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

Joseph R. Krieger\*, Ashwin Sreenivasan, Ron Heintz

*NOAA – Alaska Fisheries Science Center, Auke Bay Laboratories, 17109 Point Lena Loop Rd., Juneau, AK, 99801, USA*

A B S T R A C T

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

temperatures). Each 50 l tank held 10 fish at a flow rate of 4 l min$^{-1}$. Ambient temperatures for each tank treatment were adjusted to treatment temperatures at a rate of 1 °C–2 °C per day and fish were allowed to acclimate for a period of 2 weeks. Following the acclimation period, fish were weighed to the nearest 0.01 g (wet mass) and measured to the nearest 1 mm (TL) to establish initial condition for the growth experiment (week 0). Fish were remeasured in the same manner 3 weeks later at the conclusion of the growth study (week 3). Fish in each tank were implanted with a uniquely numbered tag to allow tracking of individual fish growth throughout the experiment. Lengths and weights of fish in replicate tanks at both the initial and final measurements were not statistically discernible (t-test, P < 0.05; Table 1) between tanks of the same temperature, suggesting similar growth within treatments. As such, individual temperature treatments are discussed and analyzed as pooled tank replicates.

Temperature-dependent growth and consumption models were constructed by regressing observed individual specific growth rate (SGR), length, and consumption values against temperature for all tanks in the experiment. Models of SGR, length, and consumption were developed using a three-parameter polynomial function. In each case, inclusion of the third parameter produced an optimum R$^2$ value without unnecessarily over parameterizing the model. SGR was parameterized as % wet weight gain d$^{-1}$ based on observed individual growth in each temperature treatment. Consumption was parameterized as % final wet weight consumed d$^{-1}$ based on individual consumption. Models were fit using the "nls" function in R (Baty et al., 2015). A one-way analysis of variance (ANOVA) was used to assess differences in treatment response among temperature groups. If significant differences were found, a Tukey's Post-hoc test was performed to examine among group variation.

Using observed consumption values, we developed the consumption function of a Wisconsin-type bioenergetics model; uniquely parameterized for YOY sablefish. Bioenergetic models have been used to understand how fish growth and consumption vary with temperature and other environmental factors (Hansen et al., 1993; Deslauriers et al., 2017). Wisconsin-type bioenergetics models use species-specific information on growth, consumption, and respiration to derive temperature-dependent response functions which are then used to fit allometric relationship between individuals and physiological response (Adams and Breck, 1990; Hartman and Hayward, 2007).

Our consumption parameters of the Wisconsin bioenergetics model were derived from weight and consumption data from the 2016 trials. Fish were hand fed to satiation each day from a pre-weighed amount of Pacific cod fillets. Any food not consumed after 3 h was removed from the tank and weighed to determine how much food was consumed by a tank on a given day. Daily prey consumption (g g$^{-1}$ d$^{-1}$) was calculated for each fish, and the mean daily rate over the 23-d feeding trial allowed calculations of maximum daily consumption (Cmax).

### 2.1. Data analysis

SGR based on mass of YOY sablefish were determined using the following equation:

$$SGR = 100 * (e^g - 1), \tag{1}$$

where g is the instantaneous growth coefficient determined by the equation:

$$g = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}, \tag{2}$$

where $W_i$ is the wet weight (g) of an individual fish at time $t_i$. Consumption estimates for fish within a tank were expressed as the percentage of final wet body mass consumed per day using:

**Table 1**

Temperature-dependent response in Length Gain (mm d$^{-1}$), Specific Growth Rate (SGR; % final wet weight d$^{-1}$), Consumption (% final wet weight consumed d$^{-1}$), and Residual Condition Factor (from log-log length-weight regression) from 2016 feeding trials. Values are expressed as tank averages of mean individual growth ± standard deviation. Superscript letters designated statistically similar groupings in each category. Weight (g) and length are expressed as mean ± standard deviation.

| Temp Treatment (°C) | Initial Weight (g) | Final Weight (g) | Initial Length (TL mm) | Final Length (TL mm) | Length Gain | SGR | Consumption | Residual Condition Factor |
|---|---|---|---|---|---|---|---|---|
| 5 | 158.1 ± 31.9 | 187.2 ± 34.8 | 259.1 ± 15.8 | 268.5 ± 15.1 | 0.41 ± 0.11[d] | 0.74 ± 0.131[c] | 3.47 ± 0.56 | −0.004 |
| 8 | 168.6 ± 28.6 | 210.7 ± 32.1 | 264.7 ± 15.1 | 279.1 ± 15.1 | 0.62 ± 0.08[cd] | 1.09 ± 0.16[b] | 4.51 ± 0.65 | −0.002 |
| 12 | 161.1 ± 25.8 | 239.4 ± 33.9 | 263.5 ± 13.6 | 290.05 ± 13.9 | 1.16 ± 0.13[ab] | 1.66 ± 0.2[a] | 6.18 ± 0.56 | 0.002 |
| 16 | 161.9 ± 27.6 | 249.3 ± 41.4 | 261.3 ± 14.1 | 291.6 ± 15.5 | 1.32 ± 0.26[a] | 1.84 ± 0.36[a] | 6.91 ± 1.11 | 0.011 |
| 20 | 149.5 ± 25.2 | 195 ± 33.7 | 253.8 ± 14.7 | 273.4 ± 14.4 | 0.85 ± 0.33[bc] | 1.1 ± 0.39[b] | 7.23 ± 2.15 | −0.011 |

$$C_i = \frac{100 * \left(\frac{\Delta W_i}{\sum \Delta W_i}\right) * \frac{\sum(F_0 - F_r)}{\sum t}}{W_f},$$ (3)

where $C_i$ is the estimated consumption of an individual fish expressed as percent final body weight per day, $\Delta W_i$ is the difference in weight of an individual fish between the first and last day the fish was fed, $\Sigma \Delta W_i$ is the total weight difference of all fish in the tank over that time, $W_f$ is the final weight of the fish, $F_0$ is the mass of food offered to fish within a treatment tank, $F_r$ is the mass of food recovered, and $\Sigma t$ is the number of days fish were fed.

A log-log transformed length-weight regression was performed on data for surviving fish at the end of the experiment and resulting length-weight residuals were averaged among temperature replicates. Departures from the pooled mean were interpreted as an index of condition for fish grown at each temperature collected at the conclusion of the experiment.

Parameterization of the consumption function of the Wisconsin bioenergetics model was derived from the mean daily consumption rate of fish from the 2016 trial:

$$C = C\text{max} * f(T) * p(C\text{max}),$$ (4)

where $C$ is weight-specific consumption rate (g g$^{-1}$ d$^{-1}$), $C$max is the maximum daily feeding rate (g g$^{-1}$ d$^{-1}$), $f(T)$ is a temperature dependence function, and $p(C$max$)$ represents the feeding level expressed as a proportion of $C$max. Maximum feeding rate was computed as an allometric function of fish weight:

$$C\text{max} = CA * W^{CB},$$ (5)

where $CA$ is the intercept for consumption allometric mass function, $CB$ is the slope for consumption allometric mass function, and $W$ is the weight (g) of fish. The temperature ($T$) dependence function ($f(T)$) used to model YOY sablefish consumption was that described in Deslauriers et al. (2017):

$$f(T) = V^X * e^{(X*(1-V))},$$ (6)

where:

$$V = (CTM - T)/(CTM - CTO)$$

$$X = \left(Z^2 * \left(1 + \frac{40}{Y}\right)^{0.5}\right)^2 / 400$$

$$Z = \ln(CQ) * (CTM - CTO)$$

$$Y = \ln(CQ) * (CTM - CTO + 2)$$

Parameter values for $CTO$ (optimal temperature for consumption) and $CTM$ (maximum water temperature above which consumption ceases) were derived from temperature-dependent consumption responses. $CQ$ (Q$_{10}$ temperature coefficient) was set at 2.2 based on a previous study of Sablefish bioenergetics (Harvey, 2009). The proportionality constant ($p$) was held at 1 for both the 2016 and 2017 trials since all fish were fed *ad libitum*.

### 2.2. Model validation

To assess the performance of our growth model developed from the 2016 YOY sablefish trials, we projected growth from initial mass measurements of the 2017 YOY sablefish (195 mm–273 mm TL) to final mass measurements 5 weeks later and compared the predicted values to the observed final values from the 2017 experiment. Fish in the 2017 trials were held at conditions identical to those described above for the 2016 except for minor differences in specific temperatures and range of temperatures (6.5 °C, 12.7 °C, 16.8 °C, and 22 °C). Initial mass values ($W$) were set based on average mass of fish at the 2017 feeding trial (120 g). The growth model was validated by comparisons between observed and estimated final mass of the 2017 YOY sablefish using
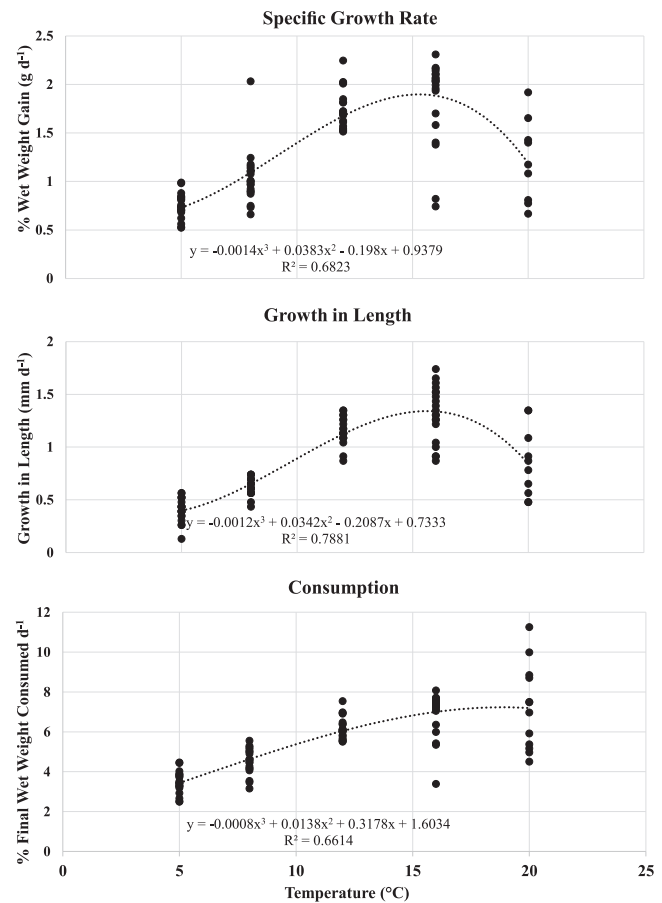


**Fig. 1.** Temperature-dependent specific growth rate (SGR), growth in length, and consumption, for YOY sablefish (218–289 mm TL). Values are based on individual values of fish from each temperature treatment following 3 weeks of growth at each temperature. A third-order polynomial function describing the temperature-dependent physiological response of each parameter is given.

three criteria (Mayer and Butler, 1993): (1) mean absolute percent error calculated as:

$$E\% = 100 * \frac{\left[\sum \left(\frac{W_o - W_p}{W_o}\right)\right]}{n},$$ (7)

where $W_o$ represents observed values, $W_p$ predicted values and $n$ the number of pairs; (2) modelling efficiency:

$$E_F = 1 - \sum (W_o - W_p)^2 / \sum (W_o - W_m)^2,$$ (8)

where $W_o$ and $W_p$ are the same as previously and $W_m$ is the mean of observed values; and (3) a paired sample *t*-test.

Mean absolute percent error is a measure of deviance based on the differences between predicted and observed value, where lower percent error is reflective of closer value agreement. Modelling efficiency is a dimensionless statistic which relates model predictions to observed data using a range of 0–1 with values closer to 1 representing "near-perfect" models (Mayer and Butler, 1993).

The parameters for the consumption function of the bioenergetics model developed from the 2016 feeding trials were also validated by the comparison of observed and estimated food consumption rates from the 2017 feeding trials using the same three criteria detailed above. These validation criteria were chosen both for their robustness in their ability to evaluate model performance (Mayer and Butler, 1993) and their use in the evaluation of other bioenergetics models (Karjalainen et al., 1997; Zweifel et al., 2010).

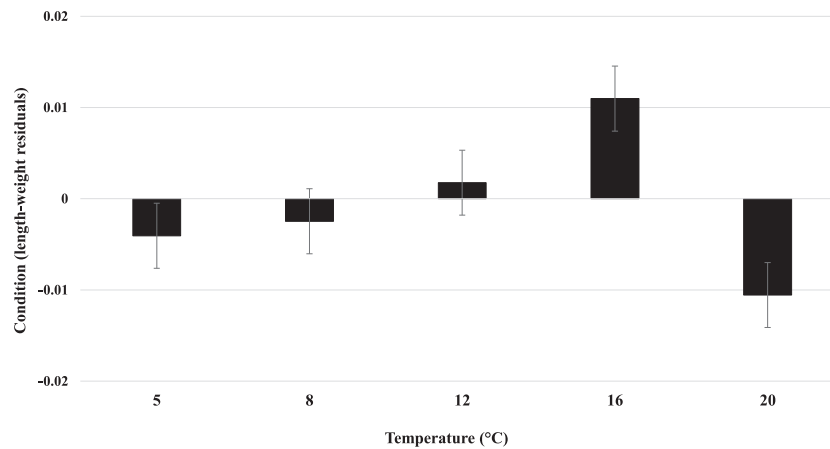All statistical analyses were performed using R-v 3.1.3 (R

**Fig. 2.** Temperature-dependent condition factor of YOY sablefish (218–289 mm TL). Condition is based on the length-weight residuals of fish following 3 weeks of growth at each temperature. Mean ( ± SD) values are based on individuals from duplicate tanks at each temperature.

Development Core Team, 2008).

## 3. Results

Temperature exerted clear effects on growth rate of YOY sablefish (ANOVA, F = 39.8, P < 0.001). Though fish were able to survive at all temperatures, dramatic reductions in growth were observed for fish at low (5 °C, 8 °C), and high (20 °C) temperatures. In the 20 °C treatment YOY sablefish mortality started after 1 week, with only 50% of fish surviving to week 3. As such, final analysis was based on fish that survived the duration of the experiment (n = 20 for 5 °C, 8 °C, 12 °C, and 16 °C treatments; n = 10 for 20 °C treatment). Daily individual growth in length varied from 0.13 mm d$^{-1}$ to 1.74 mm d$^{-1}$ (Fig. 1). For wet weight, individual SGR ranged from 0.52 to 2.31% wet weight d$^{-1}$ (Fig. 1). The general trend exhibited by fish was a rapid increase in growth rate from 5 °C to 12 °C, a more gradual rise from 12 °C to 16 °C, and a sharp decline at 20 °C. Tukey's post-hoc tests comparing growth rates among treatments demonstrated a significant difference between the middle range of temperatures and the endpoints of ≤ 8 °C and 20 °C (Table 1). The third order polynomial used to describe individual SGR as a function of temperature explained 68.2% of the observed variation. Using this function, maximum SGR was estimated at 15.1 °C (Fig. 1). Solving the SGR model equation for zero, 22.4 °C is the predicted temperature at which growth stops or becomes negative for YOY sablefish (death). Indeed, fish from our 2017 experiments were unable to withstand prolonged exposure to 22 °C water on *ad libitum* ration, resulting in high mortalities and subsequent dismissal of growth and consumption data from this treatment in our analysis. Based on these observations, CTM for our consumption function in the Wisconsin bioenergetics model was set at 22.4 °C.

Consumption rates increased sharply with temperature to ~ 18 °C, then gradually rising until appearing to approach an asymptote near 20 °C (Fig. 1; Table 1). The third order polynomial used to describe

individual consumption as a function of temperature explained 66.1% of the observed variation. The highest consumption rate generated from this polynomial function corresponded to a temperature of 17.6 °C. The maximum consumption parameter (CTO) was therefore set to 17.6 °C.

Residuals of the length-weight regression of fish taken at the end of the experiment showed a clear distinction in fish condition among temperature treatments. YOY sablefish condition was above average at 12 °C and 16 °C and below average at 5 °C, 8 °C, and 20 °C (Fig. 2). The narrow thermal range of positive condition, which overlaps with the similarly narrow range for optimal SGR, suggests YOY sablefish growth and development may be dramatically hindered by small shifts in local water temperatures.

We incorporated data from the 2016 feeding trials to estimate the consumption parameters of our bioenergetics model (Table 2). Maximum daily consumption was lowest at 5 °C, peaked at 16 °C, and declined at 20 °C (Fig.3). The power function used to describe the allometric relationship between weight and consumption was based on feeding data from the 16.0 °C treatment since this temperature was closest to our estimated CTO from the 2016 trials (Cmax = 0.1159 * W$^{-0.°93}$). Consumption parameters for the Wisconsin bioenergetics model derived for YOY sablefish are presented in Table 2.

Our consumption parameters developed from the 2016 trials were able to provide reasonable estimates of maximum daily consumption of fish in the 2017 trials. Mean absolute percent error of the bioenergetics model was 8.30%, modelling efficiency was calculated at 91.8%, and no significant difference was found between observed and estimated consumption rates (paired sample *t*-test, P = 0.47). Estimates of Cmax from the model consumption function were within one standard deviation (SD) of observed mean weight-adjusted consumption rates for all temperature treatments. Consumption was slightly underestimated in for fish in the 6.5 °C and 16.8 °C temperature treatments (8.03% and 4.97%, respectively) and overestimated in the 12.7 °C treatment (11.1% ; Table 3).

Applying the model developed for YOY sablefish SGR from the 2016 trials to YOY sablefish from the 2017 trials showed agreement between observed and predicted biomass gains. We fitted the SGR model from the 2016 trials (Fig. 1) with averaged tank temperatures used in 2017 trials and projected biomass gained through the end of a 5-week growth experiment. Variation between observed and predicted biomass from the 2017 temperature treatments was minimal (Table 4), and biomass values did not differ significantly (paired sample *t*-test, P > 0.05 for all comparisons). Mean absolute percent error was 1.5% and modelling efficiency was calculated as 99.9%. These results corroborate our SGR model for YOY Sablefish (218–289 mm TL) feeding at maximum ration across a range of temperatures.
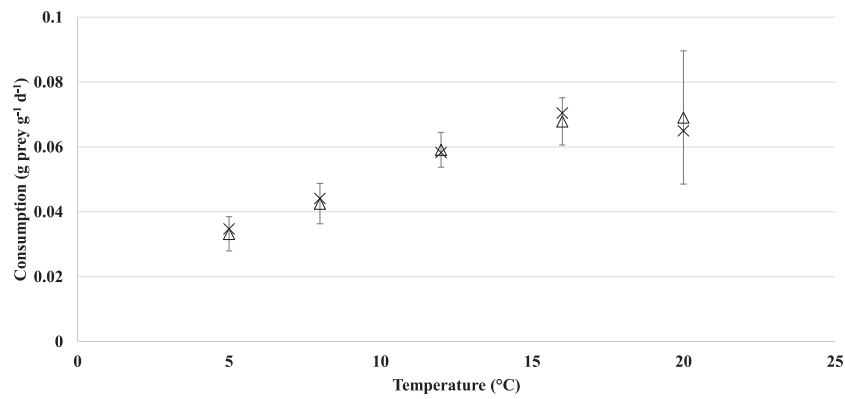
**Table 2**
Parameters of the consumption function of bioenergetics model calculated for YOY sablefish based on 2016 feeding trials.

| Parameter | Abbreviation | Coefficient |
|---|---|---|
| Intercept | CA | 0.1159 |
| Slope | CB | −0.093 |
| Optimum water temperature (T) | CTO | 17.6 |
| Maximum water temperature (T) | CTM | 22.4 |
| Temperature quotient | CQ | 2.2 |
| Initial Weight (g; 2017 trials) | W | 120 |

**Fig. 3.** Mean ( ± SD) prey consumption rates from the 2016 (hollow triangles) trials for YOY Sablefish during laboratory experiments. Estimates of consumption rates calculated using the consumption function of the bioenergetics model (X) are provided for reference.

**Table 3**
Comparison of observed *versus* predicted consumption rates from 2017 laboratory trials. Predicted consumption rates (g consumed $d^{-1}$) were estimated using the consumption function parameters derived from 2016 trials presented in Table 2. Observed consumption rates are treatment mean values ± standard deviation.

| Trial Year | Temp. Treatment (°C) | Observed Consumption | Predicted Consumption | Variation (% difference) |
|---|---|---|---|---|
| 2017 | 6.5 | 5.09 ± 0.63 | 4.68 | 8.03 |
| 2017 | 12.7 | 5.65 ± 1.14 | 6.32 | −11.1 |
| 2017 | 16.8 | 9.24 ± 1.15 | 8.78 | 4.97 |

**Table 4**
Comparison of observed *versus* predicted mean tank biomass from 2017 YOY sablefish trials as predicted by the SGR model developed from 2016 trials (Fig. 1).

| 2017 Trial Temperatures (°C) | 2017 Observed Biomass (g) | 2017 Predicted Biomass (g) | Variation (% difference) |
|---|---|---|---|
| 6.9 | 4175.7 | 3778.9 | 9.5 |
| 12.7 | 4559.2 | 4655.1 | −2.1 |
| 16.8 | 1007.1 | 1035.9 | −2.9 |

## 4. Discussion

We found sablefish performance (SGR and condition) was optimum within a thermal range of 12 °C – 16 °C. Outside of these endpoints, dramatic declines in performance were observed, with mortalities occurring following prolonged exposure to water temperatures of ≥ 20 °C. To corroborate these observations, we compared YOY sablefish temperature-dependent growth and consumption from feeding trails conducted in 2016 to a second, independent trial conducted in 2017 and found that the model developed for growth of the 2016 fish accurately predicted growth of fish in 2017, while the consumption function provided reasonable estimates of maximum consumption rates. These data expand on previous studies of YOY sablefish by linking temperature-dependent performance of individuals through their first summer, into the fall, and the onset of winter.

Our hypothesis that the thermal optima for YOY sablefish would shift to lower temperatures with increased size and age was supported. For smaller-sized sablefish (50–102 mm TL), Sogard and Olla (2001) found optimal growth occurred within a range of 16 °C – 20 °C and that consumption increased until 22 °C before dramatically declining. In that same study, fish were maintained and even thrived at temperatures of 20 °C; the temperature at which significant mortalities were found to occur in our experiment. Sogard and Spencer (2004) found similar results for sablefish (36 mm – 50 mm TL) held at 20 °C on varying ration levels. Comparisons of YOY sablefish from different size classes indicates a shift in thermal tolerance and physiological response as fish grow and begin to settle in benthic coastal habitat which occurs in the wild when fish achieve ∼ 200 mm TL in size (Rutecki and Varosi, 1997;

Sigler et al., 2001). The transition from relatively warm to relatively cold water tolerance in sablefish is not surprising, as adults are found at depths exceeding 300 m where water temperatures average 4 °C – 6 °C. However, understanding the influence of environmental perturbations during this transition is critical for understanding impacts to early recruitment.

Decreased optimal temperature for growth with increased juvenile age is consistent with observations in other species such as Arctic cod *Boreogadus saida* (Laurel et al., 2017), and Pacific cod (Hurst et al., 2010; Sreenivasan and Heintz, 2016). Growth rates observed for YOY sablefish are among the fastest ever reported for teleosts under experimental conditions (Sogard and Olla, 2001). Rapid growth during the early age-0 stage is critical for sub-arctic marine fishes surviving their first overwintering period (Heintz et al., 2013). In the summer, higher temperature for optimal performance of small YOY sablefish in the neuston likely is an adaption to maximize first summer growth before transitioning to colder, deeper water in the fall. As YOY develop, growth rate is likely reduced as energy allocation is reprioritized from protein synthesis (somatic growth) to lipid accumulation. This ontogenetic shift in temperature-performance sensitivity and energy allocation probably is an important adaption for survival, as size- and resource-dependent starvation in the winter are increasingly becoming recognized as important regulating factors in high latitude fisheries (Heintz et al., 2013; Laurel et al., 2016, 2017).

Estimated maximum consumption rates derived from the YOY sablefish consumption function demonstrated reasonable correspondence to observed trends in the 2017 laboratory trials. The high modeling efficiency score, low absolute percent mean error, and close match

between observed and predicted consumption values all compare favorably to bioenergetics models developed for other species (Kitchell et al., 1977; Zweifel et al., 2010). For example, Karjalainen et al., (1997) developed consumption parameters for a bioenergetics model for coregonids, roach *Rutilus rutilus*, and perch *Percu fluviutilis* and reported a modeling efficiency score of 0.90, 0.97, and 0.93, respectively. In the same study, mean absolute percent error ranged from 10% to 24%. These validation results corroborate the ability of our consumption parameters to accurately describe the feeding response of YOY sablefish.

While a promising first step in describing bioenergetic relationships of YOY sablefish, a complete Wisconsin bioenergetics model requires species-specific information on energetics, temperature-dependent consumption, respiration and growth response, as well as information on prey quality (proximate composition; Deslauriers et al., 2017). Harvey (2009) developed parameters for a sablefish bioenergetics model by incorporating species-specific information from a number of previous studies. However, parameter values in that study were derived from information collected at multiple life-stages and a variety of diet and temperature scenarios. In the present study, we demonstrated how growth and consumption response can change dramatically with ontogeny, even over the course of several weeks. In order to accurately assess the physiological response and resulting condition of sablefish to varying temperature and diet scenarios, life-stage specific parameter estimates are needed. A logical next step from the present study should explore sablefish and prey energetics and include the development of respiration parameters needed to outfit the respiration function of the bioenergetics model.

Sablefish have traditionally been described as belonging to one of two major stocks. The northern stock, comprised of fish found in the GOA and waters of British Colombia, and the southern stock encompassing those fish that are found in the waters of the continental USA (Hanselman et al., 2013). The majority of studies examining temperature-dependent effects on sablefish have occurred with individuals collected from the southern stock; for example, Sogard and Olla (2001) used fish from areas near Oregon, USA. However, sablefish of the North Pacific Ocean are known to migrate great distances and significant gene flow is thought to occur between the northern and southern populations (Kimura, 1980; Gharrett et al., 1982; Tripp-Valdez et al., 2012). In a recent study, Jasonowicz et al. (2016) used restriction site-associated DNA sequencing to assess the population genetic structure of sablefish collected in bottom trawl and long-line surveys from throughout their known range. The authors of that study were "unable to find evidence that would suggest there are genetically distinct populations for Sablefish with their North American range" (p. 383; Jasonowicz et al., 2016). In addition, tagging studies (Kimura and Zenger, 1997; Hanselman et al., 2015) and recently developed individual-based models (Siddon et al., 2016) have demonstrated that adults traverse great distances; covering the expanse of ocean within and between the GOA and coastline of the continental USA. Thus, although the changes in physiological response to temperature through ontogeny outlined above were observed for fish collected from the northern extent of the known range for sablefish, our findings likely have implications for sablefish throughout the northeast Pacific.

Given the large geographic range and narrow window of thermal optima observed through early development, sablefish are particularly vulnerable to changes in local water temperatures, and may be disproportionately impacted by climate change driven habitat alteration. Changes by as little as a degree or two can have major physiological implications. Whereas elevated temperatures above 20 °C may be lethal, temperatures below 12 °C may have non-lethal effects on growth and energy allocation. While YOY sablefish have been shown to prioritize lipid accumulation over somatic growth at colder temperatures (Sogard and Spencer, 2004), presumably as a buffer against resource scarcity, reduced length-at-age may lead to increased predation risk. The balance between protein (growth) and lipid synthesis in

response to variable temperature and diet quality has clear implications on survival through early development and resulting recruitment success. Future work to understand how lipid and protein synthesis is prioritized during the sablefish's first year of life is a crucial next step in order to further our understanding how changes in temperature will impact YOY sablefish physiology. In addition, expanding laboratory trials to include not only likely temperature scenarios of YOY sablefish but also diet regimes, would provide more accurate parameter values for inclusion in future bioenergetics models, a better understanding of recruitment variability, and valuable input as ecosystem indicators for more effective ecosystem-based management.

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