Effects of hypoxia on food consumption and growth of juvenile striped bass (*Morone saxatilis*)

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ABSTRACT

Hypoxia and an apparent temperature–oxygen squeeze have been reported for many coastal ecosystems and reservoirs with striped bass *Morone saxatilis*. Studies have identified limits of dissolved oxygen (DO) for this species, but interactive effects of concurrent temperatures and low DO have not been addressed. We conducted laboratory experiments on juvenile (23 g) striped bass consumption and growth in a 4×3 factorial design using 4 temperatures (20, 23, 27, and 30 °C) and 3 DO levels (2 mg L^{-1}, 4 mg L^{-1} and saturation). Temperature did not affect striped bass food consumption, but consumption increased with increased DO levels. Growth was related to DO as well as to the interaction between temperature and DO, and striped bass growth was strongly curtailed below 4 mg L^{-1} DO. Laboratory results were used to derive an equation to apply the effects of environmental DO level to striped bass bioenergetics models. Overall results should be useful to predict changes in striped bass habitat quality in response to changes in hypoxic conditions.

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1. Introduction

The frequency and severity of eutrophication-induced hypoxia have increased in marine and freshwater ecosystems (e.g., Diaz and Rosenberg, 2008). As a consequence, large-scale restoration programs to reduce nutrient loading have begun in places like the Chesapeake Bay (Boesch et al., 2001). The Chesapeake Bay is the largest estuary in North America. Large portions of the mesohaline channel of the middle region of Chesapeake Bay have dissolved oxygen (DO) levels below 50% saturation during summer months when seasonal density stratification limits re-aeration of bottom waters (Officer et al., 1984; Cooper and Brush, 1991; Hagy et al., 2004; Kemp et al., 2005). Chesapeake Bay has experienced severe hypoxia since at least the 1950's but the magnitude, extent and duration may have increased in recent years (Cooper and Brush, 1991; Hagy et al., 2004). In many areas, bottom waters (and sometimes up to <10 m water depth) are often hypoxic (<2 mg L^{-1}) from late spring to early fall. What is the overall impact of this large volume of hypoxic water on ecosystem production in general and the quantity of suitable pelagic habitat available for fishes, in particular?

Striped bass, *Morone saxatilis*, is a key commercially, recreationally and ecologically important species in the Chesapeake Bay (e.g., Richards and Rago, 1999). Striped bass populations in Chesapeake Bay have fluctuated widely for the past few decades. Numerous factors may have contributed to fluctuations in striped bass stocks, including variation in the volume of the bay characterized by hypoxia. Although striped bass can actively avoid areas with low DO, summertime temperatures in the upper portions of the water column may reach levels that are beyond the range of the species' optimal temperature for growth and consumption (i.e., >25 °C, Hartman and Brandt, 1995a,b). This temperature–oxygen "squeeze" can lead to several consequences for striped bass populations that range from direct mortality (from thermal or respiratory stress) of individuals that fail to occupy suitable habitat to a reduction in consumption and/or growth by being forced to live in suboptimal habitats (Coutant, 1985; Coutant and Benson, 1990). In addition to the Chesapeake Bay, the temperature–oxygen squeeze has been demonstrated to affect striped bass in the Hudson River, the Connecticut River, and reservoirs in Alabama, Tennessee, and Texas as well as the San Francisco Bay, Sacramento and San Joaquin deltas (Coutant, 1985; Matthews et al., 1985; Moss, 1985). For the Chesapeake Bay, Costantini et al. (2008) argued that hypoxia could have a short-term positive effect on overall striped bass growth if prey are forced to concentrate above the oxycline which might increase predator–prey encounter rates if temperatures are right (i.e., not too warm). It is thus important to quantify the direct 'tradeoff' in temperature and oxygen habitat to striped bass consumption and growth.

What is the direct effect of lowered oxygen on fish? A number of studies have examined the mortality thresholds of species to hypoxia

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(e.g., Vaquer-Sunyer and Duarte, 2008). Dissolved oxygen concentrations below 1 mg L^{-1} are generally fatal to most fish species, including striped bass (Fry, 1971) although individual species tolerances differ widely (Vaquer-Sunyer and Duarte, 2008). Fewer studies have looked at the indirect (Fry, 1971) effects of hypoxia on fishes. Low DO levels (usually between 2 and 4 mg L^{-1}) have been shown to directly affect food consumption, growth, reproduction, distribution and behavior of fish in both the field and in the laboratory (Kramer, 1987; Breitburg et al., 1997, 2001; Aku and Tonn, 1999; Wannamaker and Rice, 2000; Robb and Abrahams, 2003; Thomas et al., 2006). Hypoxia has been shown to decrease consumption and growth in species such as cod (*Gadus morhua*) and striped bass (Cech et al., 1984; Chiba, 1988; Chabot and Dutil, 1999).

Consumption and growth of fishes are also strongly affected by temperature. Under thermally stratified conditions, fish tend to select strata corresponding to optimal temperatures for growth (Brandt et al., 1980; Jobling, 1981; Olla et al., 1985). If warmer surface waters exceed the preferred temperatures of fish, then consumption and growth will likely decline when the fish are forced to inhabit these areas. The extent of the difference between the preferred temperature and the environmental temperature will determine how severe this effect may be. Striped bass are generally tolerant of a wide range of water temperatures. Juvenile (<100 g) striped bass have higher preferred temperatures than adults but metabolism and consumption fall off at much greater rates than for adults at warmer temperatures (Hartman and Brandt, 1995a). Thus, if hypoxic or anoxic conditions in the bottom waters of the bay force striped bass to move into thermal regimes in upper waters that are less than optimal (Pihl et al., 1991), the temperature–oxygen squeeze may be more severe for juvenile striped bass than for adults.

Few studies have quantified the *interaction* of DO and temperature on growth, food consumption, or distribution (although see Breitburg et al., 1994; Buentello et al., 2000). Coutant (1985) examined distributions and general condition of striped bass juveniles and adults in response to temperature and DO levels, and found evidence of stress in larger fish simultaneously exposed to reduced DO level and rising temperatures. What remains unanswered is how do differing DO levels affect food consumption and growth of striped bass? Further, is there an interaction between temperature and DO level on growth and/or consumption?

Our main objective in this study was to quantify the effects of hypoxia on food consumption and growth by striped bass under various experimental temperatures. Specific objectives were to: (1) Quantify the effects of DO concentration on temperature-specific food consumption by age-0 striped bass, (2) Quantify the effects of DO concentration on temperature-specific growth of striped bass, and

(3) Determine if there is an interaction between temperature and (low) DO concentration on striped bass bioenergetics.

2. Methods

2.1. Laboratory experiments

Experiments were conducted with similar-sized age-0 striped bass (23 g) obtained from the Potomac Electric Power Company's fish hatchery in Chalk Point, Maryland. All experiments were conducted at the Great Lakes Center Aquatic Research Laboratory (Buffalo, New York). Fish were maintained in large flow-through tanks filled with filtered city water.

Experiments were conducted using a 4×3 factorial design with four water temperature levels and three DO concentrations. The four experimental water temperatures were 20, 23, 27 and 30 °C (all ± 1.0 °C). Fish were acclimated to each temperature for a minimum of two weeks prior to each experiment. These experimental temperatures were chosen because they represent the range of temperatures that occurs during summer periods of hypoxia in Chesapeake Bay. Targeted DO levels of 100% saturation, 4 and 2 mg L^{-1} (± 1.0 mg L^{-1}) were obtained by bubbling nitrogen gas through air stones and measured every 4 h with a calibrated YSI model 58 DO meter. Water in the experimental tank was partially (50%) changed twice during the experiment to ensure adequate pH, ammonia and nitrite/nitrate levels. Photoperiod was maintained constant at 15 h of light per day.

Each experiment lasted for 10 d with a single fish exposed to a randomly selected combination of DO and temperature. Sixty fish were used for the experiment (Table 1), and the number of fish used for each treatment combination ranged from 3 to 8. Each fish was used only once. Mortality of individuals in the combinations of low DO and high temperature treatments forced us to have fewer replicates at the 20 and 30 °C treatments because these were the last temperature levels conducted. All fish were acclimated to the experimental tank for 48 h before the beginning of the experiment and were deprived of food for 24 h preceding the experiment to standardize gastric evacuation. Throughout the experiment, food was maintained *ad libitum* to encourage maximum consumption and consisted of live, pre-weighed emerald shiners (*Notropis antherinoides*). Total food consumption by striped bass was estimated by summing the weight of shiners consumed throughout the experiment. Individual striped bass were anesthetized with tricaine methanesulfonate and weighed at the beginning and end of each trial to the nearest 0.1 g wet weight. Growth (weight gain or loss) during the experiment was calculated as the difference between final and initial weights. Results of food consumption and growth were converted to standard units

Table 1
Summary of mean values of consumption and growth data with standard deviation (SD) and 95% confidence intervals (CI).

Temperature	2 mg L^{-1}		4 mg L^{-1}		Saturated	
	Consumption (g g^{-1} d^{-1})	Growth (g g^{-1} d^{-1})	Consumption (g g^{-1} d^{-1})	Growth (g g^{-1} d^{-1})	Consumption (g g^{-1} d^{-1})	Growth (g g^{-1} d^{-1})
20 °C	0.00748	−0.00557	0.02124	0.00012	0.01823	0.00625
SD	0.00555	0.00218	0.00923	0.00259	0.01497	0.00299
CI	0.00544	0.00214	0.00904	0.00253	0.01694	0.00338
N	4	4	4	4	3	3
23 °C	0.00729	−0.01108	0.02204	−0.00349	0.03455	0.00912
SD	0.00517	0.01016	0.01662	0.00397	0.01014	0.00618
CI	0.00507	0.00996	0.01330	0.00318	0.00811	0.00495
N	4	4	6	6	6	6
27 °C	0.01378	−0.01024	0.02779	−0.00241	0.03544	0.00494
SD	0.01689	0.00493	0.02287	0.00752	0.02583	0.00323
CI	0.01170	0.00342	0.01694	0.00557	0.02067	0.00259
N	8	8	7	7	6	6
30 °C	0.01978	−0.00067	0.03189	−0.00025	0.02459	0.00012
SD	0.01815	0.01053	0.00808	0.00240	0.01611	0.00633
CI	0.01779	0.01032	0.00792	0.00235	0.01579	0.00620
N	4	4	4	4	4	4

($-$g food g fish^{-1} d^{-1}, or g growth g fish^{-1} d^{-1}) to standardize for fish weight and to facilitate insertion into a bioenergetics model. A two-way analysis of variance was used to test the effect of water temperature, DO and the two-factor interaction on striped bass food consumption and growth. Post hoc tests evaluated the effects of DO upon consumption and growth within a temperature treatment. Significance level was set to $\alpha = 0.1$ in all tests.

2.2. Bioenergetics model

We used results of the laboratory experiments to modify components of the bioenergetics model for striped bass. Bioenergetics models can be used to (1) estimate food consumption based on observed growth rates, thermal history, and diet, or (2) simulate growth of fish under different conditions of diet, prey availability and water temperature. For this application, we used the bioenergetics model of Hartman and Brandt (1995a) to estimate the growth of striped bass based on measured food consumption and water temperature (option 2 above). Therefore, the striped bass energy budget can be summarized by the following equation:

$$\text{Growth} = \text{Consumption} - (\text{Metabolism} + \text{Wastes}). \tag{1}$$

Since food consumption is used as an 'input' to calculate growth, we modified only the consumption part of the model (i.e., we applied the laboratory results on the effects of hypoxia on food consumption; Fig. 1). The metabolism and waste components of the model were not modified, even though hypoxia may have an effect on these components as well. For this application, we used the model assuming that food availability is unlimited as for the laboratory experiments. Consequently, estimates of growth generated with the modified bioenergetics model are for maximum possible growth under conditions of unlimited food. However, field studies employing bioenergetics models typically find wild fish feed at levels of 40–60% of C_{max} (Hartman and Hayward, 2007). For Chesapeake Bay striped bass, Hartman and Brandt (1995b) found that age-0 striped bass fed at about 50% of maximum consumption in the field. Therefore to evaluate our bioenergetics model on more realistic conditions, we also modeled the growth of striped bass under a 50% of maximum consumption scenario.

The Hartman and Brandt (1995a) consumption component of the bioenergetics model under unlimited food conditions (C_{max}) has size- and temperature-dependent functions:

$$C_{max} = f(W) \cdot f(T) \tag{2}$$

where W is weight (g) and T is temperature (°C). Size dependency is defined on the basis of an allometric function. For this application, we used a fish at 22.6 g, which was the mean weight of fish used in laboratory experiments. The temperature dependency is modeled with the Thornton and Lessem (1978) algorithm and it is the product of two sigmoidal curves with a range from 0 to 1.

We modified Eq. (2) to incorporate the effects of hypoxia on food consumption using the following model:

$$C_{max} = f(W) \cdot f(T) \cdot f(DO) \tag{3}$$

Oxygen dependency $f(DO)$ was fit with a quadratic model and ranged from 0 to 1. Even under normoxic conditions striped bass in our experiments ate less than fish similar in size in Hartman and Brandt (1995b). This was likely due to differences in consumption between fish fed large, live shiners (the current study) and fish fed small, chopped anchovy prey (Hartman, 1993). The laboratory data of Fig. 1 were converted to a range from 0 to 1 by dividing mean consumption value at DO levels of 2 and 4 mg L^{-1} by the highest mean consumption level observed under saturated oxygen conditions
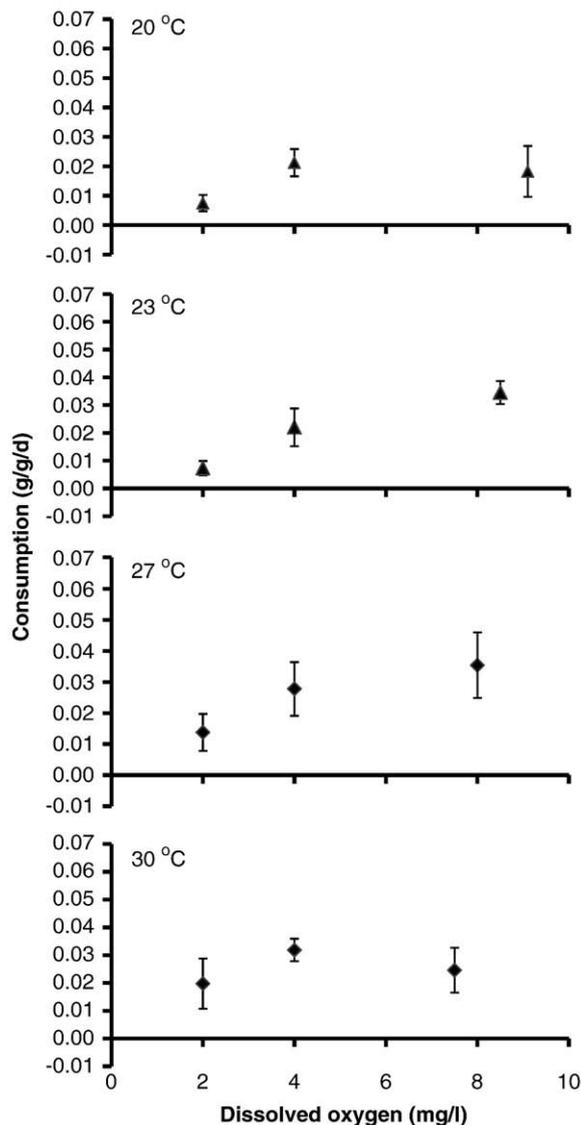

Fig. 1. Food consumption (g food g fish^{-1} d^{-1}) of striped bass maintained at DO levels of 2, 4 mg L^{-1} and 100% saturation, and at four temperatures. Error bars represent standard error.

(0.0346 g g^{-1} g^{-1} at 23 °C). Because DO concentrations at different temperatures represent different levels of oxygen saturation, we chose to express oxygen in terms of percent saturation (%-Sat) level rather than concentration. We used the following equation (Wetzel, 1983) to obtain the saturated oxygen concentration [DO]$_{SAT}$ at various temperatures:

$$[DO]_{SAT} = 14.4 + 0.332T + 0.00342T^2. \tag{4}$$

The resulting model relates $f(DO)$ to the percent saturation of oxygen with the following equation (Fig. 2):

$$f(DO) = -0.1874 + 0.0257\%\text{Sat} - 0.00014\%\text{Sat}^2. \tag{5}$$

In general, oxygen saturation levels of 50% produced a reduction in food consumption of about 25% (i.e., $f(DO) = 0.75$). We assumed that no food consumption occurs at DO levels less than 13% saturation (i.e., $f(DO) = 0$).
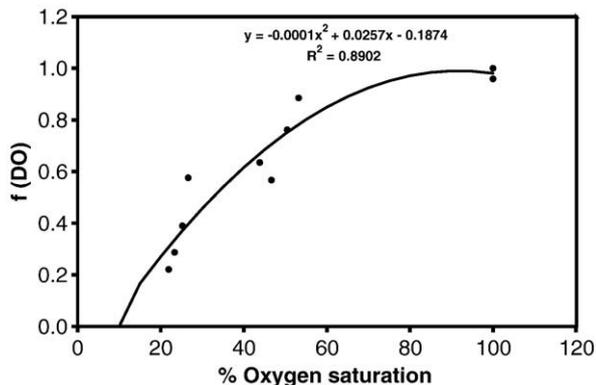
Fig. 2. Graphical representation of f(DO), the oxygen dependence proportional multiplier of maximum consumption, plotted as a function of percent oxygen saturation.

3. Results

3.1. Laboratory experiments

3.1.1. Food consumption

Striped bass food consumption differed significantly among DO levels, but we found no significant effect of temperature or the interaction of temperature and oxygen on consumption rate (Tables 1 and 2). Post hoc Tukey's tests ($df = 48$, $\alpha = 0.1$) revealed significant differences in consumption rate between each DO level across all temperatures with consumption generally increasing with DO level (Fig. 1). Overall, mean consumption at 2 mg L^{-1} was lower than at 4 and 8 mg L^{-1} at all temperatures and mean consumption at 4 mg L^{-1} was lower than 8 mg L^{-1} at intermediate (optimal) temperatures of 23 and 27 °C but not at 20 and 30 °C.

3.1.2. Growth

Striped bass growth differed significantly among DO levels (Tables 1 and 2) and we found a significant ($\alpha = 0.1$) interaction of temperature and oxygen. We found no significant effect of temperature on growth. Post hoc Tukey's tests confirmed that growth was higher at 4 mg L^{-1} than 2 mg L^{-1} and growth at 8 mg L^{-1} exceeded both lower DO levels at 20, 23 and 27 °C. In general, there was a linear relationship between DO level and growth (Fig. 3). However, at the 30 °C treatment there were no significant differences in growth among DO levels. For all experimental temperatures, DO levels of 2 and 4 mg L^{-1} on average resulted in no growth or negative growth (i.e., weight loss).

3.2. Bioenergetics models

Our newly derived bioenergetics consumption sub-model (Fig. 4) shows that maximum food consumption by age-0 striped bass can be

Table 2
Analysis of variance summary table for the effect of water temperature and dissolved oxygen on food consumption and growth of age-0 striped bass.

| Source of variation	df	Sum of squares	Mean square	F-value	Pr>F
Food consumption					
Temperature (°C)	3	0.00084	0.00028	0.91	0.394
Oxygen (mg L^{-1})	2	0.00027	0.00137	4.99	0.011
Temperature × oxygen	6	0.00087	0.00014	0.52	0.787
Error	48	0.01817	0.00027		
Growth					
Temperature (°C)	3	0.000087	0.00020	0.84	0.479
Oxygen (mg L^{-1})	2	0.001350	0.00067	19.47	<0.0001
Temperature × oxygen	6	0.000420	0.00007	2.02	0.081
Error	48	0.001664	0.00003		
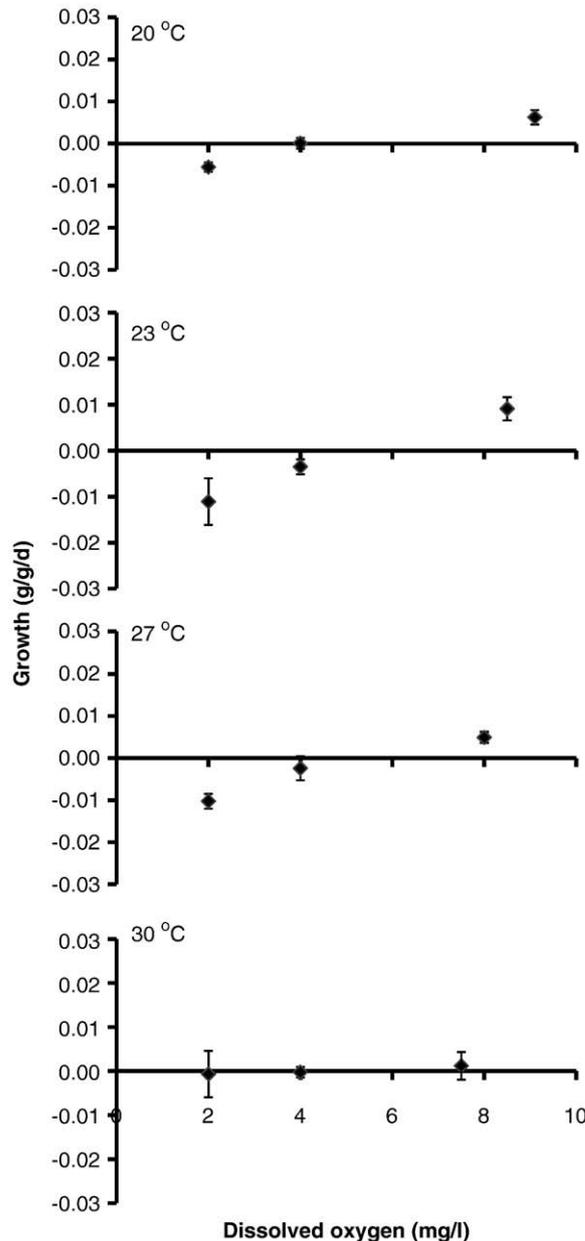
Fig. 3. Growth (g g^{-1} d^{-1}) of striped bass maintained at DO levels of 2, 4 mg L^{-1} and 100% saturation, and at four temperatures. Error bars represent standard error.

estimated for a variety of water temperature and DO combinations. In general, maximum food consumption predicted by the model was relatively unaffected by DO concentrations >60% of saturation (4.5 to 5.1 mg L^{-1}). At any temperature, food consumption was reduced by about 40 and 80% at DO concentrations of 4 and 2 mg L^{-1}, respectively, and no consumption occurred at DO ≤ 1 mg L^{-1}.

Similar to consumption, the maximum growth by age-0 striped bass remained relatively unchanged with DO>60% of saturation (Fig. 5). At most temperatures, growth was reduced by about 50% when DO reached 50% of saturation. The minimum DO concentration required for positive growth varied with water temperature due to the different saturation concentrations at different temperatures. For temperatures in the range 12 to 20 °C, the minimum DO concentration for positive growth was about 2.0 mg L^{-1}. As temperatures increased from 20 to 27 °C, the minimum DO concentration for positive growth increased from 2.0 to 4.5 mg L^{-1}. No growth was possible at temperatures above 28 °C.
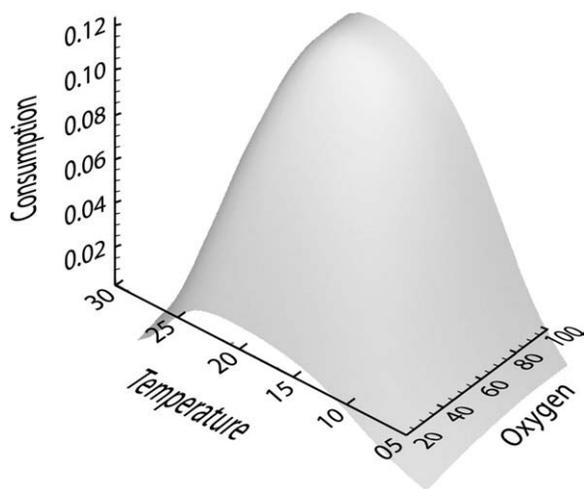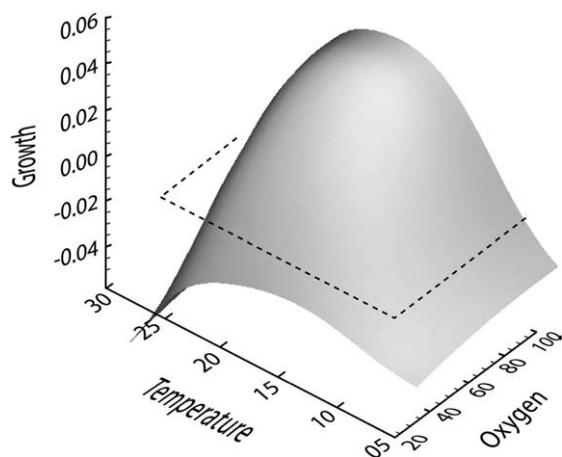
Fig. 4. Bioenergetics model prediction of striped bass maximum food consumption (g food g fish^{-1} d^{-1}) for a 22.6 g fish as a function of water temperature (°C) and DO concentration (% saturation).

Fig. 6. Bioenergetics model prediction of striped bass growth (g g^{-1} d^{-1}) as a function of water temperature (°C) and DO concentration (% saturation) of a 22.6 g fish feeding at 50% of C_{max}.
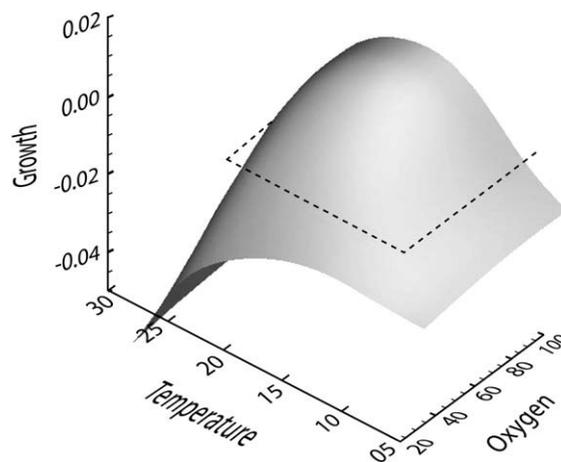
When striped bass bioenergetics were constrained by more realistic feeding levels, the influence of DO and temperature on growth was more dramatic (Fig. 6). When striped bass are modeled to consume 50% of maximum consumption, growth capacity was greatly diminished. At this feeding level growth is substantially curtailed with no growth at temperatures above 25 °C for any DO level and no growth >22 °C at 40% of DO saturation.

4. Discussion

Overall, the laboratory results indicated that striped bass food consumption and growth decline as DO levels decline but the overall impact on growth depends on environmental temperature. Other studies have also shown reduced consumption and growth of fishes under hypoxia (Chabot and Dutil, 1999; Thetmeyer et al., 1999; Buentello et al., 2000; Pichavant et al., 2000, 2001; Taylor and Miller, 2001). A level of 4 mg L^{-1} is often considered the limit of stressful oxygen concentration (Thursby et al., 2000; although see Vaquer-Sunyer and Duarte, 2008). In terms of growth, continuous exposure to DO concentrations of 4 mg L^{-1} (at 23, 27 and 30 °C) or below (at all temperatures) caused striped bass to lose weight even though food was always unlimited. Previous experiments on the effects of DO levels on striped bass have also shown that DO<3–4 mg L^{-1} adversely

affects appetite and can cause physiological stress (Chittenden, 1971). Obviously, the effects of low DO on striped bass growth in estuaries will depend on the degree of exposure to the stress and, to some extent, on the environmental temperature. The lack of an overall significant effect of temperature per se on food consumption was not unexpected since Hartman and Brandt (1995a) found that maximum food consumption of striped bass at saturated DO levels is similar from 18 to 28 °C. They also found that food consumption declined sharply at temperatures of 30 °C or more.

We applied the effects of environmental DO level to fish bioenergetics models. Fish bioenergetics models are widely used to estimate fish growth or consumption. Through 2006, over 250 journal articles have been published based upon the Wisconsin bioenergetics model (Hartman and Kitchell, 2008). Published models exist for over 40 species of fish, including striped bass (Hartman and Brandt, 1995a). Most models consider only water temperature and occasionally salinity (Vernberg, 1998; Buckel et al., 2005) as environmental variables affecting fish physiological rates. Such bioenergetics models have been spatially linked to prey distributions to arrive at measures of habitat quality in the Great Lakes (Goyke and Brandt, 1993; Hook et al., 2003) and Chesapeake Bay (Luo and Brandt, 1993; Luo et al., 2001). Despite the widespread concern regarding hypoxic volumes in the Great Lakes, the Gulf of Mexico, and other coastal areas, ours is one of the first models to mechanistically incorporate DO levels as a limiting factor in fish growth models (although see Costantini et al., 2008).

Our modification of the striped bass bioenergetics model should have importance in evaluating the impact of increasing hypoxic volumes in the Chesapeake Bay. Hypoxic volumes (<2 mg L^{-1}) in the bay increased about 3-fold from 1950 to 2001 with the trend increasing rapidly over the last 20 years (Hagy et al., 2004). Incorporation of our bioenergetics model into spatial models can quantify habitat changes for striped bass related to changes in DO and thermal conditions within the Chesapeake Bay. This approach can be used to forecast and backcast historical conditions, potentially identifying ecological tipping points by integrating striped bass abundance, disease, and normoxic volume in the bay.

Our findings that no growth was possible for juvenile striped bass at >25 °C when feeding at realistic levels has major implications for the growth and health of Chesapeake Bay striped bass stocks. It appears that the temperature–oxygen squeeze speculated by Coutant (1985) exists and it is intensifying (Hagy et al., 2004). If under normoxic conditions and realistic feeding levels (50% of *ad libitum*) juvenile striped bass cannot achieve positive growth at 25 °C, then virtually none of the bay's mid-region volume supports growth during

Fig. 5. Bioenergetics model prediction of striped bass growth (g g^{-1} d^{-1}) as a function of water temperature (°C) and DO concentration (% saturation) of a 22.6 g fish feeding at C_{max}.

the summer months. Growth is further compromised under hypoxic conditions suggesting that during summer most areas within the bay lead to a growth deficit. Under these growth and thermal conditions juvenile striped bass may be concentrated in volumes where growth is maximized leading to the potential for increased competition, disease and mortality.

Dissolved oxygen levels are influential in restricting growth and ultimately habitat quality of striped bass. Ours is not the first study to explore striped bass relative to thermal and hypoxic conditions. Coutant (1985) and Coutant and Benson (1990) suggested the concept of a temperature–oxygen squeeze for Atlantic coastal striped bass, and Chiba (1988) conducted laboratory experiments with striped bass under hypoxic conditions. However, neither of these studies evolved into a bioenergetics model that could be applied to evaluate and quantify habitat quality. The Chiba (1988) study did not control for temperature, and temperatures during a single trial fluctuated as much as 5 °C. Thus, ours is the first study to quantify consumption and growth of striped bass while controlling both temperature and DO levels. Our experiments however were only done on small juveniles and cannot be extrapolated without caution to larger striped bass.

Individual fish response to all experiments was highly variable. Hartman (1993) also found a high degree of individual variability when working with juvenile striped bass. This variability, particularly in our laboratory study, may yield insights into how individuals respond to environmental stressors such as high temperatures and hypoxia. Observations in the laboratory suggest that striped bass respond to stressful temperatures or hypoxia in one of two ways. Some fish become inactive — apparently attempting to minimize energy expenditures while waiting for conditions to improve. Others responded by rapid swimming within test chambers in an apparent effort to swim out of the stressful conditions. It is not difficult to speculate that this dual behavior is evolutionarily significant — allowing populations to persist under extreme thermal or hypoxic events.

Since cultural eutrophication is such a widespread problem facing fisheries management, the ability to quantify the effects of hypoxia on fish consumption and growth (and also fish growth potential) would represent a tremendous advantage to fisheries managers. Nutrient loading and oxygen depletion has become such a common problem that methods developed to measure, evaluate, and understand the progression of the effects of nutrient load (increasing or decreasing) on oxygen, and hence fish production, would be of tremendous benefit to a great many aquatic ecosystems. Problems with low summer growth (or summer kill) associated with low DO levels have been demonstrated for years, but rarely quantified beyond a lethal level. The ability to incorporate these oxygen effects with some measure of estimated oxygen depletion (or increase) from nutrient loads would provide a mechanism to predict changes in fish habitat quality (e.g., Price et al., 1985; Brandt and Kirsch, 1993).

Acknowledgements

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