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Growth of young-of-year sablefish (*Anoplopoma fimbria*) in response to temperature and prey quality: Insights from a life stage specific bioenergetics model

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ABSTRACT

The first year is typically a bottleneck for juvenile fishes and survival at this stage can be dictated by environmental conditions affecting growth, such as temperature and food availability. Shifts in environmental conditions—and the resulting effects on growth—are of particular concern for high latitude species, which are experiencing more pronounced impacts of climate change. We measured effects of temperature on growth, consumption, and respiration of young-of-year (YOY) Sablefish (218–289 mm TL; *Anoplopoma fimbria*) in laboratory trials. Physiological response functions were used to outfit a novel, life stage specific bioenergetics model. Average daily growth rates ranged from 0.82 to 3.42 $g\ d^{-1}$ (46.7 to 122 $J\ g^{-1}\ d^{-1}$), with optimum growth occurring at 12–16 °C and declining substantially outside of this range. We then validated the model by comparing model estimates of growth to known growth rates for a separate cohort of Sablefish reared under controlled conditions. Sensitivity analysis indicated that the consumption-related parameters had the greatest influence on model outputs. As such, consumption parameters should be determined with care. Finally, we used the model to characterize the conditions necessary for wild YOY Sablefish to successfully settle from neustonic to demersal stages by modeling temperature-prey scenarios that reflect the transition from neustonic offshore to demersal nearshore habitats observed over the period from August to October. Our findings suggest that Sablefish in the Gulf of Alaska could thrive under warming ocean conditions given sufficient food, which corroborates reports of high Sablefish recruitment events following a marine heat wave in 2014.

1. Introduction

Understanding the physiological and behavioral response of an organism to its environment is fundamental to understanding ecological processes (Begon et al., 1986; Odum, 1997) and is of tremendous practical value for anticipating climate change effects on harvested species. However, knowledge of biological responses to environmental drivers is often incomplete (Stearns, 1992; Hendry and Stearns, 2004) and limited to the most well-studied life stages of a species (Kennedy and Gray, 1993). Stages of life history are defined by developmental milestones (e.g., beginning of exogenous feeding, gonad development) that often lead to changes in resource use or physiological responses to external factors (Hendry and Stearns, 2004). Knowledge of ontogenetic shifts in response to environmental variability can be especially crucial for early life history stages of fishes because they are susceptible to mortality through combinations of biotic (e.g., predation, resource availability; Garvey et al., 1994; Garvey and Marschall, 2003) and abiotic (e.g., temperature and oxygen; Chandler and Bjornn, 1988; Einum and Flemming, 2000) factors. Knowledge of physiological responses of larvae and juveniles to shifts in environmental conditions is critical for understanding how a changing ocean will ultimately affect survival through the first year, which is typically a bottleneck for fish populations (Diana, 2004).

Shifts in environmental conditions and the resulting effects on physiological processes are of particular concern for fish found in higher latitudes, which are experiencing more pronounced impacts of climate change. Fish in arctic and subarctic regions experience severe winter conditions, such as resource scarcity and temperatures often nearing lower thermal limits (Hurst, 2007). Larval and juvenile fishes in higher latitudes are more dependent on successful foraging and

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favorable habitat conditions during summer and fall growth periods in order to obtain a suitable size and physiological state to survive through their first winter (Heintz et al., 2013). Thus, external forces that alter resource availability or local environmental conditions during early development will have a disproportionate effect on overwinter survival and recruitment rates. For fishes in the Gulf of Alaska (GOA), this may pose a more acute problem, as a recent marine heat wave has been implicated in widespread changes in community structure and composition of fisheries (Cavole et al., 2016). Yet, the effects of these phenomena on recruitment dynamics resulting from changes in physiological condition of larval and juvenile fishes remain unclear.

Sablefish (*Anoplopoma fimbria*), an economically important groundfish in the North Pacific, may be particularly susceptible to changes in environmental conditions given its unusual early life history. During early development, Sablefish prioritize energy for protein synthesis (somatic growth) over lipid accumulation; their growth rates under laboratory conditions are among the highest observed in teleosts, > 3 mm or 3–6% body weight d^{-1}, (Sogard and Spencer, 2004). This strategy of rapid growth is important to survival, but the conditions necessary for maintaining these rates under natural conditions are unknown. Once young Sablefish reach a size to near 125 mm TL, they transition from surface waters to nearshore benthic habitats where they spend their first winter (Maloney and Sigler, 2008). During this transition to nearshore habitat, growth rates slow and thermal tolerances shift to colder temperatures (Krieger et al., 2019). These internal and external changes could have pronounced effects on the physiological condition of young Sablefish through early developmental stages. If young-of-year (YOY) Sablefish are to survive their first winter they must acquire sufficient lipid reserve during their first summer and fall (i.e., critical size hypothesis; Beamish and Mahnken, 2001; Heintz et al., 2013). Thus, factors influencing physiological condition of young Sablefish during this time can have implications for Sablefish recruitment success.

In fisheries, bioenergetics models have been used to understand how fish growth and consumption respond to variable environmental conditions (e.g., temperature, prey quality; Kitchell et al., 1977; Deslauriers et al., 2017). Bioenergetics models use species-specific information to equate consumption to growth, diet, and temperature- and size-dependent respiration rates affording the ability to quantify environmental effects on growth or consumption (Kitchell et al., 1977). Harvey (2009) parameterized a bioenergetics model for Sablefish using values derived from the literature and incorporating information collected from multiple life stages. However, given that many fish undergo pronounced morphological and physiological transitions through ontogeny (Werner and Gilliam, 1984; Stearns, 1992), a general bioenergetics model derived of life stage indiscriminant information may not accurately describe physiological responses of YOY Sablefish to environmental conditions. For instance, Krieger et al. (2019) identified distinct shifts in rates of growth, consumption, and condition as a function of temperature between larger sized (218–289 mm TL) YOY Sablefish and those of smaller sized (50–102 mm TL) YOY Sablefish from a previous study (Sogard and Olla, 2001). Similarly, Sreenivasan and Heintz (2016) found distinct differences in rates of both growth and consumption of juvenile Pacific Cod (*Gadus microcephalus*; 135–194 mm TL) compared to rates of smaller sized juveniles (49–52 mm TL) described by Hurst et al. (2010).

In this study, our objectives were to: 1) use controlled laboratory conditions to parameterize a stage specific bioenergetics model describing the growth of YOY sablefish (218–289 mm), 2) validate the model by estimating the growth of a separate cohort of fish grown under controlled conditions, and 3) use the model to identify the conditions necessary for wild YOY to successfully settle from the neustonic to demersal stages.

2. Methods

2.1. Growth and consumption experiments

Growth and consumption were measured for wild-caught YOY Sablefish during two separate feeding experiments, in 2016 and 2017. Experimental conditions for Sablefish reared during the 2016 study are similar to those described below for the 2017 study and are detailed in Krieger et al. (2019). The primary difference between the two years was that the 2017 study grew fish over a longer period of time (7 weeks compared to 3 in 2016) and included additional temperature treatments within the range of temperatures that experimental fish were exposed to in the 2016 study (5 °C, 8 °C, 12 °C, 16 °C, and 20 °C; Krieger et al., 2019). The 2017 study was carried out over a period of seven weeks, from October 24 to December 15. YOY Sablefish were collected in surface trawls (Nordic 264 rope trawl, 10.2 cm mesh and 0.8 cm cod end) approximately 40 to 60 km south of Kayak Island, Alaska, USA (latitude 56.761°N, longitude −144.307°W) in August 2017. Fish were transported to Auke Bay Laboratories, Juneau, AK, and housed in the onsite flow-through seawater facility. Fish were initially quarantined in separate holding tanks at 7 °C and fed once weekly to satiation. Fish were held in these conditions for a period of six weeks in an effort to maintain their size at capture for the start of the feeding study. During quarantine and subsequent feeding studies, fish were fed on a ration of chopped fillets of frozen Pacific Cod.

Following the quarantine period, fish were randomly assigned to 1 of 4 temperature treatments: 6.5 °C, 12.7 °C, 16.8 °C, or 19.5 °C, and held on a natural day / night photo cycle. Within each temperature treatment, fish were divided into 2 tanks for a total of 8 tanks (4 temperatures, each with 2 tanks). At the start of the experiment, each 50 L tank held 14 fish at a flow rate of 4 $L\ min^{-1}$. Tank temperatures were gradually changed from 7 °C to their desired treatment temperatures at a rate of 1–2 °C per day over a one week period. Once all tanks were at their experimental temperature, fish were allowed to acclimate for a period of two weeks. Following this acclimation period, fish in each tank were implanted with a uniquely numbered t-bar anchor tag (Floy Tag & Manufacturing Inc.) to allow tracking of individual fish growth throughout the experiment. Each fish was measured to the nearest 1 mm (TL) and weighed to nearest 0.01 g (wet mass) to establish initial condition for the growth experiment (week 0). Fish were re-measured two weeks (week 2), five weeks (week 5), and seven weeks later at the conclusion of the growth study (week 7). Lengths and weights of fish in replicate tanks were not statistically discernible between tanks of the same temperature at each measurement period (*t*-test, $P > .05$; Table 1). As such, individual temperature treatments were analyzed as pooled tank replicates.

Two Sablefish from each treatment tank ($n = 16$ total fish) were sacrificed at week 0 to determine their energy density values ($J\ g^{-1}$); energy density was also determined for Pacific Cod prey used in this study. Sampled fish were euthanized in a solution of tricaine methanesulfonate (MS-222; 0.025 $g\ l^{-1}$) and stored individually at −20 °C until analysis. Energy densities of Sablefish and Pacific cod were measured by bomb calorimetry. Whole fish (excluding stomach contents from sampled Sablefish) were homogenized while frozen to a puree of uniform color and consistency from which random aliquots were selected for chemical analysis. Samples for bomb calorimetry were dried and combusted using a Parr 6725 semi-mirco bomb calorimeter. Dried-homogenates were pressed into pellets weighing at least 25 mg prior to combustion.

2.2. Bioenergetics model parameterization

Our bioenergetics model for YOY Sablefish was developed following the general form of the fish bioenergetics model, which uses the core thermodynamic equation:

Table 1
Length (TL mm) and wet weight (g) measurements of YOY Sablefish measured at set intervals throughout the 2016 and 2017 feeding experiments. Values are mean (± standard deviation) tank measurements for each temperature treatment.

		Sampling period							
		Initial		Week 3		Week 5		Week 7	
Year	Temperature (°C)	Length	Weight	Length	Weight	Length	Weight	Length	Weight
2017	6.5	238.9 (10.7)	97.6 (14.5)	250.9 (10.3)	129.7 (17.2)	264.1 (10.6)	149.1 (19.0)	269.7 (10.7)	159.9 (21.9)
	12.7	244.8 (12.1)	101.1 (15.3)	265.0 (12.4)	141.3 (19.9)	289.9 (13.7)	190.0 (29.9)	NA	NA
	16.8	245.1 (12.3)	103.7 (16.9)	269.7 (13.7)	150.9 (25.0)	298.7 (12.0)	201.4 (34.8)	NA	NA
2016[a]	5	259.1 (15.8)	158.1 (31.9)	268.5 (15.1)	187.2 (34.8)	NA	NA	NA	NA
	8	264.7 (15.1)	168.6 (28.6)	279.1 (15.1)	210.7 (32.1)	NA	NA	NA	NA
	12	263.5 (13.6)	161.1 (25.8)	290.1 (13.9)	239.4 (33.9)	NA	NA	NA	NA
	16	261.3 (14.1)	161.9 (27.6)	291.6 (15.5)	249.3 (41.4)	NA	NA	NA	NA
	20	253.8 (14.7)	149.5 (25.2)	273.4 (14.4)	195 (33.7)	NA	NA	NA	NA

[a] From Krieger et al., 2019

$$C = G + R + SDA + U + F \tag{1}$$

where the rate of consumption C, is equal to the change in growth G, plus the sum of energy costs of respiration R, specific dynamic action SDA, excretion U, and egestion F over a specified time interval. The units or currency of the model are joules per gram of fish per day (J g^{-1} d^{-1}). The C and R terms represent functions that are directly dependent on fish weight (W, in grams) and temperature (T, °C). Estimates of optimal and maximum temperatures and Q_{10} rate (e.g., rate at which standard respiration increases with a 10 °C increase) are typically derived empirically or through direct observations, and drive the temperature-dependence functions ($f(T)$) for both consumption and respiration (Table 2). For a more detailed description of these equations and their derivation see Kitchell et al., 1977 and Deslauriers et al. (2017). In mature fishes, growth G can also describe energy that is allocated to gonadal development; however, the fish used in our experiment were not reproductively mature. As such, energy allocated to growth was assumed to be solely for somatic growth. In the present study, C and G are estimated by feeding trials and Eq. (1) is rearranged to solve for R.

Species-specific parameters for the YOY Sablefish bioenergetics model were derived from laboratory trials during the 2016 feeding study and taken from available literature when not measured directly. The growth G parameter was determined for individual fish using specific growth rates (SGR) calculated using the following equations (Laurel et al., 2016; Koenker et al., 2018; Krieger et al., 2019):

$$SGR = 100 * (e^{g}-1) \tag{2}$$

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

$$g = \frac{\ln WW_2 - \ln WW_1}{t_2 - t_1} \tag{3}$$

where WW_i is the wet weight (g) of an individual fish at time t_i, and $i = 1$ is the initial measurement and $i = 2$ is the final measurement over a specific interval. SGR of individual fish, in units of % final wet weight gained per day (g d^{-1}), were then divided by 100 and multiplied by the mean energy density of YOY Sablefish (Table 3). This provided the growth term G for the bioenergetics model in units of J g^{-1} d^{-1}.

Table 2
Equations used in the life stage specific bioenergetics model.

Physiological Function	Equation
Respiration	$R = RA * W^{RB} * f_R(T) * ACT * w$, where $f_R(T) = \mathrm{RV}^{\mathrm{RX}} * e^{(\mathrm{RX} * (1\text{-}\mathrm{RV}))}$ $\mathrm{RV} = (RTM - T) / (RTM - RTO)$ $\mathrm{RX} = \mathrm{RZ}^2 * (1 + (1 + 40 / \mathrm{RY})^{0.5})^2) / 400$ $\mathrm{RZ} = \ln(RQ) * (RTM - RTO)$ $\mathrm{RY} = \ln(RQ) * (RTM - RTO + 2)$ $w = 13{,}560$ J * g $O2^{-1}$
Consumption	$C = CA * W^{CB} * P * f_C(T)$, where $f_C(T) = \mathrm{V}^{\mathrm{X}} * e^{(\mathrm{X} * (1 - \mathrm{V}))}$ $\mathrm{V} = (CTM - T) / (CTM - CTO)$ $\mathrm{X} = \mathrm{Z}^2 * (1 + (1 + 40 / \mathrm{Y})^{0.5})^2) / 400$ $\mathrm{Z} = \ln(CQ) * (CTM - CTO)$ $\mathrm{Y} = \ln(CQ) * (CTM - CTO + 2)$
Specific dynamic action	$S = \mathrm{SDA} * (C - F)$
Egestion	$F = \mathrm{FA} * C$
Excretion	$U = \mathrm{UA} * (C - F)$

Details on the parameterization of the consumption function of the bioenergetics model are described in Krieger et al. (2019) and are summarized here. The consumption function was derived from the mean daily consumption rate:

$$C = Cmax * f_C(T) * p(Cmax) \tag{4}$$

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

Table 3
Parameter values (± standard deviation) for YOY Sablefish bioenergetics models. Source of individual parameter value denoted by superscript and listed below.

Parameter	Description	YOY Sablefish
CA	Intercept for consumption allometric function (g $g^{-1}d^{-1}$)	0.1159[b]
CB	Slope for consumption allometric function	-0.093[b]
CQ	Q_{10} for consumption	2.2[b]
CTO	Optimal temperature for consumption (°C)	17.6[b]
CTM	Maximum temperature for consumption (°C)	22.4[b]
RA	Intercept for respiration allometric function (g O_2 $g^{-1}d^{-1}$)	0.0259[a]
RB	Slope for respiration allometric function	-0.359[a]
RQ	Q_{10} for respiration	1.9[c]
ACT	Activity Multiplier	1[c]
RTO	Optimal temperature for respiration (°C)	20[a]
RTM	Maximum temperature for respiration (°C)	24[a]
SDA	Specific dynamic action	0.163[d]
UA	Excretion	0.047[c]
FA	Egestion	0.104[d]
ED Pred	Energy density of predator (Sablefish, J g^{-1})	6230 ± 470[a]
ED Prey	Energy density of prey (J g^{-1})	3082 ± 318[a]

Source
[a] Current Study
[b] Krieger et al. (2019)
[c] Sullivan and Smith Jr. (1982)
[d] Hanson et al. (1997)

$$Cmax = CA * W^{CB} \quad (5)$$

where *CA* is the intercept of the mass-dependent consumption function, *CB* is the slope of the mass-dependent consumption function, and *W* is the weight (g) of an individual fish. For the weight parameter *W* we used average initial wet weights for each temperature treatment. The temperature (*T*) dependence function ($f_C(T)$) used to model YOY Sablefish consumption is shown in Table 2. Optimal temperature for consumption (*CTO*) and maximum water temperature above which consumption ceases (*CTM*) values were developed by Krieger et al. (2019). The value for Q_{10} (*CQ*) was calculated using the temperature-dependent consumption equation derived by Krieger et al. (2019). The proportionality constant (*p*) was held at 1 since all fish were fed *ad libitum*.

We used the *U* (excretion) value from Sullivan and Smith Jr. (1982) who measured metabolic functions of Sablefish from a range of sizes and ages, including YOY and age-1 individuals. Since we did not directly estimate *SDA* and *F* in our study, we used the values presented in another Sablefish bioenergetics model by Harvey (2009) who in turn derived these values from Hanson et al. (1997).

The respiration function of the bioenergetics model is derived as:

$$R = f_R(W) * f_R(T) * ACT \quad (6)$$

where *R* is the specific rate of respiration (g O_2 g^{-1} fish d^{-1}), ($f_R(W)$) is a weight dependence function for respiration, ($f_R(T)$) is a temperature dependence function for respiration, *W* is the weight (g) of fish as defined above, and ACT is an activity multiplier that scales respiration with activity level.

To estimate *R* for individual fish, we rearranged the bioenergetics equation (Eq. (1)) to solve for *R*, given values of *G*, *C*, *SDA*, *U*, and *F*. Individual respiration values (in J g^{-1} d^{-1}) were then converted into g O_2 g^{-1} fish d^{-1} (*R*) using the oxy-calorific coefficient value of 13,560 J g O_2^{-1}. The temperature dependence function for respiration ($f_R(T)$) used to model YOY Sablefish performance is shown in Table 2. We set *RTO* to the highest temperature at which we observed fish to survive through the duration of experimental trials (20 °C). *RTM* was set to 24 °C based on observations of mortalities at prolonged exposure to this temperature in smaller sized YOY Sablefish (Sogard and Olla, 2001). The *ACT* coefficient was set to 1, because the activity of fish was assumed to be included in the routine metabolic rate.

We solved Eq. (6) for ($f_R(W)$) and used non-linear regression to estimate intercept and slope parameters of the allometric function of respiration rate and weight:

$$f_R(W) = R/(f_R(T) * ACT) = RA * W^{RB} \quad (7)$$

where *RA* is the intercept of the allometric respiration function, *RB* is the slope of the allometric respiration function, and *W* is the weight (g) of fish as defined above. To estimate the *RA* and *RB* parameters, we calculated $R/(f_R(T) * ACT)$ at a given temperature (5 °C) and determined its statistical relationship with *W* by fitting a power function to the data. Separate models were fitted to data from each temperature treatment; for the bioenergetics model, we used *RA* and *RB* parameters derived from the fitted model for the 5 °C treatment because it had the highest coefficient of determination, R^2, a standard measure of goodness of fit. Respiration parameters are shown in Table 3.

2.3. Model validation

To assess the performance of our bioenergetics model developed from 2016 YOY Sablefish trials, we determined growth based on the initial and final mass measurements of 2017 YOY Sablefish. Fish from the 2017 19.5 °C treatment were excluded from this study due to high rates of mortality (Table S1), which were likely caused by unintended spikes in water temperatures that occurred at the onset of the growth study. These spikes in water temperature were a result of failures in water valve controls responsible for regulating mixtures of hot and cold water to these tanks. Similarly, issues with water flow that occurred mid-way through the experiment are likely responsible for the high rates of mortality experienced in the 12.7 °C and 16.8 °C treatments during 2017, which caused us to terminate the feeding study in these tanks after 5 weeks. Each tank and treatment operated on an independent water control valve system, which isolated temperature and flow anomalies to individual tanks. As a result, final weight measurements used to evaluate model predictions were taken only from experimental trials and time points for which no adverse flow conditions occurred and fish experienced positive growth (Table 1). Average initial weights (g) from each temperature treatment were used as the initial condition (*W*) and the final observed weight (g) from each simulation was used for comparisons with model estimates (Table 1).

We validated the bioenergetics model by comparing the observed and estimated final mass of YOY Sablefish using three criteria (Schaeffer, 1980; Mayer and Butler, 1993): (1) a paired sample *t*-test; (2) mean absolute percent error calculated as:

$$E\% = 100\left[\sum\left(\frac{y_o - y_p}{y_o}\right)\right]/n \quad (8)$$

where y_o represents observed values, y_p predicted values and *n* the number of pairs; and (3) a metric of modeling efficiency (Mayer and Butler, 1993):

$$E_F = 1 - \sum(y_o - y_p)^2/\sum(y_o - y_m)^2 \quad (9)$$

where y_o and y_p are the same as previously and y_m is the mean of observed values.

Mean absolute percent error is a measure of deviance based on the differences between predicted and observed value, with models scoring error values of less than 10% generally considered “acceptable representations” (Kleijnen, 1987). Modeling efficiency is a dimensionless statistic which relates model predictions to observed data. Efficiency values range from negative infinity to 1, with values of less than 0 indicating that model-predicted estimates are worse than using observed means, while values closer to 1 represent “near-perfect” models (Mayer and Butler, 1993).

2.4. Model sensitivity

An error analysis was performed to determine the sensitivity of our bioenergetics model to uncertainty in parameter estimation. We used Monte Carlo simulation to evaluate the influence of all model parameters on estimates of *G* (Bartell et al., 1986). Model parameters were randomly drawn ($n = 8000$) from normal distributions with means equal to estimated parameter values (Table 3) and coefficients of variation (CV) of 2%, 10%, and 20% (after Bartell et al., 1986 and Harvey, 2009). We fixed the *p*(*Cmax*) parameter at 1 because all fish were fed *ad libitum* and did not vary the predator and prey energy density parameter values since these were directly obtained from fish utilized in this study. Temperature was fixed at 5 °C. To assess model sensitivity, we used relative partial sum of squares (RPSS) derived from a multiple linear regression of *G* against all parameters (Bartell et al., 1986). RPSS quantifies the influence of a given parameter on the model output after the influence of all other parameters has been removed. The sum of RPSS across parameters is equal to the R^2 value of the multiple linear regression and describes the relative importance of direct parameter effects on *G* (Bartell et al., 1986).

Bioenergetics model simulations were run using Fish Bioenergetics 4.0 (Deslauriers et al., 2017). Statistical analyses and model sensitivity analysis were performed using R-v 3.1.3 (R Development Core Team, 2008).

2.5. Bioenergetics model application

During the neustonic stage of YOY sablefish development,

Table 4

Prey species and corresponding energy density values (kJ g^{-1} wet weight) used to generate growth scenarios. All prey species represent actual prey retrieved from stomachs of young of year Sablefish except for Pacific Cod which was used in the laboratory experiments.

Prey item	Energy density
Ctenophora	0.92
Hyperiidae	2.67
Pacific Cod (*Gadus macrocephalus*)	3.08
Lingcod (*Ophiodon elongatus*)	3.71
Mysidae	4.04
Pacific Herring (*Clupea pallasii*)	4.65
Pink Salmon carcass (*Oncorhynchus gorbuscha*)	5.30
Shiner Perch (*Cymatogaster aggregata*)	6.00
Nereidae	6.24

Table 5

Temperature profiles used to model growth under field conditions. Values for each profile show the number of days at each temperature and the cumulative number of degree days (CDD).

	Warm profiles		
	Initial temperature	Final temperature	
Profile	15 °C	10 °C	CDD
1	77	0	1155
2	70	7	1120
3	63	14	1085
4	56	21	1050
5	49	28	1015
6	42	35	980
7	35	42	945
8	28	49	910
9	21	56	875
10	14	63	840
11	7	70	805

	Cool profiles		
	Initial temperature	Final temperature	
Profile	13.5 °C	8.5 °C	CDD
1	77	0	1039.5
2	70	7	1004.5
3	63	14	969.5
4	56	21	934.5
5	49	28	899.5
6	42	35	864.5
7	35	42	829.5
8	28	49	794.5
9	22	56	773
10	14	63	724.5
11	7	70	689.5

individuals are transported primarily by ocean convection towards nearshore nursery areas where they become more demersal (Mason et al., 1983; Shotwell et al., 2014). We used the model to identify the conditions necessary for wild YOY Sablefish to successfully settle from the neustonic to demersal stages, by simulating YOY sablefish growth over a 77-day period under varying ration, diet quality, and temperature conditions. The simulation period corresponds to the date range over which fish were observed in the field, from their neustonic phase (i.e., collected in NOAA survey beginning August 5th) to post-settlement (i.e., collected during a field survey ending October 21st).

Model simulations included different combinations of ration levels, dietary energy density, and water temperature (total of 594 scenarios). Ration sizes (*p* in Table 2) were set at 55%, 75% and 100% of C*max*. Dietary energy densities ranged from 0.92 kJ g^{-1} to 6.2 kJ g^{-1} and reflected the energy densities of common prey items observed in stomachs of age − 0 Sablefish sampled in St. John Baptist Bay (Coutré et al., 2015); energy densities of common prey types were determined as described previously (Table 4). The average size of neustonic YOY sablefish in the eastern GOA was used as the starting size of fish in simulations (34 g) and was calculated from catch data collected during the 2017 NOAA survey (described above). To evaluate the viability of simulation outputs we compared projected final size to the range of sizes observed in field sampled post-settlement YOY Sablefish (110 g and 240 g) that were caught using hook-and-line in St. John Baptist Bay on the west coast of Baranof Island in October 2017 by University of Alaska Fairbanks researchers (Callahan and Beaudreau, unpublished data). Scenarios that produced fish sizes within the range of sizes observed during 2017 field sampling (110 g to 240 g) were considered to be reasonable approximations of possible conditions leading to observed growth in the 2017 cohort (i.e., "viable" simulations).

The thermal experience of fish that successfully settled was unknown, consequently we examined a range of thermal experiences for each combination of ration size and dietary energy density. We constructed temperature scenarios that would reflect the transition from neustonic offshore to demersal nearshore habitats over the period from August to October. Average sea surface temperature during the August 2017 NOAA survey was 13.5 °C. Average October 2017 temperature from two temperature loggers placed near the seafloor at depths of 20–25 m in St. John Baptist Bay was approximately 9.0 °C. We constructed 11 thermal profiles reflecting cooler conditions, with 13.5 °C and 8.5 °C as starting (surface) and ending (approximate bottom) temperatures, respectively (Table 5). In addition, we generated 11 thermal profiles reflecting warmer conditions (i.e., with 15 °C and 10 °C as starting and ending temperatures, respectively; Table 5). We used the average sea surface temperature observed on 2016 NOAA surveys for YOY Sablefish (15 °C) as the initial temperature and subtracted 5 °C to maintain the same thermal range as the cool scenario. Each profile reflected a different transition point from surface to bottom temperatures within the 77 day simulation period; for example, in 'profile 2' under observed conditions, fish growth was modeled at a temperature of 13.5 °C for 70 days then at 8.5 °C for 7 days. The cumulative number of degree days (CDD; Trudgill et al., 2005) was calculated for each profile to aid in data visualization and interpretation. To calculate CDD, we multiplied the number of days a profile was set at a specific temperature by that temperature. For example, CDD for 'profile 2' under the warm scenarios (Table 5) was calculated as (70 days × 15 °C) + (7 days × 10 °C) = 1120.

3. Results

Growth and consumption of YOY Sablefish showed strong relationships with temperature in the laboratory. During the 2016 feeding trials, average SGR ranged from 0.74 to 1.84% wet weight d^{-1}, equating to average daily growth rates of 46.7–122.0 J $g^{-1}d^{-1}$ or 0.82–3.42 g d^{-1} (Table 6). Daily growth rates increased with temperature from 5 °C to 16 °C, then sharply declined at 20 *°C. M*aximum daily consumption rates followed a similar trend with values steadily increasing with temperature until leveling around 16 °C and 20 °C (Table 6).

The power function used to describe the allometric relationship between weight and respiration was expressed as $R = 0.0259 * W^{-0.359}$

Table 6

Temperature-dependent specific growth rate (SGR; % wet weight gain d-1), growth (J g-1d-1), and maximum consumption rate (J g-1d-1) from 2016 feeding study of YOY Sablefish. Values are expressed as averages of mean individual growth / consumption (± standard deviation) per treatment.

Temp treatment (°C)	SGR	Growth	Max consumption
5	0.74 (0.13)	46.70 (7.94)	107.1 (16.67)
8	1.09 (0.16)	61.25 (9.59)	139.1 (19.53)
12	1.66 (0.20)	108.7 (12.14)	190.5 (16.84)
16	1.84 (0.36)	122 (15.97)	224.2 (23.42)
20	1.10 (0.39)	71.25 (23.51)	222.7 (63.38)

Table 7
Model performance of the life stage specific bioenergetics model. Observed and predicted final wet weight (g) are calculated from 2016 and 2017 laboratory trials.

Trial year	Temp treatment (°C)	Growth duration	Final observed weight	YOY model estimates
2016	5	3 Weeks	187.2 (34.0)	187.84
2017	6.5	7 Weeks	159.9 (21.9)	169.25
2016	8	3 Weeks	210.7 (31.3)	210.64
2016	12	3 Weeks	239.4 (13.5)	224.05
2017	12.7	5 Weeks	190 (29.9)	178.56
2016	16	3 Weeks	249.3 (40.3)	235.30
2017	16.8	5 Weeks	201.4 (34.8)	214.23
2016	20	3 Weeks	195 (32.0)	206.78
		Validation assessment		YOY model value
		Paired T-Test		0.47
		Mean Absolute Percent Error (%)		4.6
		Modeling Efficiency (0–1)		0.84

Model parameters used to generate weight estimates are listed in Table 3. Duration of each model simulation was dependent on temperature treatment and study year. Observed weights are based on treatment averages (± standard deviation). Results of the three validation criteria are also provided.

($F = 7.35$, p-value $= .014$, $R^2 = 0.29$). As such, the RA and RB parameters of our bioenergetics model were at 0.0259 and − 0.359, respectively. All respiration parameters for the bioenergetics model derived for YOY Sablefish are presented in Table 3.

3.1. Model validation

Final weight predictions based on modeled growth of YOY Sablefish from 2016 and 2017 feeding studies using YOY life stage specific bioenergetics parameters were similar to observed values in both study years (Table 7). Mean absolute percent error of the bioenergetics model was 4.6%, modeling efficiency was calculated at 84%, and no significant difference was found between observed and estimated final weights (paired sample t-test, $P = .47$). All estimates of weight from the model were within one standard deviation of observed mean final wet weights for all temperature treatments. Final weight was slightly underestimated in four of eight treatments (range of 0.03–6.8%) and overestimated in the remaining four (range of 0.34–6.0%; Fig. 1).

3.2. Sensitivity analysis

The highest RPSS values from each CV level were generally from consumption-related parameters. The *CA* parameter, the intercept for consumption allometry, explained the most variability at all levels of CV (Fig. 2). The *CB*, *CQ*, and *CTO* parameters were always ranked between 2nd and 5th highest in terms of RPSS values. *RB*, the allometric slope of respiration, was the most influential respiration-related parameter, ranking among the top 5 RPSS values at all CV levels. The least influential parameters, those with the lowest RPSS values, were the maximum and optimal temperatures of respiration, the activity multiplier, and the coefficients of egestion, excretion, and specific dynamic action. The majority of these parameter values were obtained from the literature and were not directly derived in this study. Model R^2 values were high (0.783–0.992) across all levels of CV runs, indicating that changes in the response variable G were primarily due to direct parameter effects rather than a result of interaction effects among parameters and nonlinear relationships between G and parameter values (Bartell et al., 1986).

3.3. Application

Modeling the growth potential of fish collected in pelagic habitats in 2017 and comparing the results with observed sizes of YOY sablefish in October provided insight into the range of possible ration sizes, diet qualities, and thermal experiences leading to observed growth. Environmental conditions that produced final weights falling within the range of weights observed among YOY sablefish in October were considered viable. Rations below 55% of C*max* failed to produce any viable outcomes. The number of viable simulations was optimized when consumption was set to 75% of C*max*. The percentage of viable simulations increased from 7% to 53% as consumption rates increased from 55% to 75% of C*max* and then declined to 47% when consumption equaled C*max*.

Consumption of higher energy prey compensated for lower consumption rates in producing viable outcomes. For fish feeding at 75% of

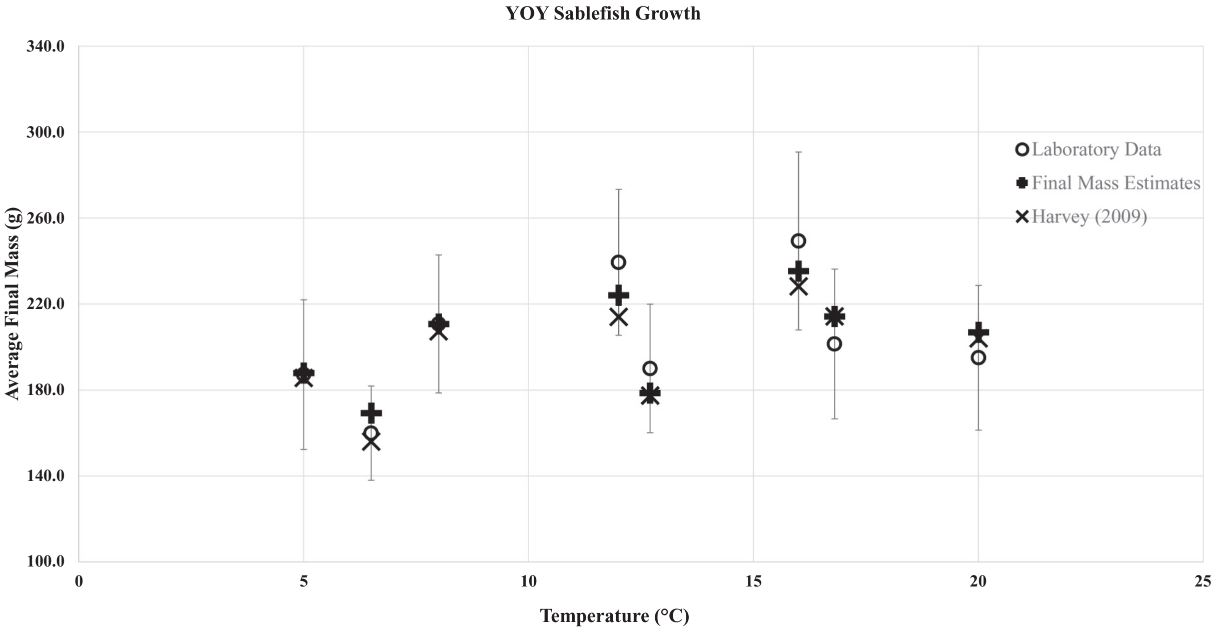

Fig. 1. Mean (± SD) final mass (g) from 2016 and 2017 laboratory experiments (**O**) and estimates of final mass calculated using our life stage specific bioenergetics model (+) and the life stage indiscriminate model of Harvey (2009) (**X**).

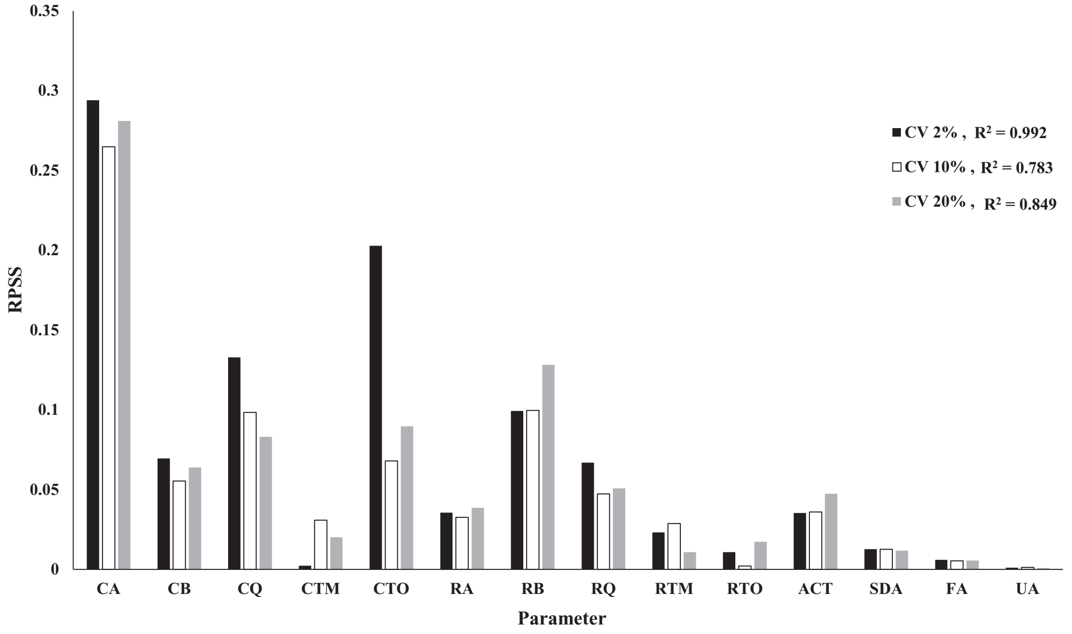

Fig. 2. Sensitivity analysis of the bioenergetics model for YOY Sablefish. Parameters were drawn from normal distributions around the means from Table 3 (with the exception of prey and predator energy densities), and coefficients of variation (CV) of 2%, 10%, or 20%. Relative partial sums of squares (RPSS) indicate parameter influence on model output (*G*), while the R^2 indicates the total variability explained by the fitted linear model.

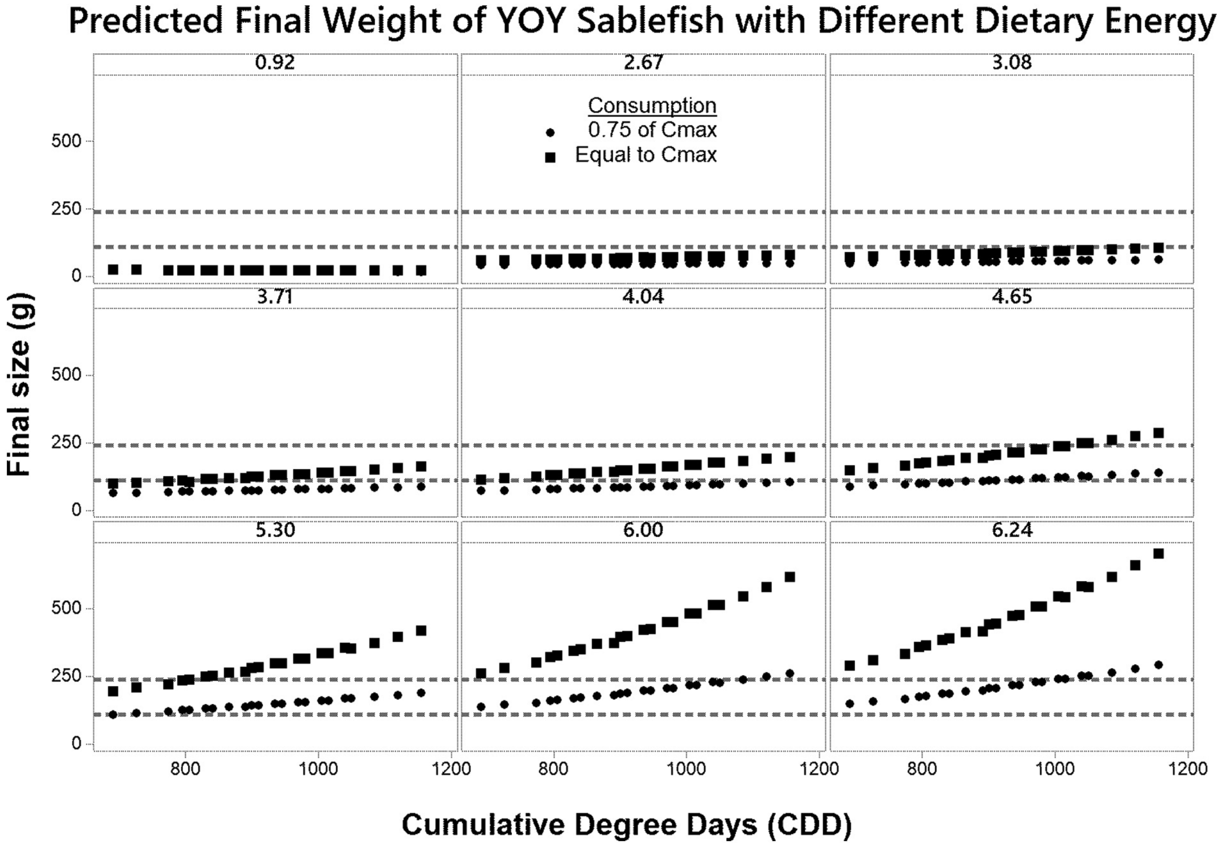

Fig. 3. Predicted final mass of YOY sablefish under differing environmental conditions. Fish were grown from and initial mass of 34 g for 77 days under differing combinations of dietary energy density (shown in panel headings) and temperature profiles (cumulative degree days or CDDs). Curves in each panel show the relation between temperature units and final size for consumption rates (*p*) equal to 75% and 100% of C*max*. The gray horizontal lines in each panel show the range of weights observed among YOY sablefish settled in demersal habitats in October of 2017.

C*max*, most of the viable simulations (84%) were observed when dietary energy density averaged 5.3 kJ g^{-1} or more (Fig. 3). The predicted final size exceeded the observed range at the highest energy density (6.24 kJ g^{-1}), while the lowest dietary energy density that produced viable simulations was 4.65 kJ g^{-1}. For fish feeding at C*max*, the lowest dietary energy density that produced viable simulations was 3.71 kJ g^{-1}, and 92% of the viable simulations occurred when fish diets ranged between 3.71 kJ g^{-1} and 4.65 kJ kJ g^{-1}. Energy densities greater than 5.30 kJ g^{-1} tended to produce fish with weights in excess of the observed range (Fig. 3).

Similarly, higher energy diets compensated for low CDD values to produce viable outcomes. For example, when dietary energy density averaged 4.65 kJ g^{-1}, only thermal profiles ≥934.5 CDDs (50% of simulations) produced viable outcomes for fish feeding at 75% of C*max*. When dietary energy density increased to 6.0 kJ g^{-1} lower temperatures (i.e., 689.5 to 1085 CDDs) produced viable outcomes (Fig. 3). For fish feeding at C*max*, the 7 warmest thermal profiles produced viable outcomes when dietary energy densities averaged 3.71 kJ g^{-1} and all thermal profiles produced viable outcomes when dietary energy densities averaged 4.04 kJ g^{-1}. At dietary energy densities exceeding 4.04 kJ g^{-1}, warm thermal conditions produced fish that were larger than the observed range of weights.

4. Discussion

We developed a life stage specific bioenergetics model for YOY Sablefish using a novel temperature-dependent respiration function derived from experimental trials in conjunction with previously developed models explaining temperature-dependent growth and consumption for YOY Sablefish fed at maximum ration. To corroborate the performance capabilities of our model, we compared model simulated growth across a range of temperature scenarios between two independent experimental trials. We found that the YOY bioenergetics model derived from the 2016 feeding experiments accurately predicted growth of fish in all temperature treatments from both 2016 and 2017 feeding trials. We then applied our model to estimate the growth of YOY sablefish under real-world conditions using environmental inputs generated from multiple field surveys. Our experimental data and life stage specific model provide an improved understanding of the physiological response of YOY Sablefish to varying temperature and prey conditions and can be used as a tool for projecting Sablefish growth responses to future environmental changes.

4.1. Model performance

The sensitivity analysis indicated that the consumption-related parameters had the greatest influence on model outputs. This is not surprising given that other parameters in the bioenergetics model equation are calculated based on the consumption function (i.e., egestion, excretion, specific dynamic action). These parameters have also been found to be the most influential in other studies (Bartell et al., 1986; Harvey, 2009; van der Lee et al., 2017). Indeed, the consumption parameters combined to generate an R^2 value of 0.77 in the 2% CV run and > 0.6 in the 10% and 20% CV runs. Therefore, consumption parameters should be determined with care, given their strong influence on model outputs (Bartell et al., 1986; Deslauriers et al., 2017).

The parameters derived from the temperature-dependent respiration function were less influential on model outputs. With the exception of *RB*, all respiration parameters scored relatively low RPSS values from our Monte Carlo simulations. Thus, while temperature-dependent respiration is an integral component of the bioenergetics modeling framework, its relative effect on overall growth in YOY Sablefish is of lesser importance. This further supports the notion that a thorough understanding of temperature-dependent consumption aspects may be most beneficial for understanding growth response of young Sablefish.

While our model provides robust estimates of growth, there are still some sources of uncertainty in the model parameters. For example, many factors can affect the physiology and survival of captive fish that are not experienced by individuals in the wild, such as potential injury and stress during capture and transport to the lab. On the other hand, wild fish also experience factors that affect their physiology and survival in ways not experienced by captive individuals, such as predator avoidance and foraging behavior. While captive fish may experience different metabolic rates compared to those in the wild, there are few other alternatives for parameterizing bioenergetics models. The vast majority of fish bioenergetics models are parameterized from experimental data (see Deslauriers et al., 2017), which inevitably leads to some uncertainty in parameter values. Our best attempt to account for this uncertainty is to conduct rigorous sensitivity analyses and validate model outputs with data collected from field surveys; both of which have been done in this study.

In addition, although we determined the majority of the bioenergetics parameters from direct measurements of captive YOY Sablefish, some parameter values were drawn from the literature (Table 3). However, those not directly measured (egestion, excretion, specific dynamic action, *RQ*, and *ACT*) generated an R^2 of < 0.12, and had relatively little influence on model outputs. In addition, our estimates of the coefficients for the allometric respiration function were empirically determined, whereas Kitchell et al., 1977 theoretically defined the parameters for a 1 g fish at *RTO*. While we did not measure *RA* and *RB* under those conditions, our ability to accurately predict growth for fish from an independent experiment justifies the method.

4.2. Growth under variable temperature and prey conditions

Application of the laboratory derived growth model revealed the dependence of YOY Sablefish on high rations to achieve observed post-settlement sizes. Simulations involving ration levels below 75% of C*max* led to few viable outcomes regardless of thermal profiles or diet quality. Estimates of relative feeding rates for juvenile Walleye Pollock (*Gadus chalcogrammus*) and Pacific Cod in another study from the GOA were well below 75% of C*max* (Holsman and Aydin, 2015), suggesting that our model either underestimates C*max* or that Sablefish require greater rations than these two gadids. The latter explanation is consistent with previous studies which suggest that Sablefish employ an early life history characterized by maximum consumption and selection for rapid growth during their neustonic residence (Sogard and Olla, 2002). Indeed, the apparent dependence on high quantities of suitable prey may partially explain the episodic recruitment cycles that have been characteristic of Sablefish over the last several decades (Sigler et al., 2001; Hanselman et al., 2018). In years where conditions favor the occurrence of one or more key prey species, young Sablefish may thrive and survive to recruit into the fishery at high rates. Previous studies have postulated that Sablefish recruitment dynamics and year-class strength may be strongly mediated by local environmental conditions (such as prey availability) experienced early in life (Schirripa and Colbert, 2006; Shotwell et al., 2014). If this is correct, identifying the abundance and availability of essential prey species may help to provide an early indicator of Sablefish recruitment success in future cohorts.

This strategy of maximizing growth also requires that juvenile Sablefish consume an energy rich diet in relatively warm temperatures. Sablefish sampled in the neuston in August must have experienced at least 934.5 CDDs and consumed diets averaging at least 4.65 kJ g^{-1} to grow to the sizes observed in nearshore habitats the following October. Based on the simulations, Sablefish required at least 33 days at a surface temperature of 15.0 °C followed by 44 days at 10 °C to reach a viable size. Individuals feeding at C*max* for the entire period could have reached a viable size with fewer CDDs, allowing them to spend less time in the neuston; however, their diets would still have needed to average at least 3.71 kJ g^{-1}, equivalent to a diet composed of fish (i.e., Lingcod (*Ophiodon elongatus*) and Pacific Herring (*Clupea pallasii*) and Mysidae

(Mysis shrimp). The need to consume high energy diets points to the importance of piscivory for juvenile Sablefish. Pelagic YOY Sablefish typically consume pteropods, amphipods, calanoid copepods and euphausiids (Sigler et al., 2001), most of which have relatively low energy densities (Davis et al., 1998). Post-settlement juvenile Sablefish consume predominantly fish (Coutré et al., 2015), which commonly have energy densities exceeding 3 kJ g^{-1}; fish prey identified in juvenile Sablefish stomachs include Shiner Perch (*Cymatogaster aggregata*), Lingcod, Pink Salmon carcasses (*Oncorhynchus gorbuscha*) and Pacific Herring (Coutré et al., 2015; Callahan et al., unpublished data). Further examination of the possible link between the onset of piscivory in YOY Sablefish and recruitment success is warranted (Sogard, 2011).

Our findings suggest that Sablefish could thrive under warming ocean conditions given sufficient food. Their flexibility as generalist predator allows them to shift among seasonally pulsed prey (e.g., salmon, herring; Coutré et al., 2015). The potential for quick growth during early life stages may allow juvenile Sablefish to achieve larger sizes prior to their first winter, increasing the odds of survival. A record high Sablefish recruitment event coinciding with a marine heat wave in 2014 in the GOA (Hanselman et al., 2018) provides preliminary support for the hypothesis that Sablefish may be resilient to some degree of continued ocean warming.

4.3. Conclusions

In both years of our laboratory trials, we found that temperature had clear effects on growth of YOY Sablefish. Growth was maximized at 12–16.8 °C. Fish held at temperatures outside of this range grew an average of 25% and 12% less at lower temperatures in 2016 and 2017, respectively, and 22% less at higher temperatures in 2016. While these differences are considerable and could potentially affect overwinter survival and recruitment success, a discussed above, laboratory conditions do not reflect those experienced by wild fish. For instance, the laboratory fish were fed *ad libitum* which likely does not reflect typical prey fields found in the wild and may mask the effect of sub-optimal temperatures on YOY Sablefish growth and development. In addition, laboratory fish likely expend less energy to obtain prey compared to wild fish. Wild YOY Sablefish encountering less abundant or lower quality prey would grow more slowly at a given temperature, as was demonstrated in the modeled growth simulations. If growth is hindered during the late summer or fall it could prevent YOY fish from reaching a sufficient size or condition to survive the winter (Heintz et al., 2013). A fruitful area of future inquiry would be to evaluate the condition of wild caught sablefish in the spring immediately following their first winter. In this way we could better understand the physiological toll that is taken on Sablefish during this critical period of their early life history and the fall condition necessary to sustain them through this period of time.

While bioenergetics models are used extensively (Deslauriers et al., 2017), many are predominately derived empirically from combining observations from numerous studies, and few have been independently validated. This study is unique in that we both validated the model using laboratory data and corroborated it with real world data collected from multiple field surveys. Our study contributes to an improved mechanistic understanding of relationships between Sablefish and habitat conditions through early ontogeny, which will provide insight into potential survival bottlenecks and shifts in Sablefish production under future climate scenarios.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2020.151340.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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