$) were maintained. Feeding rates were lowest at 20% DO followed by higher feeding rates at 40% and $\geq 70\%$. At 20°C these differences were not significant although the differences in feeding rates between the DO treatments were significant at 28°C (Figure 9).

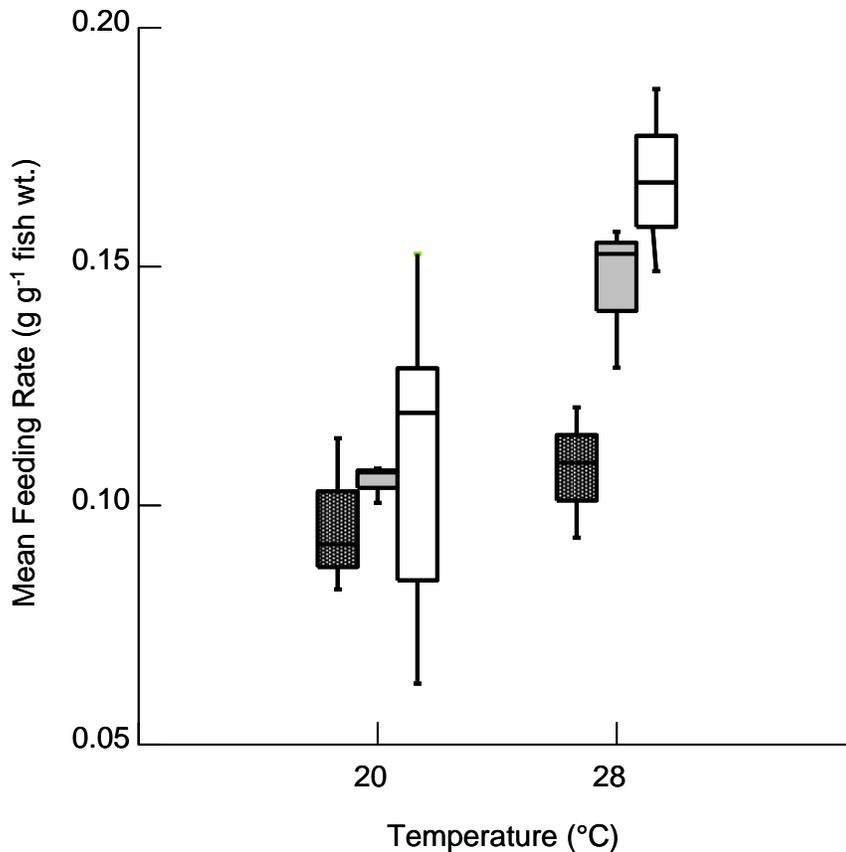


Figure 9. Mean daily feeding rates of YOY white perch at temperatures 20 and 28°C and percent dissolved oxygen saturations of 20% (black hatched boxes), 40% (grey filled boxes), and $\geq 70\%$ (unfilled boxes). Boxes indicate the median (horizontal line), the first and third quartiles (box edges), and ± 1.5 times the inner quartile range (whiskers).

The best fitted surface response equation for feeding rate (FR) as a function of temperature (T) and DO was: $FR = 7.8 \times 10^{-4} * T + 4.5 \times 10^{-5} * T^2 - 3.9 \times 10^{-4} * DO - 4.1 \times 10^{-6} * DO^2 + 6.2 \times 10^{-5} * T * DO + 3.6 \times 10^{-2}$. The total model was found to be significant ($F = 32.2$; $DF = 5$; $p < 0.001$) as well as the linear terms ($F = 78.27$; $DF = 2$; $p < 0.001$); the quadratic terms were not significant ($p = 0.5$). In contrast to the growth rate response surface, the lack of fit test was not significant ($p = 0.18$), indicating that quadratic terms were well fit to the data in predicting a maximum. Overall, feeding rate increased with increasing DO and temperature, with highest

feeding rates (0.19 g g^{-1} fish wt) occurring at the warmest temperature (28°C) and highest DO levels ($\geq 70\%$ DO). Feeding rate was more sensitive to changes in DO at warmer temperatures. Feeding rate increased from 0.09 to 0.19 g g^{-1} fish wt between 20 and $\geq 70\%$ DO at 28°C compared to 0.04 to 0.06 g g^{-1} fish wt at 12°C for the same DO levels (Figure 10).

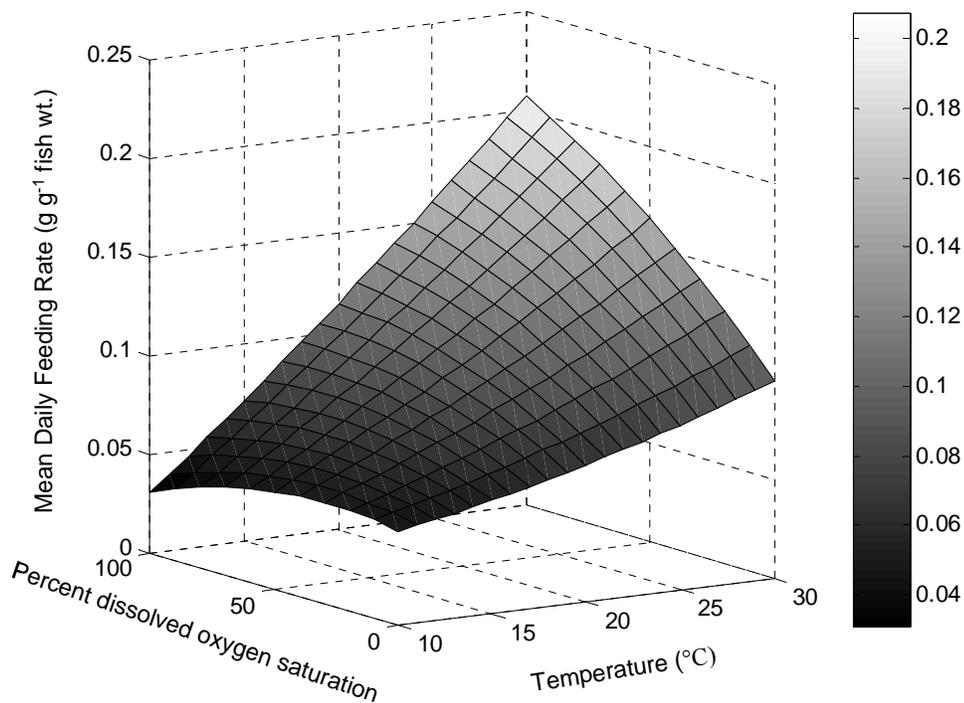


Figure 10. Mean daily feeding rate as a function of temperature and dissolved oxygen. Surface contours are calculated from the equation given in the text.

Consumption as a Function of Mass

Among YOY white perch between 3 and 9 grams, 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.

(interaction; $p = 0.53$; consumption: 0.20). A regression fitted to the data was not significant, indicating no relationship between weight and maximum consumption ($p = 0.4$; Figure 11). As a result, data was not adjusted for differences in fish size among experimental units.

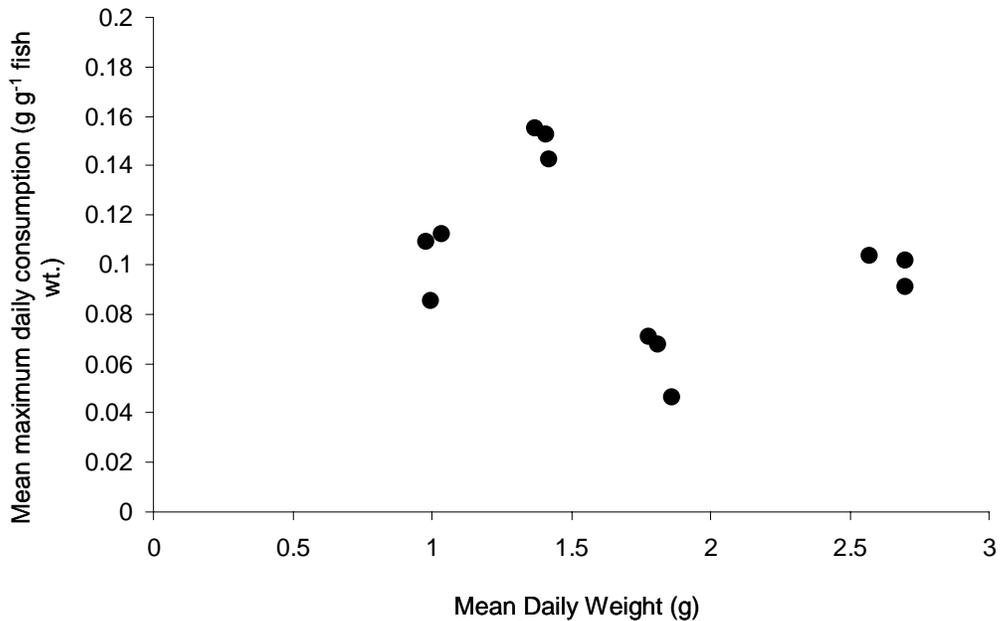


Figure 11. Mean daily fish weight versus maximum consumption relationship for YOY white perch. Four weight classes were looked at 3, 5, 6, 9 g reported here in dry weight units.

Gross Growth Efficiency

In general, growth gross efficiency was greater at higher temperatures and higher DO levels. At 20 and 28°C, gross growth efficiency was about 15% while at lower temperatures it declined to values close to zero (Figure 12).

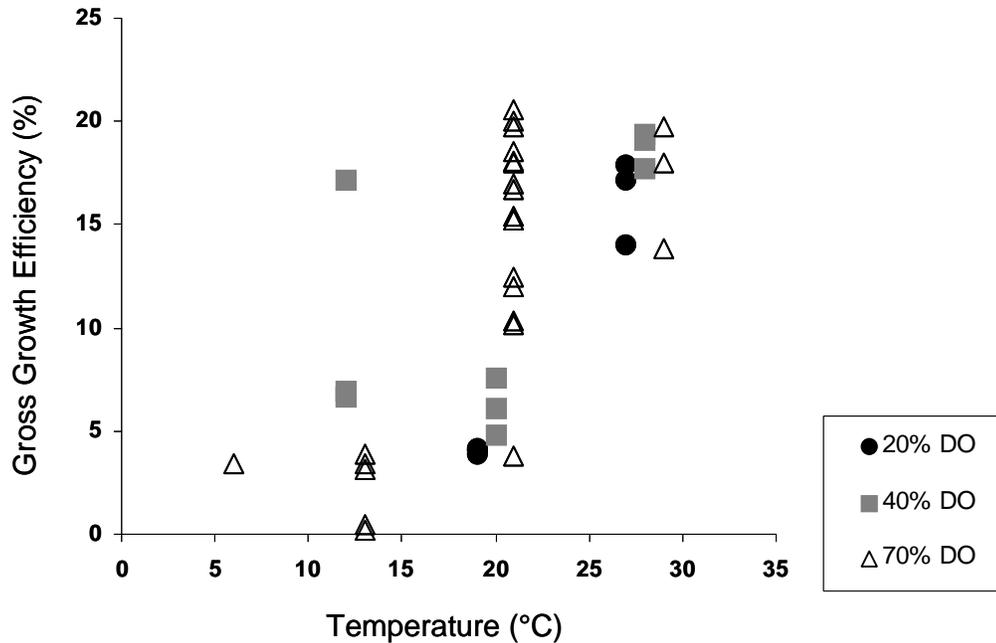


Figure 12. Gross growth efficiencies of YOY white perch at temperatures 6, 12, 20, and 28°C and percent dissolved oxygen saturation combinations of 20, 40, and $\geq 70\%$. Data points were offset slightly to aid presentation.

For summertime temperatures (20 and 28°C), temperature ($F = 105.96$; $DF = 1, 13.3$; $p < 0.001$), DO ($F = 15.56$; $DF = 2, 15.3$; $p < 0.001$), and their interaction ($F = 15.3$; $DF = 2, 13.3$; $p < 0.001$) significantly influenced gross growth efficiency. At 20°C, greater variability was observed between DO treatments, ranging from 4% growth efficiency at 20% DO to 15% growth efficiency at $\geq 70\%$ DO. In contrast, at 28°C, gross growth efficiencies ranged from 16 to 18% over the same DO range. Gross growth efficiency is a ratio of growth over consumption. Therefore, a fish that is not feeding and growing at a slow rate can have the same ratio of a fish that experiences equivalent rates of high growth and consumption. For instance, one fish at 20% DO and 28°C consumed 0.46 g and grew 0.09 g resulting in a gross growth efficiency of 18%. Alternatively, a fish at $\geq 70\%$ DO and at 28°C consumed 0.84 g food and grew 0.15 g which leads to the same gross growth efficiency of 18%, even though the fish

grew and consumed almost twice as much (Figure 13). Recall that gross growth efficiency is an index of energy assimilation rather than overall metabolic performance.

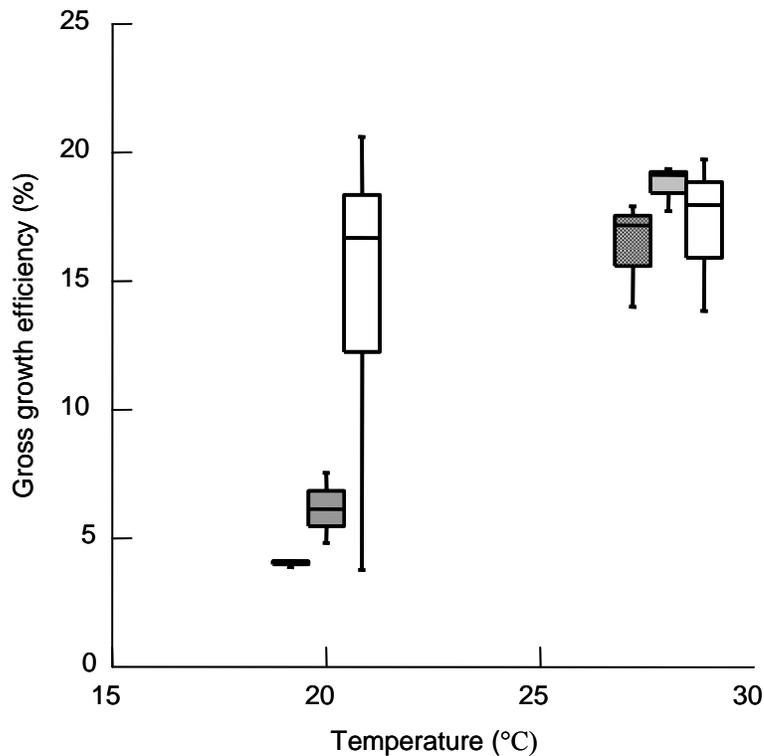


Figure 13. Gross growth efficiencies of YOY white perch at temperatures 20 and 28°C and percent dissolved oxygen saturations of 20% (black hatched boxes), 40% (grey filled boxes), and $\geq 70\%$ (unfilled boxes). Boxes indicate the median (horizontal line), the first and third quartiles (box edges), and ± 1.5 times the inner quartile range (whiskers).

Routine Metabolism

Routine metabolism was significantly associated with temperature and the interaction between temperature and DO. Temperature explained 48% of the variance in oxygen consumption rates (T: $F = 10.96$; $DF = 1$; $p = 0.001$; Interaction: $F = 8.49$; $DF = 1$; $p = 0.004$). Oxygen consumption rates ranged from 10.85 to 58.63 $\text{mg O}_2 \text{ g}^{-1} \text{ day}^{-1}$ with highest values at higher temperatures (Figure 14).

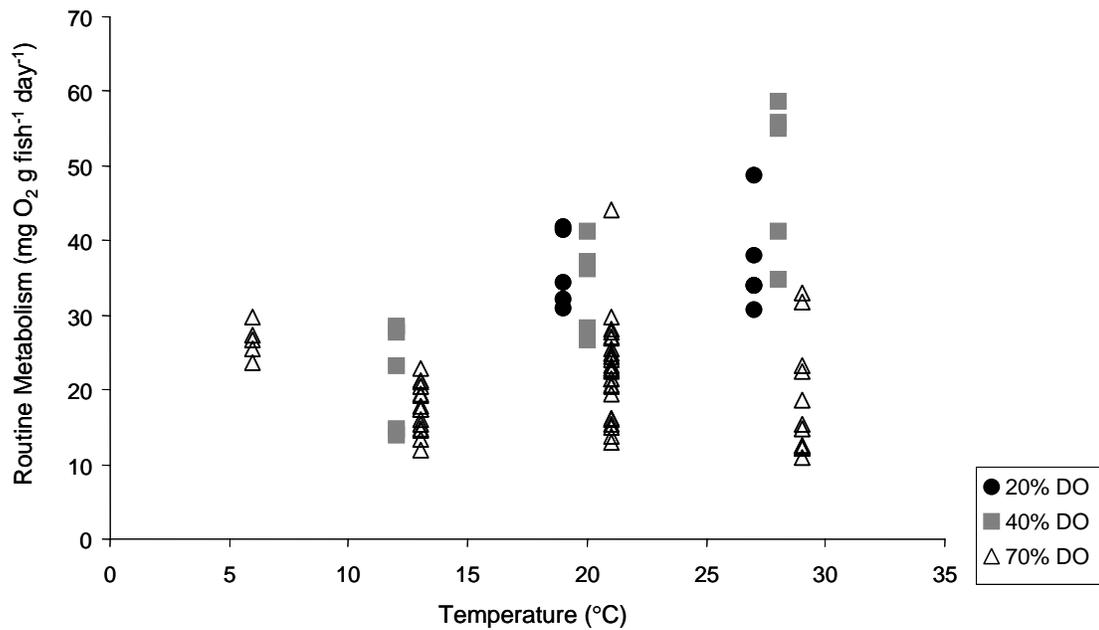


Figure 14. Oxygen consumption of YOY white perch at temperatures 6, 12, 20, and 28°C and percent dissolved oxygen saturation combinations of 20, 40, and $\geq 70\%$. Data points were offset slightly to aid presentation.

At summer temperatures of 20 and 28°C, DO significantly affected oxygen consumption ($F = 37.04$; $DF = 2, 28.3$; $p < 0.001$) as well as the interaction between temperature and DO ($F = 5.97$; $DF = 2, 28.3$; $p = 0.007$). Oxygen consumption showed a more pronounced difference between DO levels at 28°C, with a range of 10.9 to 41.2 mg O₂ g fish⁻¹ day⁻¹. At 20°C the difference between DO levels was much less ranging from 12.9 to 24.4 mg O₂ g fish⁻¹ day⁻¹ (Figure 15).

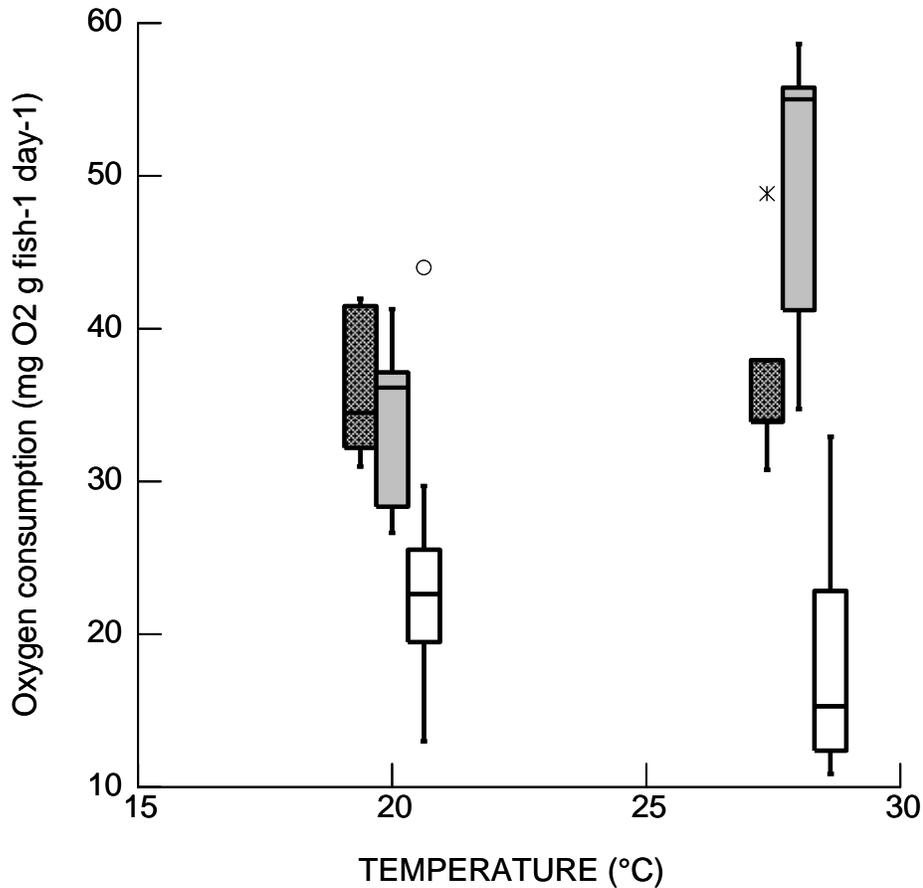


Figure 15. Oxygen consumption for summertime treatments 20 and 28°C and percent dissolved oxygen saturations of 20% (black hatched boxes), 40% (grey filled boxes), and $\geq 70\%$ (unfilled boxes). Boxes indicate the median (horizontal line), the first and third quartiles (box edges), and ± 1.5 times the inner quartile range (whiskers).

The fitted surface response equation for routine metabolism (RM) as a function of temperature (T) and DO was: $RM = 2.7 \cdot T - 6.1 \times 10^{-3} \cdot T^2 + 1.9 \cdot DO - 1.5 \times 10^{-2} \cdot DO^2 - 3.6 \times 10^{-2} \cdot T \cdot DO - 39.4$. The total model was significant ($F = 18.22$; $DF = 5$; $p < 0.001$) as well as the linear, quadratic, and cross-product functions ($F = 34.99$; $DF = 2$; $p < 0.001$; $F = 3.13$; $DF = 2$; $p = 0.05$; $F = 14.88$; $DF = 1$; $p < 0.001$ respectively). There was a significant lack of fit of the model however ($F = 9.82$; $DF = 3$; $p < 0.0001$), which is again likely due to low statistical power or biased distribution of DO treatments levels occurring at the lowest temperatures (12°C). In general, routine

metabolism increased with increasing temperature and decreasing DO levels. The highest routine metabolism ($58.6 \text{ mg O}_2 \text{ g fish}^{-1} \text{ day}^{-1}$) occurred at 28°C and $40\% \text{ DO}_{\text{sat}}$. Similar to growth and feeding rates, routine metabolism appears to be more sensitive to changes in DO at higher temperatures than at lower temperatures (Figure 16).

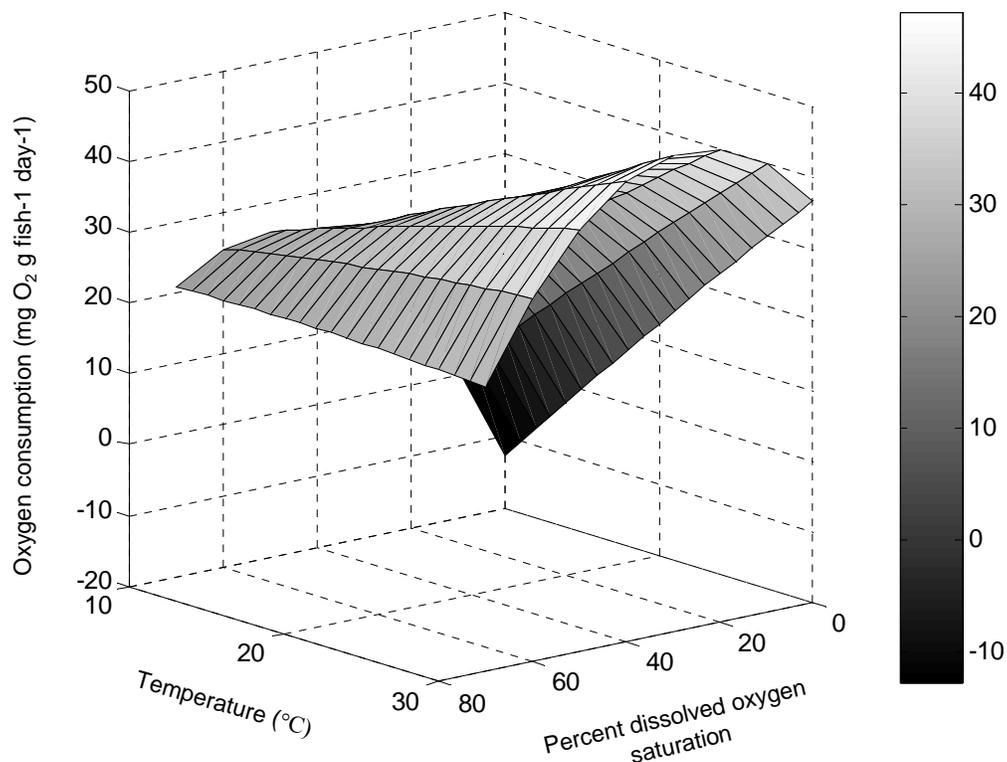


Figure 16. Mean oxygen consumption as a function of temperature and dissolved oxygen. Surface contours are calculated from the equation given in the text.

Calorimetry

In general, energy density increased with increasing DO levels. Energy densities ranged from 21.61 to 23.89 KJ g^{-1} dry weight across temperature and DO treatments with highest values at high DO saturations. A multiple linear regression

analysis indicated that DO significantly affected energy densities ($F = 14.38$; $DF = 1$; $R^2 = 0.18$; $p < 0.001$). Neither temperature nor its interaction with DO significantly influenced energy density (Figure 17).

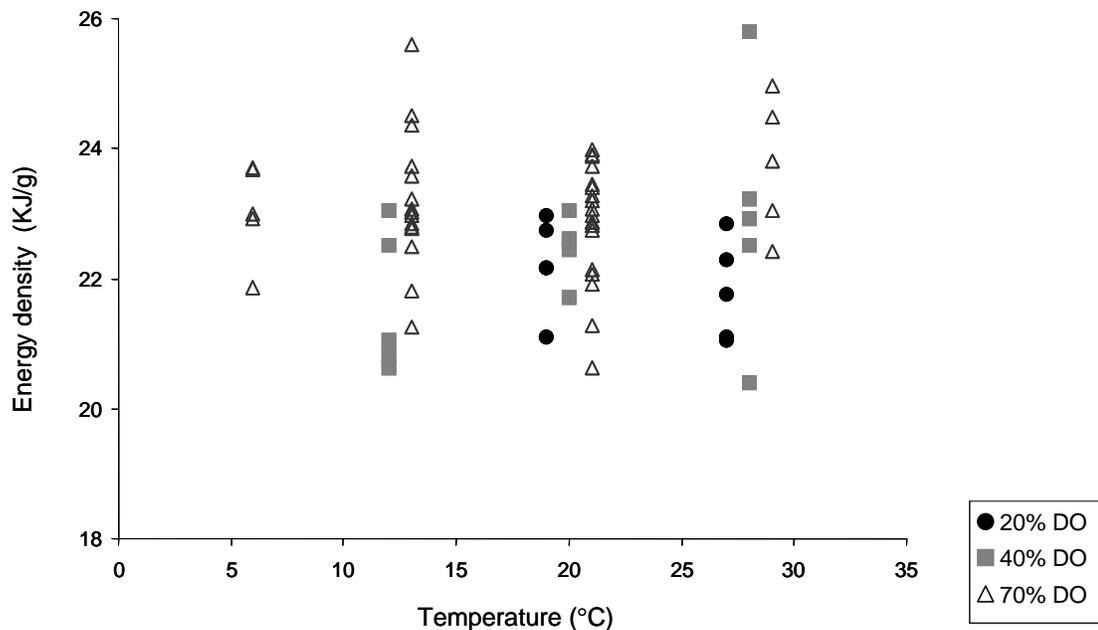


Figure 17. Energy density of YOY white perch at temperatures 6, 12, 20, and 28°C and percent dissolved oxygen saturation combinations of 20, 40, and $\geq 70\%$. Data points were offset slightly to aid presentation.

In analyses looking at summer temperatures of 20 and 28°C, DO significantly affected energy densities ($F = 4.39$; $DF 2, 39$; $p = 0.02$). Again, neither temperature nor the interaction between temperature and DO was significant. Within each temperature treatment, lowest energy density occurred at 20% DO_{sat} treatments followed by 40% and then 70% DO (Figure 18). To determine if there was a positive relationship between conversion efficiency and energy density, I performed a correlation analysis. No significant relationship was found ($p = 0.62$).

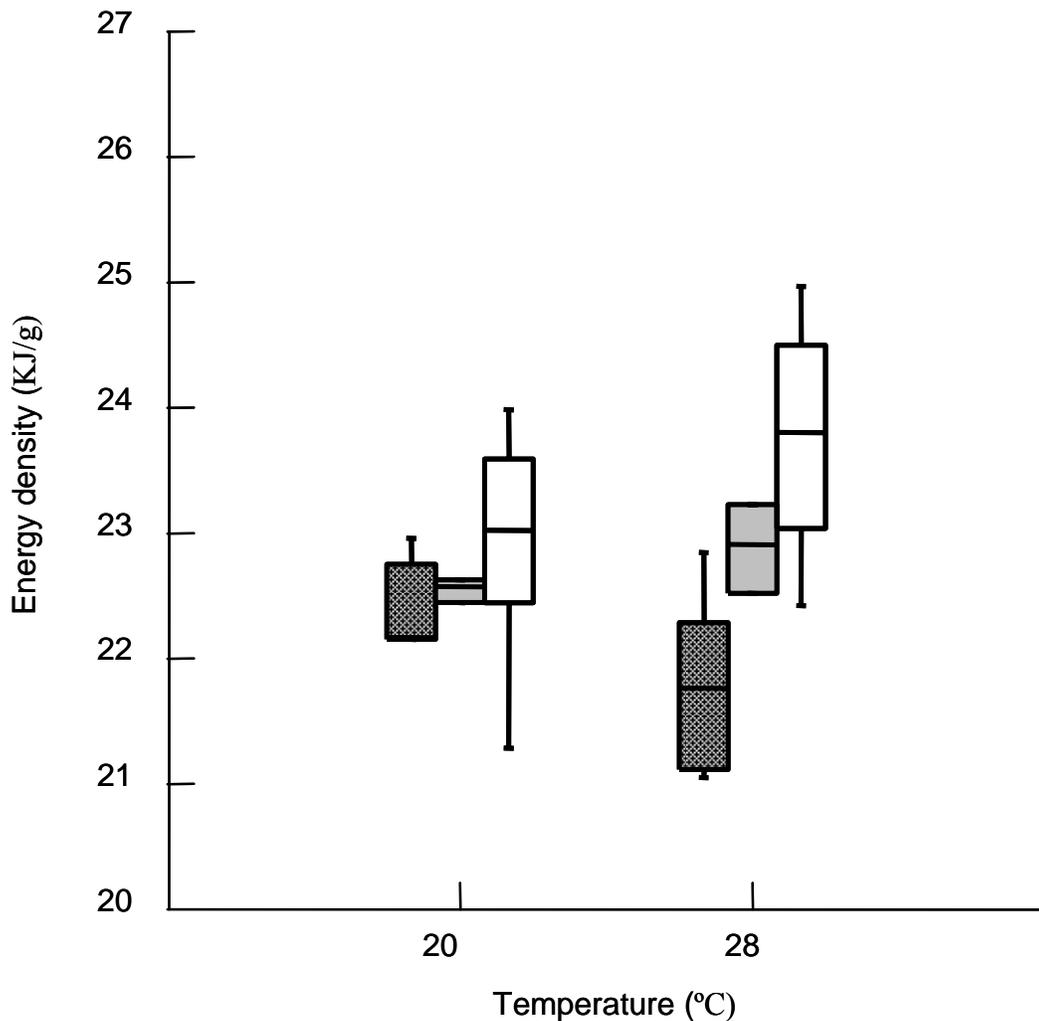


Figure 18. Energy Densities of juvenile white perch for summertime treatments 20 and 28°C and percent dissolved oxygen saturations of 20% (black hatched boxes), 40% (grey filled boxes), and $\geq 70\%$ (unfilled boxes). Boxes indicate the median (horizontal line), the first and third quartiles (box edges), and ± 1.5 times the inner quartile range (whiskers).

Egestion

Egestion was significantly associated with temperature ($F = 18.28$; $DF = 2$, 12 ; $p < 0.001$), but not DO ($p = 0.57$) or their interaction ($p = 0.40$). Egestion as a proportion of consumption ranged from 0.03 to 0.07. No distinction could be made

between the DO treatments. Egestion increased between 12 and 20°C and decreased from 20 to 28°C (Figure 19).

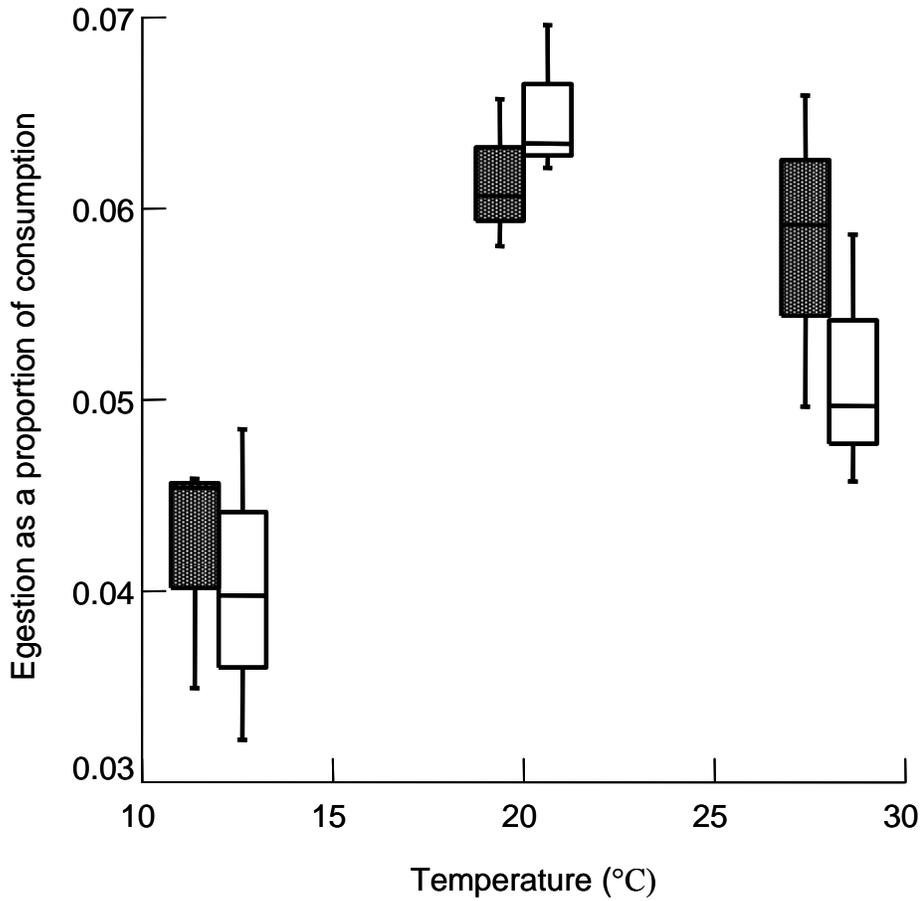


Figure 19. Egestion rates for YOY white perch at 40% dissolved oxygen levels (shaded bars) and $\geq 70\%$ dissolved oxygen levels (open bars) across three different temperatures (12, 20, and 28°C). Boxes indicate the median (horizontal line), the first and third quartiles (box edges), and ± 1.5 times the inner quartile range (whiskers).

Energy Budgets

Energy allocated towards growth increased with increasing temperatures. Energy for growth at 12°C ranged from 0 to 0.09 KJ across DO levels, which corresponded to 0-20% of the overall energy consumed. Conversely, energy for

growth at 28°C ranged from 0.51 to 0.97 KJ across DO levels, which represented 42-52% total consumed energy. Within each temperature treatment, energy for growth generally increased with increasing DO level. This was evident for total energy consumed as well. Energy allocated towards routine metabolism ranged from 0.26 KJ at 28°C and $\geq 70\%$ DO_{sat}, to 0.69 KJ at 28°C and 40% DO. In general, % energy allocated towards routine metabolism decreased with increasing DO saturation (Figure 20). Very little (<2%), if any, energy remained for feeding metabolism (SDA) and active metabolism at 28°C for 20 and 40% DO_{sat} (Figure 20). The constructed energy budgets probably under-estimate SDA as this typically ranges between 9-16% (Hanson et al. 1997). This may have occurred due to an overestimation of routine metabolism. Although no mortality was seen for DO treatments of 20 and 40% at 28°C, the very high routine metabolism values could suggest a stress response. Similarly, high estimates for routine metabolism could have led to the relatively few instances where total energy allocations exceeded 100% (Figure 20). Still, the departures from 100% are relatively small and are within what would be expected for experimental error. Modeled proportion for excretion may have also resulted in total energy allocations exceeding 100%. Finally, the energy estimate for egestion was taken from the center treatment of 20°C, 4 salinity, and $\geq 70\%$ DO; and could have biased application at lower DO levels.

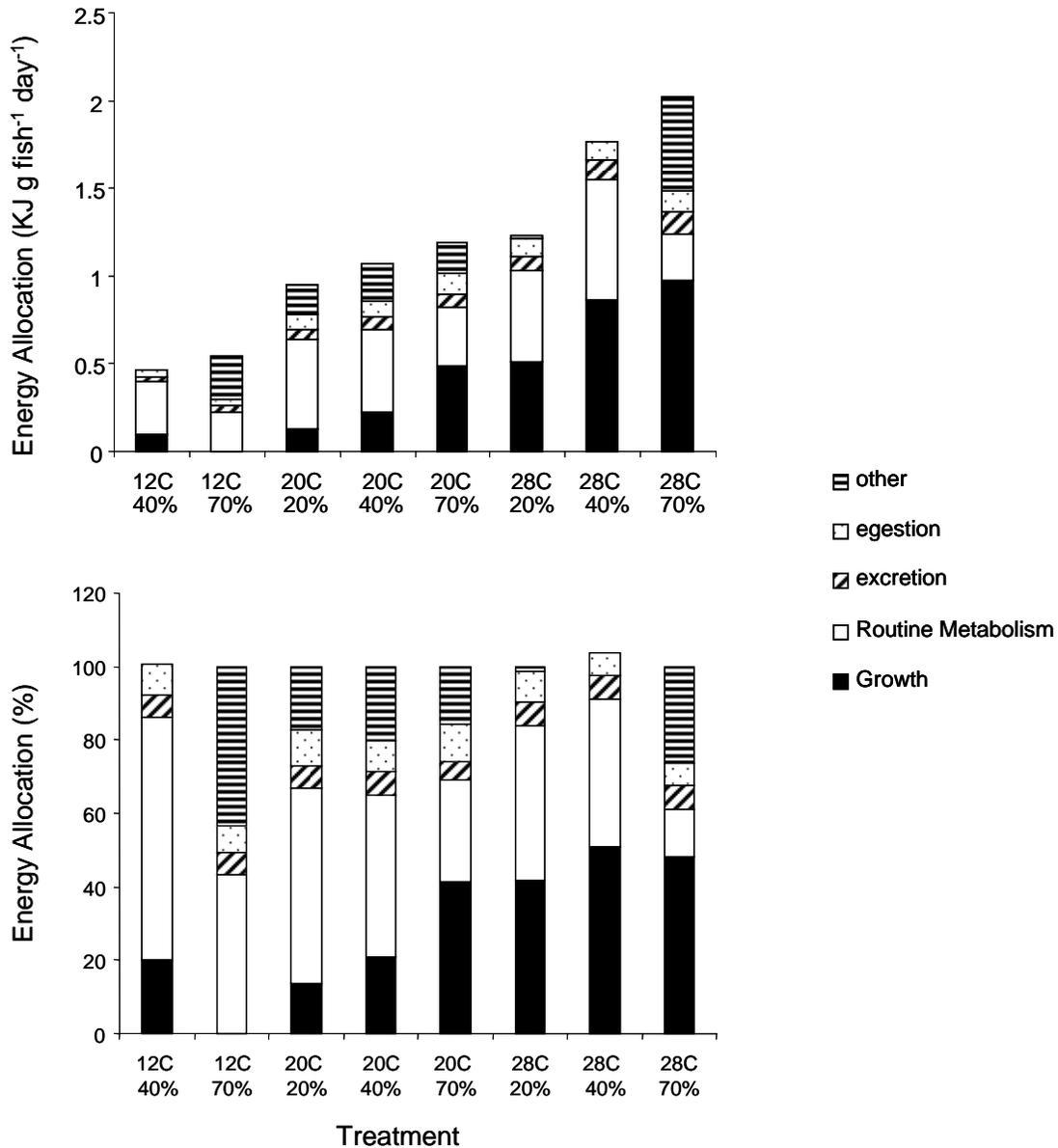


Figure 20. YOY white perch energy budgets for eight different treatments. Top graph shows total energy allocation in KJ g fish⁻¹ day⁻¹. Bottom graph is percent of total energy allocation. Temperatures are 12, 20 and 28°C and percent dissolved oxygen levels are 20, 40, and ≥70%.

Parameter Validation

Experimental growth rates ranged from 0.0071 to 0.0359 in g day⁻¹ while field growth rates ranged from -0.0029 to 0.0259 g day⁻¹. Average growth rates for the Potomac (0.02 g day⁻¹) and the Patuxent (0.01 g day⁻¹) were more similar to

experimental growth rates at 20°C (0.01 g day⁻¹) than experimental growth rates at 28°C (0.03 g day⁻¹; Figure 21). To determine if there were significant differences between the experimental and field growth rates, I performed a one-way analysis of variance using the 28°C experimental growth rate data and the Potomac growth rate data since there was greater overlap in temperature between the two. The growth rates significantly different (F = 56.71; DF = 1, 25; p < 0.001). I would expect that experimental growth rates would be higher than field growth rates as experimental fish were fed twice a day *ad libitum*. Based upon the energy budget developed for 28°C, ≥70% DO, and salinity of 4 and an average Potomac growth rate of 0.02 g day⁻¹, I estimated a total consumption of 0.91 for wild juveniles, 63% of the value obtained for experimental fish.

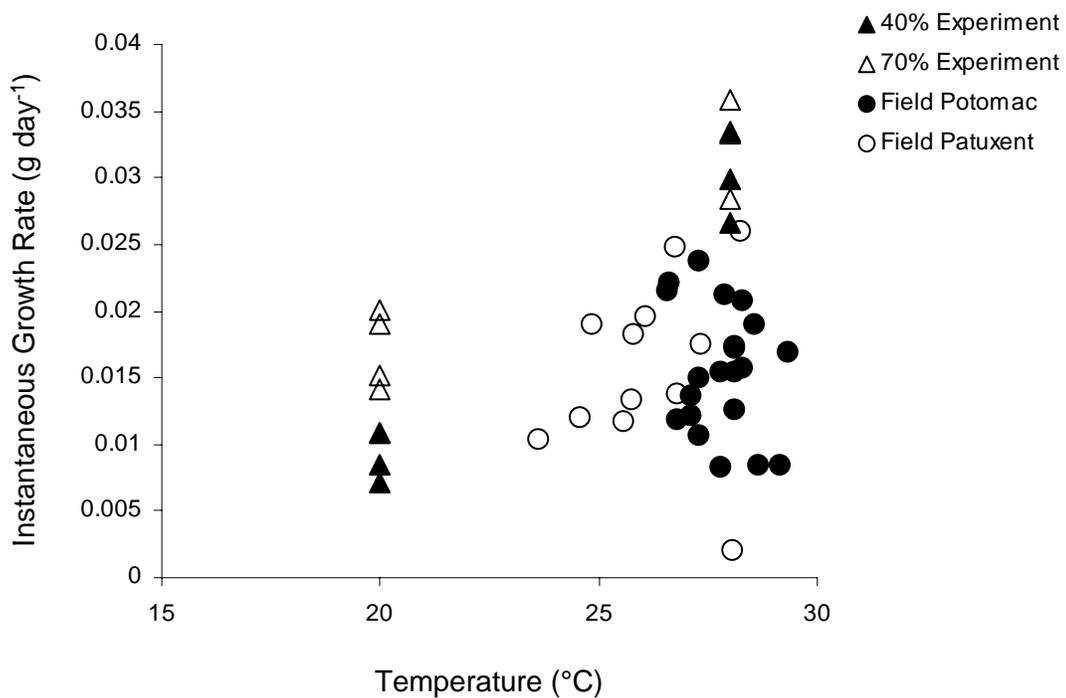


Figure 21. Experimentally and field derived instantaneous growth rates of YOY white perch. Field growth rates were measure from two sub-estuaries of the Chesapeake Bay: the Potomac and the Patuxent. Experimental Data looked at temperatures treatments 20 and 28 °C and dissolved oxygen treatments 40 and ≥70%.

Discussion

In this study, YOY white perch exhibited a broad range of physiological responses to temperature and DO, but not salinity. White perch increased growth and feeding in warmer, more oxygenated waters. In hypoxic environments, white perch experienced increased respiratory cost and decreased growth and feeding. The results suggest that estuarine gradients in temperature and DO but not salinity have strong influences on habitat suitability as measured by scope for growth.

Salinity Effects

Contrary to my hypothesis that YOY white perch would experience greatest growth and feeding at oligohaline (0.5-5) salinities, preliminary results revealed no significant effect of salinity on growth or feeding. These results agree with studies performed on juvenile striped bass from South Carolina (Secor et al. 2000) and bluefish (Buckel et al. 1995) but differ from studies performed on white perch (Kerr and Secor in press), Maryland striped bass (Secor et al. 2000), juvenile weakfish (Lankford and Targett 1994), juvenile turbot (Imsland et al. 2001), juvenile fat snook (Rocha et al. 2005), juvenile green sturgeon (Allen and Cech 2007), and a number of other estuarine species including channel catfish, goldfish, rainbow and brown trout, striped bass, and Gulf sturgeon, all of which show significant differences in physiological performance under salinity gradients (Altinok and Grizzle 2001; Table 1).

Salinity can interact with above-optimal temperature to negatively impact metabolic processes such as routine metabolism (Wuenschel et al. 2004b). On the

other hand, similar to results observed here, other studies failed to detect a significant interaction with temperature and salinity (Buckel et al. 1995; Niklitschek and Secor in press). The effect of salinity remains unclear, perhaps due to confounding effects of taxonomic or life-stage specific effects (Morgan and Iwama 1991). For example, Secor et al. (2000) found that salinity tolerance differed among genetic strains of striped bass with a Maryland striped bass strain showing a physico-chemical preference for oligohaline salinities (7) while no salinity preference was seen in a South Carolina strain.

A possible explanation for limited or nil salinity effects could stem from the euryhaline nature of white perch. Most species studied thus far (Table 1) have been facultative estuarine fishes. White perch in Chesapeake Bay are obligate estuarine fish and therefore, would have adapted to variable salinity conditions common to estuaries. As a result, white perch may not exhibit the same range of physiological responses to salinity as facultative users. Secondly, the range of salinity evaluated here may have been insufficient to elicit a response. At salinities ≥ 16 , physiological responses might have been detected. In experiments on the congeneric white bass (*Morone chrysops*), Heyward et al. (1995) found that fish reared in salinities of 12 and below were significantly larger than fish reared at salinities of 16 and 20. Similarly, Bardonnnet and Jatteau (2008) looked at Allis shad (*Alosa alosa*) salinity tolerance for salinities ranging from 0 to 30. While Allis shad could easily handle intermediate salinity conditions (salinity of 10 and less), they showed very low survival rates at higher salinities of 20 and 30. This study only looked at the salinity range at which Chesapeake Bay white perch are normally seen (0-13; Setzler-

Hamilton 1991). Further studies need to be done to determine if this range is determined by energetics or whether other factors such as increased predation pressure keep white perch from higher salinity habitats.

Temperature Effects

Temperature appeared to drive patterns in growth, feeding, and egestion rates. From 6°C to 28°C, average instantaneous growth rates increased from slightly negative growth rates to 0.28 g d⁻¹. Higher growth rates were due to higher consumption which increased over 4-fold from 0.03 to 0.14 g g⁻¹ fish wt between 6 and 28°C but also due to an increase in conversion efficiency which increased from 0 to 17% over the same temperature range. Between temperatures 20 and 28°C, gross growth efficiencies ranged from 10-20%, which was moderately less than for weakfish, which ranged 14-26% at the same temperature range (Lankford and Targett 1994) and substantially less for bluefish juveniles, measured at 20-28% for a temperature range of 18-24°C (Buckel et al. 1995). Brett and Groves (1979) noted that gross growth efficiencies for juvenile fishes typically range between 10 and 25% depending on environmental conditions, which conform to the results reported here. Interestingly, I observed no difference in energy density associated with temperature.

Super-optimal responses were not detected for the highest temperature level tested (28 C). Without evidence of declining growth at higher temperatures, maximum growth rates cannot be predicted. Similarly, feeding rates and gross growth efficiency also continued to increase at the highest temperature treatment. These results could suggest that white perch are well adapted to thermal conditions in the Chesapeake Bay, where summer water temperatures can reach 29°C (Chesapeake Bay

Program http://www.chesapeakebay.net/status_weather.aspx? Menu item=19787). At the other extreme, the lower limit for positive growth for YOY white perch was estimated to be approximately 12°C ($5.8 \times 10^{-4} \text{ g day}^{-1}$) as no positive growth was detected at 6°C ($-3.8 \times 10^{-4} \text{ g day}^{-1}$).

Temperature had a significant effect on egestion and routine metabolism. Egestion increased from 12°C to 20°C and then decreased from 20 to 28°C. A similar response was seen in gut evacuation rates of walleye larvae, which showed a thermal optimum at 20°C (Johnston and Mathias 1996). I measured an average egestion rate of 8% of total energy intake across treatments. This is similar to proportions developed by Hartman and Brandt (1995a) for juvenile striped bass (10% of total energy intake) as well as comparable to what has been reported for juvenile Atlantic sturgeon (10%, Niklitschek and Secor in press). My egestion estimate for the center treatment at $\geq 70\%$, 20C, and 4 salinity was 10% of the total energy intake. However, for treatments with higher and lower temperatures as well as treatments with lower DO, egestion estimates were less. Routine metabolism decreased by a factor of 1.5 from 6 to 28°C at $\geq 70\%$ oxygen saturation. This is contrary to the prevailing view and supporting literature which indicates that increasing temperature accelerates metabolism (Fry 1971). For instance, studies on routine metabolism have detected increases of 5-fold for round goby (Lee and Johnson 2005) or 2.5-fold for European sea bass (Claireaux and Lagardere 1999) between winter and summer time oxygen consumption.

Dissolved Oxygen Effects

Fry (1971) described oxygen as a limiting factor: a reduction in oxygen should depress the metabolic rate beyond a threshold effects level. Accordingly, I observed that growth rate decreased with decreasing oxygen saturation below 40%. At 20°C growth rates declined 3-fold from 0.018 g d⁻¹ at ≥70% DO to 0.006 g d⁻¹ at 20%. On the other hand, at 28°C, growth rates declined 33% (0.03 to 0.02 g d⁻¹) between ≥70 and 20%. For white perch, a threshold DO level probably occurs between 20 and 40% DO at warmer temperatures and between 70 and 40% at cooler temperatures. Similar to white perch, low DO saturation has been shown to significantly decrease growth in Atlantic sturgeon (Secor and Gunderson 1998; Niklitschek and Secor in press), channel catfish (Buentello et al. 2000), mummichog (Stierhoff et al. 2003), juvenile spot, and Atlantic menhaden (McNatt and Rice 2004). However, species show large differences in their tolerance to low DO. Atlantic sturgeon experienced a decrease in growth with DO levels below ≥70% (Secor and Gunderson 1998; Niklitschek and Secor in press); channel catfish showed decreases in growth around a DO saturation of 30%, while species such as spot, menhaden and mummichog which have very high hypoxia tolerances exhibited growth effects at about 10-15% DO saturations (Buentello et al. 2000; Stierhoff et al. 2003; McNatt and Rice 2004).

The lack of growth at low DO saturation can be explained in part by decreased feeding rates, increased routine metabolism, and decreased gross growth efficiency. Lowest feeding rates were observed at 20% DO, followed by 40% and then ≥70%. At 20°C, feeding rates ranged from 0.096 at 20% DO to 0.11 g g⁻¹ fish weight at ≥70% DO while at 28°C feeding rates increased 2-fold from 0.1 to 0.2 g g⁻¹ g fish

weight over the same DO range. Reduced feeding in response to hypoxia has been reported for several studies (Stierhoff et al. 2006; Niklitschek and Secor in press) and could indicate a behavioral strategy for conserving energy and maximizing metabolic scope under hypoxic conditions (Brett and Groves 1979). Gross growth efficiencies ranged from 4-15% at 20°C and from 16-19% at 28°C. While not apparent in gross growth efficiency responses, white perch are experiencing very different metabolic demands between DO levels. This is readily seen in routine metabolism values between DO levels. At 20°C, oxygen consumption increased from 22.67 to 36.22 mg O₂ g⁻¹ fish day⁻¹ from ≥70% to 20% DO, and at 28°C this range increased with values of 18.82 to 49.08 mg O₂ g⁻¹ fish day⁻¹ over the same DO range. Low gross growth efficiencies combined with high oxygen consumption values indicated an increase in maintenance requirements. Wuenschel et al. (2005) observed a similar response in grey snapper in response to salinity rather than oxygen stress.

I did not detect a strong effect of hypoxia on egestion. Niklitschek and Secor (in press) observed that under hypoxic conditions, Atlantic sturgeon increased egestion and decreased post-prandial metabolism which indicates a decrease in assimilation to compensate for a decrease in metabolic scope. White perch might be slightly more tolerant than sturgeon to low DO, or perhaps this study lacked the statistical power to detect a difference in egestion among DO levels.

Low DO also significantly decreased energy density, with lowest values at 20% DO saturation. Energy densities ranged from 5724 J/wet weight to 6331 J/wet weight. These values are comparable to energy densities calculated by Hartman and Brandt (1995b) for weakfish (6467 J/wet weight), striped bass (6858 J/wet weight),

bluefish (6077 J/wet weight) but were higher than those they measured for bay anchovy (4832.95 J/wet weight) as well as for those measured by Wuenschel et al. (2006) for gray snapper (4491 J/wet weight) and spotted seatrout (4248 J/wet weight). These values correspond to a percent dry weight of 26.5% which is the average percent dry weight of the white perch in this study. While previous studies have detected ontogenetic (Wuenschel et al. 2006), seasonal (Flath and Diana 1985), and spatial (Schultz and Conover 1997) variation in energy densities, few or no studies have studied the effect of hypoxia on energy densities. Although I did not detect an effect of hypoxia on egestion, a decrease in assimilation could account for the lower energy densities at low DO levels. Reduced consumption could have also contributed to lower energy densities.

Temperature and Dissolved Oxygen Interaction

The response surface analysis of growth indicated that warmer temperatures increased sensitivity to low DO. The lack of a significant fit could be due to low degrees of freedom or an unbalanced experimental design in which not all DO treatment levels occurred at lower temperatures. Significant interactive effects of temperature and DO on juvenile growth have been reported for several other estuarine species including Atlantic menhaden (McNatt and Rice 2004), Atlantic sturgeon (Niklitschek and Secor in press), summer flounder, and winter flounder (Stierhoff et al. 2006).

Feeding rates as well as oxygen consumption showed a significant interaction between DO and temperature. Feeding rates at 20°C were not significantly different between DO levels although consumption rates were ordered lowest to highest at

20%, 40%, and $\geq 70\%$. At 28°C the differences in feeding rates between DO levels were significant. Routine metabolism also showed a wider spread between DO treatments at 28°C than at 20°C. Significant interaction between temperature and DO saturation suggests that at warmer temperatures greater energy expenditure is required, and as a result, the limiting oxygen threshold is reached sooner (Claireaux and Lagardere 1999). Metabolic depression in the form of reduced consumption and decreased activity is an effective survival strategy (Dalla Via et al. 1994), but could ultimately lead to reduced growth, condition, and increase the possibility of predation. A three-fold decrease in growth rate, for instance, as seen between the 70 and 20% DO treatments could affect recruitment by keeping small juveniles vulnerable to predation for much longer. Further, decreased scope for metabolism due to higher basal metabolism under hypoxia, will mean less energy will be available to evade and escape predators. Therefore, hypoxia not only reduces habitat quality for juvenile growth but also may have consequences to survival and recruitment.

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.” During summer cooler bottom waters are hypoxic, but warmer surface waters may be super-optimal: elevating metabolic rates and increasing oxygen demand. The result is a “squeeze” - a narrow habitat range of suitable habitat. Studies have shown that estuarine organisms such as weakfish, spot, pinfish, croaker, menhaden, white mullet, and brown shrimp will choose to avoid hypoxic areas and move into more energetically favorable habitats (Wannamaker and

Rice 2000; Tyler and Targett 2007). However, this migration to suitable habitats could lead to overcrowding, an increase in inter- and intraspecific competition, and an increase in predator encounters. Other food-web relationships could also be affected as a result of changes in predation patterns and abundances of predators and prey (Breitburg et al. 1997). The net result of migration and mortality due to hypoxia is an overall decrease in diversity, abundance, and production of fish within those affected areas (Breitburg 2002).

Previously, it has been thought that young-of-year white perch would be less affected by the temperature-oxygen squeeze since juveniles have a higher thermal tolerance than adults and occupy shoal waters that are not subjected to stratification, and therefore hypoxia (Coutant 1985, Breitburg et al. 2003). However current Chesapeake Bay data show that even shallow, littoral habitats show large, diurnal fluctuations in dissolved oxygen saturation (<http://mddnr.chesapeakebay.net/eyesonthebay/index.cfm>), similar to that noted in other mid-Atlantic estuaries (Tyler et al. 2009). This new information indicates that even less area is available for juvenile habitat and refugia and that such habitat is energetically less favorable. In addition to the direct effects of hypoxia, young-of-the-year white perch are also subjected to the indirect effects of crowding, inter- and intraspecific competition, and an increase in predator encounters as older, adult fish move into shoal waters to avoid hypoxic, deeper water.

Not only do areas of low DO and high temperatures displace fish populations, they can also serve as barriers to other suitable habitats. For example, Maes et al. (2007) modeled environmental factors which controlled the migration of anadromous

and catadromous fish populations in a Western European estuary. They observed that under warm, summer time conditions, DO was a limiting factor and prevented the upstream migration of YOY species to nursery areas.

Limitations and validation

This study did not evaluate the possibility of compensatory growth which could be a mechanism for overcoming the negative effects of hypoxia delayed growth. Bejda et al. (1992) found that flounder exposed for 11 weeks to hypoxic conditions when returned to normal conditions for 5 weeks had growth rates twice as great as those under normoxic conditions. It was projected that by the end of the season, both hypoxic treated fish and fish kept at normoxic conditions would reach comparable size. However size selective mortality due to significant reductions in growth during the summer could minimize or negate any compensatory growth in the fall.

This study also didn't address the possibility of acclimation to hypoxia. McNatt and Rice (2004) observed that growth rates for spot and Atlantic menhaden had consistently higher growth rates during week two of their two week hypoxic experiment, which indicated acclimation to low DO. Acclimation to hypoxic conditions has also been seen in summer flounder (Taylor and Miller 2001) and mummichog (Greaney et al. 1980). Our experiment did not last long enough to evaluate the ability of white perch to acclimate to hypoxic conditions. Other ways fish might minimize the negative effects of hypoxia, which is outside the scope of this study, is through escape and avoidance behaviors (Wannamaker and Rice 2000, Tyler and Targett 2007).

In drawing inferences from bioenergetic studies, it is important to try to compare energetic responses to those observed in the field. Growth rates in the Potomac River were estimated to be about one-third less than those observed under similar conditions in the laboratory. One explanation for this difference is that experimental fish were fed *ad libitum* twice a day. If rations were limited in the field, then we would expect to see decreased growth rates. I calculated that the experimental fish would have to eat 37% less to achieve the growth rates seen in the field which is well within reason. This assumes that all other energetic components such as routine metabolism, excretion, egestion, and active and feeding metabolism were the same between the two groups. In addition to lack of food, the field fish might also have experienced hypoxic conditions; field estimated growth rates (0.02 g day^{-1}) were very similar to growth rates by fish reared under hypoxic conditions (20% DO saturation, 0.02 g day^{-1}). As field growth rates were very coarse in their estimation, comparisons should be made with caution and be general rather than specific. However, it does appear that the parameters developed in this study can be useful in modeling habitat suitability for white perch.

White perch in Chesapeake Bay

It is clear that white perch are sensitive to low DO conditions, especially during the summer at high water temperature. With the Chesapeake Bay showing increased incidence and duration of hypoxia (Hagy et al. 2004) and increasing eutrophication which in turns lead to hypoxia (Kemp et al. 2005), nursery habitat for white perch and other species could be severely curtailed which in turn might diminish overall white perch production. In 2003, the Chesapeake Bay Program in

conjunction with the Environmental Protection Agency (EPA) developed new water quality criteria for the bay. For migratory, spawning and nursery use, the current criteria calls for a “6 mg l⁻¹ averaged over 7 days with a 5 mg l⁻¹ 1-day minimum from February through May. From June through January, the shallow-water/open-water use criteria apply.” The shallow-water/open-water use criterion calls for a 7-day average of 4 mg l⁻¹ and an instantaneous minimum of 3.2 mg l⁻¹ (<http://www.bayjournal.com/article.cfm?article=2447> retrieved on November 25, 2008). This criterion corresponds to DO levels of 42-48% over a temperature range of 20 to 28C. Results from this study indicate that the current criterion is sufficiently protective for growth effects of YOY white perch. In particular, no significant differences were detected in growth or feeding rates between 40 and ≥70% dissolved oxygen treatments. Although routine metabolism was significantly higher at 40% than at ≥70%, apparently this was insufficient to decrease the scope for growth.

Bioenergetic models can be useful in assessing current habitat suitability as well as predicting future suitability under certain scenarios. Projections for trends in Chesapeake Bay resulting from climate change are still uncertain. However, most models agree that conditions will be wetter (Najjar 1999; Neff et al. 2000). Increased precipitation could increase nutrient fluxes to rivers, estuaries, and bays (Walker et al. 2000) which would increase eutrophication and hypoxia. The effects and extent of hypoxia could also intensify under climatic warming. Long term temperature data from the Chesapeake Bay show a warming trend of 0.3C per decade (Breitburg 2002; Pyke et al. 2008). Perhaps as equally important is the future impacts of urbanization on streamflow which are likely to be as large as climate change impacts (Neff et al.

2000). Bioenergetic models that can integrate multiple water quality parameters together with forage conditions (albeit not evaluated here) will become increasingly useful in making management decisions for an uncertain future.

Appendices

Table 1A. Two-way ANOVA (Type 3 test) on the fixed effects of salinity (1, 4, 8, and 12) on growth and feeding rates of YOY white perch.

Effect	Numerator degrees of freedom	Denominator degrees of freedom	F Values	Pr>F
Instantaneous growth rate				
Salinity	3	22	0.37	0.78
Temperature	1	22	4.54	0.04
Salinity x Temperature	3	22	0.53	0.67
Feeding rate				
Salinity	3	22	0.93	0.44
Temperature	1	22	69.25	<0.001
Salinity x Temperature	3	22	1.27	0.31

Table 2A. Multiple linear regression (Type 3 test) on the effects of temperature (6, 12, 20, and 28°C) and dissolved oxygen (20, 40, and $\geq 70\%$) on log-transformed growth rates, log-transformed feeding rates, oxygen consumption, and energy density of YOY white perch.

Source	Degrees of freedom	Sum of Squares	Mean Square	F Values	Pr>F	R-Square
Instantaneous growth rate						
Model	3	2.17	0.72	56.22	<0.001	0.80
Error	41	0.53	0.01			
Corrected Total	44	2.70				
Temperature	1	0.10	0.01	7.70	0.01	
DO	1	0.00	0.00	0.01	0.91	
Temperature x DO	1	0.01	0.01	0.84	0.36	
Feeding rate						
Model	3	4.32	1.44	71.04	<0.001	0.84
Error	41	0.83	0.02			
Corrected Total	44	5.15				
Temperature	1	0.07	0.07	3.29	0.08	
DO	1	0.04	0.04	1.95	0.17	
Temperature x DO	1	0.12	0.12	5.33	0.03	
Oxygen Consumption						
Model	3	4302.99	1434.33	23.57	<0.001	0.48
Error	77	4685.09	60.85			
Corrected Total	80	8988.08				
Temperature	1	666.72	666.72	10.96	0.001	
DO	1	69.38	69.38	1.14	0.29	

Temperature x DO	1	516.54	516.54	8.49	0.004	
Energy Density						
Model	2	17.24	8.62	7.20	0.002	0.18
Error	67	80.19	1.20			
Corrected Total	69	97.43				
Temperature	1	2.25	2.25	1.88	0.18	
DO	1	17.22	17.22	14.38	<0.001	

Table 3A. Two-way ANOVA (Type 3 test) on the fixed effects of temperature (20 and 28°C) and dissolved oxygen (20, 40, and ≥70%) on growth rates, feeding rates, oxygen consumption, and energy density of YOY white perch.

Effect	Numerator degrees of freedom	Denominator degrees of freedom	F Values	Pr>F
Instantaneous growth rate				
Temperature	1	13.7	122.53	<0.001
DO	2	12.8	21.14	<0.001
Temperature x DO	2	12.8	3.25	0.07
Feeding rate				
Temperature	1	12.8	30.38	<0.001
DO	2	12.4	10.54	0.002
Temperature x DO	2	12.4	4.22	0.04
Oxygen consumption				
Temperature	1	27.7	2.77	0.11
DO	2	28.3	37.04	<0.001
Temperature x DO	2	28.3	5.97	0.007
Energy Density				
Temperature	1	39	0.44	0.51
DO	2	39	4.39	0.02
Temperature x DO	2	39	0.76	0.47

Table 4A. Response surface regression analysis (Type 1 test) on the effects of temperature (20 and 28°C) and dissolved oxygen (20, 40, and ≥70%) on growth rates, feeding rates, oxygen consumption, and energy density of YOY white perch.

Source	Degrees of freedom	Sum of Squares	R-Square	F Value	Pr > F
Instantaneous growth rate					
Linear	2	0.00	0.78	84.19	<0.001
Quadratic	2	0.00	0.04	3.97	0.03
Crossproduct	1	0.00	0.00	1.02	0.32
Total Model	5	0.00	0.82	35.47	<0.001
Lack of Fit	3	0.00		3.33	0.03
Feeding rate					
Linear	2	0.06	0.78	78.27	<0.001
Quadratic	2	0.00	0.00	0.72	0.50
Crossproduct	1	0.00	0.02	3.01	0.09

Total Model	5	0.06	0.81	32.2	<0.001
Lack of Fit	3	0.00		1.72	0.18
Oxygen Consumption					
Linear	2	3786.45	0.42	34.99	<0.001
Quadratic	2	338.28	0.04	3.13	0.05
Crossproduct	1	805.21	0.09	14.88	<0.001
Total Model	5	4929.94	0.55	18.22	<0.001
Lack of Fit	3	1178.06		9.92	<0.001
Energy Density					
Linear	2	17.24	0.18	0.93	0.002
Quadratic	2	0.58	0.01	0.223	0.79
Crossproduct	1	0.02	0.00	0.02	0.89
Total Model	5	17.84	0.18	2.87	0.02
Lack of Fit	3	4.60		1.25	0.30

Table 5A. ANCOVA results for the effects of size category and feeding rate on the mean daily weight of fish. Size categories were 3, 5, 6, and 9 g.

Effect	Numerator degrees of freedom	Denominator degrees of freedom	F Values	Pr>F
Size category	3	4	8.30	0.03
Feeding rate	1	4	2.39	0.20
Size x feeding	3	4	0.85	0.53

Table 6A. Two-way ANOVA (Type 3 test) on the fixed effects of temperature (20 and 28°C) and dissolved oxygen (20, 40, and $\geq 70\%$) on gross growth efficiencies of YOY white perch.

Effect	Numerator degrees of freedom	Denominator degrees of freedom	F Values	Pr>F
Temperature	1	15.3	105.96	<0.001
DO	2	13.3	15.56	<0.001
Temperature x DO	2	13.3	15.3	<0.001

Table 7A. Two-way ANOVA (Type 3 test) on the fixed effects of temperature (20 and 28°C) and dissolved oxygen (20, 40, and $\geq 70\%$) on egestion rates of YOY white perch.

Effect	Numerator degrees of freedom	Denominator degrees of freedom	F Values	Pr>F
Temperature	2	12	18.28	<0.001
DO	1	12	0.33	0.57
Temperature x DO	2	12	1.00	0.40

Table 8A. One-way ANOVA (Type 3 test) on the fixed effect of location (experiment and Potomac) on growth rates of YOY white perch.

Effect	Numerator degrees of freedom	Denominator degrees of freedom	F Values	Pr>F
Location	1	25	56.71	<0.001

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