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Temperature-dependent growth and consumption of young-of-the-year sablefish *Anoplopoma fimbria*: Too hot, too cold or just right?

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ABSTRACT

Sablefish *Anoplopoma fimbria* are a highly valued, economically important groundfish in Alaska; however, estimated stock biomass has been in steady decline since the early 1990s, likely as a result of poor recruitment. Among several factors found to impact recruitment strength, ocean temperature often has been to affect early-life condition. Despite the importance of early-life condition in predicting cohort success, few studies have examined the thermal response of young-of-the-year (YOY) sablefish in regards to growth and development, and those focus on only a narrow size range. In this study, we measured the effects of temperature on growth and consumption rates of YOY sablefish (218–289 mm TL) in laboratory trials with fish held over 5 temperature treatments (5 °C, 8 °C, 12 °C, 16 °C and 20 °C) and maintained on *ad libitum* ration for 3 weeks. We compared growth, consumption, and body condition of fish between treatments. Specific growth rate (SGR; % wet weight gain (g) d^{-1}) was used to derive a temperature-dependent growth model, and consumption rates were used to calculate species-specific parameters for the consumption function of a Wisconsin-type bioenergetics model. Daily growth in length varied from 0.13 mm d^{-1} to 1.74 mm d^{-1} and SGR ranged from 0.52 to 2.31. SGR peaked at 15.4 °C, remained high at 12 °C and 16 °C, and steadily declined as temperatures shifted outside this range. Residuals of length-weight regressions were positive at 12 °C and 16 °C, and negative at 5 °C, 8 °C, and 20 °C. Consumption rose sharply with temperature, peaking at 17.6 °C. The narrow thermal range facilitating higher than average condition and optimal SGR indicates that YOY sablefish growth and development may be dramatically influenced by relatively small shifts in water temperatures. Further, when compared to similar studies of smaller-sized sablefish, we observed a shift with size in thermal performance, with larger fish performing better at colder temperatures compared to smaller fish. The shift in thermal performance with size is an important consideration for understanding the result of environmental perturbation on recruitment. While traditional recruitment models rely heavily on information from a single life-stage, resource use and physiological requirements often change with development. Given the widespread occurrence of anomalous thermal events in the Gulf of Alaska, a life-stage specific understanding of the effects of varying temperatures is crucial.

1. Introduction

Climate-induced changes to habitat conditions can have major effects on the productivity of marine organisms. Disruptions from optimal conditions lead to departures from homeostasis, decreasing fitness by negatively affecting survivorship, growth and/or reproduction (Diana, 2004; Portner and Farell, 2008). For poikilotherms such as fish, shifts in environmental conditions and the resulting impacts to physiological response are of particular concern for populations found in regions where more pronounced impacts of climate change processes are evident, such as those in higher latitudes (Peck et al., 2004). In these regions, fish experience severe winter conditions such as enhanced resource scarcity and temperatures often near lower thermal limits (Hurst, 2007). This places immense selective pressures on larval and juvenile fish to attain sufficient size and condition in the fall if they are to survive their first winter (*i.e.*, critical size hypothesis; Beamish and Mahnken, 2001; Heintz et al., 2013). Thus, external factors that alter resource availability or local environment will have a disproportionate effect on overwinter survival and recruitment rates.

Among the factors affecting fish condition, temperature is a dominant regulator of growth and development. Recently, anomalous warming events have occurred in the Gulf of Alaska (GOA) and throughout the northeast Pacific Ocean, with unclear implications for local fish communities. For example, in 2013 and 2014 a warm mass of

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water or "warm blob" was detected centered on the dateline (180 °W) at ~ 40 °N and extending 30 degrees of longitude and 8 degrees of latitude, covering much of the northeast Pacific Ocean (Peterson et al., 2015). This "warm blob" contained areas of water 3 °C above long-term (1982–2014) seasonal averages with increased temperatures persisting to ~ 100 m in depth. At the other end of the thermal spectrum, increases in global temperatures and shifts in climate patterns have also resulted in dramatic increases in terrestrial freshwater discharge (FWD) in the GOA, attributed to accelerated glacial volume loss and regional climatic changes resulting in precipitation increasingly falling as rain rather than snow (Radić and Hock, 2013; McAfee et al., 2014). This increase in FWD has been shown to cause a decrease in summer and fall nearshore water temperature along the Alaska coast (Spurkland and Iken, 2011). Small deviations from normal thermal conditions can have profound effects on growth rates and development, especially for young fish. This in turn impacts population dynamics by way of influencing predation risk and overwinter survival (Houde, 2008).

Although cohort and recruitment success of most fish are heavily dependent on conditions experienced through early development, significant knowledge gaps exist for many species during this period of life (Pepin, 1991; Secor et al., 2002; Young et al., 2006). Research is often focused on the most dominant or commercially valuable life history-stage, typically adults. However, shifts in physiological performance through ontogeny has been noted for many species, emphasizing the need for life-stage specific information (Pepin, 1991; Hendry and Streans, 2004).

Sablefish *Anoplopoma fimbria* are a highly valued, economically important groundfish in Alaska, generating ~ $100 million annually (Hanselman et al., 2013). However, estimated biomass for this stock has been in steady decline since the early 1990s, likely as a result of poor recruitment (Hanselman et al., 2013). Sablefish recruitment is episodic, characterized by large interannual variations in year-class strength that typify density-independent population regulation (Sigler et al., 2001). These observations suggest that sablefish recruitment dynamics and year-class strength may be strongly mediated by local environmental conditions experienced early in life (Schirripa and Colbert, 2006; Shotwell et al., 2014).

Sablefish are particularly sensitive to environmental perturbation experienced during early growth and development. In the North Pacific, sablefish spawning occurs during January-February at depths > 300 m, near the edge of the continental slope (Mason et al., 1983). Eggs develop at depth, while larvae develop near the surface in waters generally ranging from 12 °C–18 °C. Larvae are transported *via* ocean currents shoreward toward shallow, coastal inlets and estuaries along the Alaskan coast. In the fall, young-of-the-year (YOY) settle in cooler benthic coastal habitats where they remain for one or two years prior to maturation and subsequent return to deeper, open water (Maloney and Sigler, 2008). YOY sablefish experience a rapid rate of growth (> 3 mm d^{-1}), contingent on resource availability and local habitat characteristics (Sogard and Spencer, 2004). During this period of rapid growth, environmental factors are believed to play a vital role in determining year-class strength and resulting recruitment success (Mason et al., 1983; Sigler et al., 2001, 2003). Given recent anomalous climate events in the GOA, YOY sablefish may now be experiencing altered growth and development, which in turn impacts pre-winter condition and overwinter survival.

Despite the importance of early-life development, there is relatively sparse information on temperature-dependent physiological response of YOY sablefish. Previously, Sogard and Spencer (2004) grew YOY sablefish (36 mm–50 mm TL) at two temperatures (10 °C and 20 °C) on two ration treatments (*ad libitum* and low ration; 3–4% body mass d^{-1}) over a period of 15 weeks. They found that temperature and ration significantly influenced body composition with fish fed on higher ration growing significantly faster at both low and high temperatures, and those held at colder temperatures allocating more energy to lipid storage rather than protein synthesis (somatic growth). Sogard and Olla (2001) examined the influence of temperature and ration quantity on growth and conversion efficiency (g grown / g consumed) of larval and YOY sablefish (50–102 mm mean TL). On maximum ration, growth rates and efficiency increased as temperature rose from 14 °C–20 °C, with sablefish attaining growth rates of > 3 mm d^{-1}. However, growth rates and efficiency dropped significantly for fish held in temperatures outside of this range (< 1.2 mm d^{-1} at 6 °C and 8 °C, and -0.3 mm d^{-1} at 24 °C).

While informative, previous studies of early-life stage sablefish have focused on a narrow size class, representing individuals found in the summer near the neustonic zone (50 mm–150 mm TL). Sogard and Olla (1998) documented a shift in thermal tolerance as sablefish transition from early, pre-settlement YOY (63–109 mm TL) to advanced, post-settlement YOY (142–206 mm TL); smaller fish tolerating warmer water compared to larger fish. However, that study only described ontogenic changes in behavior with regards to temperature of YOY sablefish but did not describe growth and condition effects. From a physiological perspective, the transition with ontogeny from warm surface waters to colder benthic habitat is likely accompanied by marked changes in growth and condition, which to our knowledge has not previously been documented for YOY sablefish.

In this study, we measured the effects of temperature on growth rates and consumption of post-settlement YOY sablefish (218–289 mm TL) in the laboratory during two separate feeding studies. Our objectives were to: 1) identify optimal temperatures for growth and consumption of YOY sablefish with abundant resources; 2) quantify relationships between temperature and growth and consumption; 3) derive parameters for the consumption function of a Wisconsin bioenergetics model for YOY sablefish; and 4) independently assess the performance of our models by forecasting growth and consumption of YOY sablefish in a second feeding study (2017). We hypothesized that the optimal thermal range for growth, consumption, and general condition of the larger sized YOY sablefish in this study would shift to lower temperatures when compared to the optimal thermal range of smaller sized YOY sablefish in previous studies. This hypothesis was based on previous observations of behavioral shifts in thermal tolerance between sablefish of different size classes described by Sogard and Olla (1998).

2. Methods

Two separate feeding studies were conducted on wild-caught sablefish during fall 2016 and 2017. The 2016 study was carried out for a duration of 3 weeks, from Oct. 11 to Nov. 2. YOY sablefish ranging in size from 218 to 289 mm TL were collected in surface trawls (Nordic 264 rope trawl, 10.2 cm mesh and 0.8 cm codend) 40 to 100 km offshore of Baranof Island and Kruzof Island, AK. (latitude 56.940 N, longitude -136.134 W) during the month of August 2016. All fish were transported to the flow-through seawater facility at Auke Bay Laboratories, Juneau AK, where they were initially quarantined for ~ 1 month in a separate holding tank at ambient temperature (6.8 °C) prior to experiments. During quarantine, fish were fed twice weekly to satiation on a ration of chopped fillets of frozen Pacific cod *Gadus macrocephalus*. Fish were kept on this diet throughout the course of the experiment.

At the onset of the experiment following the quarantine period, fish were randomly assigned to 1 of 5 temperature treatments: 5 °C, 8 °C, 12 °C, 16 °C, and 20 °C, and held at a natural photoperiod cycle (*i.e.*, lights were turned on and off to reflect natural daylight hours). Temperatures were achieved and maintained using the water warming and cooling systems in the Auke Bay Laboratory. Daily temperature checks indicated only minor daily fluctuations in experimental temperatures of < 0.2 °C. These temperatures were chosen since they encompass the known range of temperatures YOY sablefish may experience in the GOA. Fish were held in 1 of 2 tanks for a given temperature treatment, for a total of 10 tanks in the experiment (2 tanks each at 5