



# First winter energy allocation in juvenile sablefish *Anoplopoma fimbria*, a fast growing marine piscivore

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**ABSTRACT:** Understanding how energy allocation changes with ontogeny can provide insights about survival bottlenecks during early life stages for marine fishes. Energy allocation in juvenile fish before and during their critical first winter differs among species based on life history and foraging characteristics. To improve understanding of energy–size relationships in marine fish, we examined seasonal energy allocation in sablefish *Anoplopoma fimbria*, a species with unusually fast growth rates during early life. We assessed seasonal metrics of growth and energy storage in sablefish during their first 2 yr using field collections from 2016–2019. Based on growth rates estimated from length–frequency distributions, sablefish increased rapidly in size during autumn, and growth continued but slowed through their first winter as newly settled young-of-the-year. Mean energy density (ED,  $\text{kJ g}^{-1}$ ) declined over the winter, but total energy (TE,  $\text{kJ ind.}^{-1}$ ) increased significantly between October and March, reflecting positive overwinter growth. Relationships between energy storage and length were atypical for high-latitude marine fish in that they were steepest in March, indicating that relatively large fish grew during winter with minimal energy depletion, whereas relatively small fish grew but depleted their energy stores. We propose that improved foraging success for large fish may explain this pattern. Our results suggest that sablefish benefit from achieving large sizes prior to winter and support the hypothesis that the first winter can be a survival bottleneck for sablefish. This work informs our understanding of piscivore energy allocation during early life history and our understanding of possible sablefish recruitment drivers.

**KEY WORDS:** *Anoplopoma fimbria* · Young-of-the-year · First winter · Energy density · Growth · Body condition · Nutritional stress · Gulf of Alaska

## 1. INTRODUCTION

The first winter is often a physiologically demanding period for juvenile fish, and overwinter survival can be a key determinant of recruitment success (Beamish & Mahnken 2001, Norcross et al. 2001, Beamish et al. 2004, Heintz et al. 2013). In high-latitude marine environments, food availability is generally lowest in winter, and water temperatures may approach the lower limit of thermal tolerances for some species (Hurst 2007). Pre-winter energy

stores are critical to surviving the first winter; therefore, juveniles of many fish species increase fat deposition in late summer and autumn, and survivors of winter often emerge in poorer condition than in the previous fall (Madenjian et al. 2000, Hurst & Conover 2003, Heintz & Vollenweider 2010, Sewall et al. 2019). Within a cohort, smaller fish often have reduced survival over winter compared to larger fish (Hunt 1969, Hurst & Conover 1998, Beamish & Mahnken 2001, Sewall et al. 2019) due to energy depletion allometries (Schultz & Conover 1999) and their limited

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ability to store energy. Consequently, size-selective overwinter mortality is common, with improved survival in larger individuals (Hunt 1969, Hurst & Conover 1998, Beamish & Mahnken 2001, Sewall et al. 2019).

Understanding how energy allocation strategy changes with ontogeny can provide insights about key selection pressures and survival bottlenecks during early life stages. Small fish benefit from somatic growth because larger size reduces predation risk from size-selective predators (Juanes & Conover 1994, Miranda & Hubbard 1994, Sogard 1997), increases access to higher-energy prey resources (Olson 1996, Scharf et al. 2000, Sewall et al. 2019), and improves capacity to survive starvation (Johnson & Evans 1990, Schultz & Conover 1999, Sogard & Olla 2000). Larger fish within a given year class can accumulate greater energy reserves than smaller individuals in the same cohort, and energy stores are often positively correlated with length prior to winter (Schultz & Conover 1999, Sogard & Olla 2000, Heintz & Vollenweider 2010). Size-based variation in energy allocation strategies may reflect differences in the sources of mortality for large and small individuals (Post & Parkinson 2001). For example, larger individuals may prioritize energy storage before winter to reduce their risk of starvation, whereas smaller individuals experiencing higher predation risk may prioritize somatic growth.

For juvenile fishes, the relationship between energy stores and size (length) may change between autumn and spring in a variety of ways, depending on life history and foraging decisions (Fig. 1). Empirical studies have indicated at least 4 overwinter energy allocation strategies in marine fish. First, energy stores are independent of size and remain stable over winter while fish grow in length (e.g. winter flounder *Pseudopleuronectes americanus*, Bell 2012; Fig. 1A). Second, energy stores are positively correlated with size, fish do not grow, and fish lose energy at a rate proportional to their size during winter (e.g. striped bass *Morone saxatilis*, Hurst & Conover 2001; Fig. 1B). Third, energy stores are size-dependent as in the previous scenario, but large fish lose a disproportionate amount of their energy reserves during winter, and fish do not grow (Fig. 1C). Fourth, small fish lose a greater proportion of their energy reserves than large fish during winter, and fish do not grow (Fig. 1D).

small fish over winter; all sizes exhibit limited or no growth (Fig. 1C). Small fish may avoid starvation by foraging while large fish rely on energy reserves (e.g. Paul et al. 1998, Heintz & Vollenweider 2010, Farley et al. 2011). Lastly, large fish can retain a higher proportion of their energy stores following periods of food deprivation due to decreased mass-specific metabolic costs associated with large size. In this fourth case, energy stores are size-dependent, small fish lose a disproportionate amount of energy relative to large fish over winter, and all sizes exhibit little to no growth (Fig. 1D). Evidence for the first 3 cases is based largely on species that feed on zooplankton and benthic invertebrates going into their first winter (Foy & Paul 1999, Hurst & Conover 2001, Eckmann 2004, Heintz & Vollenweider 2010, but see Morley et al. 2007), whereas the fourth case has mainly been demonstrated in laboratory starvation experiments (e.g. Schultz & Conover 1999, Sogard & Olla 2000, but see Sutton & Ney 2001). To further our understanding of energy–size relationships in piscivores, we examined energy allocation in a wild population of sablefish *Anoplopoma fimbria*.

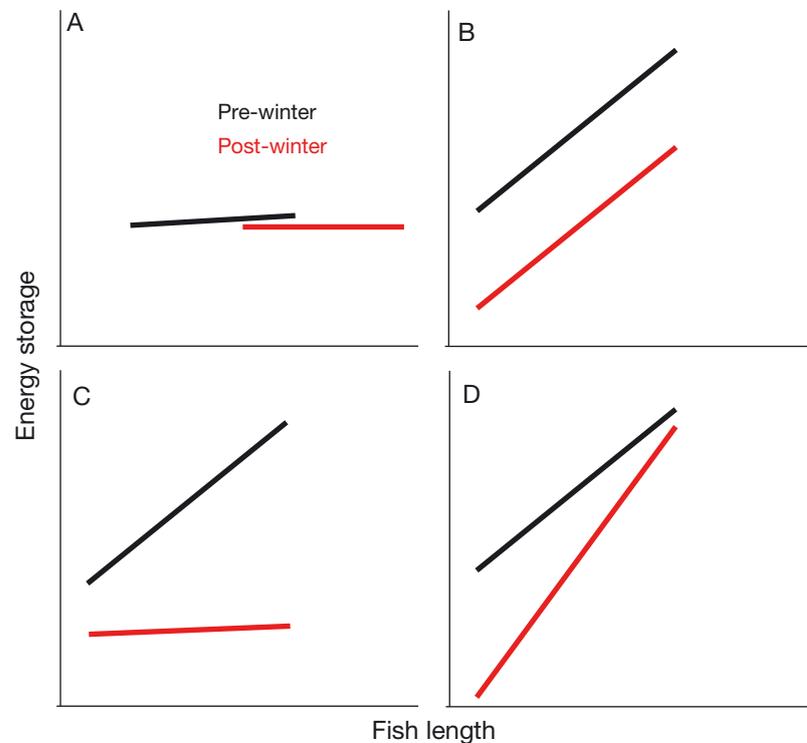


Fig. 1. Conceptual diagram of size-based energy storage patterns in juvenile fish before and after winter. (A) Fish maintain their energy stores and grow over winter. (B) Energy stores are dependent on size prior to winter and lost at proportionate rates relative to size over winter. (C) Large fish lose a disproportionate amount of their energy stores during winter relative to that of small fish, and no growth occurs. (D) Small fish lose a greater proportion of their energy reserves than large fish during winter, and fish do not grow

Sablefish is a commercially important demersal fish species that supports the third most valuable groundfish fishery in Alaska (Fissel et al. 2017). Sablefish spawn January through April on the continental slope at depths greater than 300 m, and prevailing currents transport larvae towards shore (Mason et al. 1983, Shotwell et al. 2014). Larvae hatch in spring (mean hatch date for Alaskan sablefish is 30 April; Sigler et al. 2001), rise to the surface (Kendall & Matarese 1987), and sablefish inhabit the photic zone through their first summer. In Southeast Alaska, sablefish settle into coastal bays and estuaries to spend their first winter and second summer in near-shore areas (Rutecki & Varosi 1997) before migrating towards deep adult habitat, where they recruit to the commercial fishery beginning in their third year. Sablefish recruitment in Alaska is highly variable and difficult to predict (Shotwell et al. 2014, Coffin & Mueter 2016, Hanselman et al. 2019). Consistently low recruitment from 2001–2013 led to declines in sablefish stock biomass and a consequent reduction in commercial fishery quotas in the Gulf of Alaska (Hanselman et al. 2019). In 2014, a marine heatwave in the Gulf of Alaska led to die-offs and recruitment failure of fish and sea birds (Di Lorenzo & Mantua 2016, Zador & Yasumiishi 2017, Barbeaux et al. 2018, Jones et al. 2018, Piatt et al. 2020). In contrast, sablefish recruitment reached record highs in 2014 and 2016 (Hanselman et al. 2019).

In their first year of life, sablefish become piscivorous and have some of the fastest recorded growth rates among young-of-the-year marine fish (Sigler et al. 2001, Sogard & Spencer 2004, Sogard 2011). Age-0 sablefish growth is maximized in warm water temperatures close to their upper thermal limit (Sogard & Olla 2001, Krieger et al. 2019). Given optimal conditions, the fastest-growing age-0 sablefish also store more energy than their slower-growing peers, suggesting sablefish may be less constrained by a physiological trade-off between growth and storage, though growth and energy storage were severely reduced with low food availability in laboratory experiments (Sogard & Spencer 2004). Sablefish enter winter at relatively large sizes; for example, age-0 individuals in October averaged 256 mm in length in waters off Southeast Alaska (Rutecki & Varosi 1997). Rapid juvenile growth permits an early shift to piscivory, and by August of their first summer, fish can be a major component of sablefish diets (W. Strasburger pers. comm.).

In this study, we examined how juvenile sablefish energy storage and growth vary seasonally and with body size during the first 2 yr of life. We analyzed data collected from 2 yr of field collections to evalu-

ate which of the generalized energy allocation strategies (Fig. 1) is most plausible for juvenile sablefish, based on pre- and post-winter relationships between energy storage and body size (Objective 1). We then used an expanded data set that included previous surveys by the National Marine Fisheries Service (NMFS) to explore size-specific patterns of energy storage across multiple years and seasons from their first summer as pelagic juveniles to their second fall before migration to deeper adult habitat (Objective 2). This provided inferences about the degree to which energy–size relationships vary across broader spatial and temporal scales.

## 2. MATERIALS AND METHODS

### 2.1. Study area and data acquisition

Sablefish samples were collected by 3 methods over 4 yr (see Table 1) in western Baranof Island bays and the Gulf of Alaska (Fig. 2). To address Objective 1, we collected fish by hook and line in Saint John Baptist Bay (SJBB) in 2017–2019. Some additional western Baranof Island sablefish were obtained from purse seine fishermen in September 2018. To address Objective 2, we included additional pelagic age-0 sablefish collected by the NMFS from the Gulf of Alaska in 2016 and 2017 in our analyses. Sampling methods are further detailed below.

Our 2017–2019 field sampling took place in SJBB, a known sablefish nursery area (Fig. 2). SJBB is a narrow bay ca. 3 km long and 800 m wide that opens west into Neva Strait. Depths range from approximately 25 m near the head to 70 m at the mouth, and seafloor substrate consists of soft mud and shell hash. Surveys conducted by NMFS in Southeast Alaska during the 1980s and 1990s identified SJBB as the site with most consistent juvenile sablefish catches (Rutecki & Varosi 1997). Ongoing studies at this site have informed our understanding of sablefish dispersal from nearshore areas to deep adult habitat (Maloney & Sigler 2008), vertical migrations and fine-scale movement (Coutré et al. 2017, Ehresmann et al. 2018), and foraging habits during nearshore residence (Coutré et al. 2015).

We conducted 6 sampling trips (5–6 d each) in SJBB to collect age-0 and age-1 sablefish in October 2017, April–May 2018, July 2018, October 2018, March 2019, and July 2019. This sampling design allowed us to track 2 cohorts of age-0 sablefish from the fall prior to their first winter (October), in

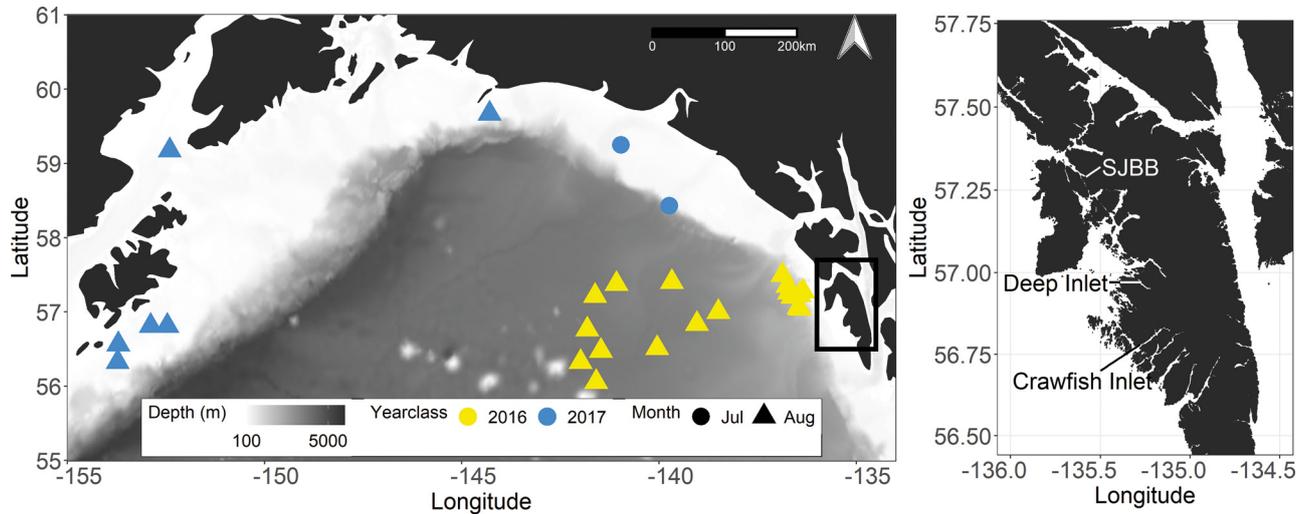


Fig. 2. Sablefish catch locations in the Gulf of Alaska from National Marine Fisheries Service surface trawl surveys (left) and from rod and reel sampling and purse seine catch on western Baranof Island (inset). Gulf of Alaska map includes data from 2016 and 2017 in July and August. SJBB: Saint John Baptist Bay

late winter/early spring (March–May), and during their second summer (July). We captured sablefish from near-bottom depths (ca. 25 m) by jigging with rod and reel, using hooks baited with squid (Coutré et al. 2015, Ehresmann et al. 2018). Fish were subsampled for laboratory analysis by retaining the first 20–30 fish caught on each trip, and additional fish were retained if the initial subsample was not representative of the length distribution of the catch. We euthanized subsampled fish with a blow to the head or an overdose of 10% eugenol (AQUI-S 20E); retained fish were stored on ice packs in a cooler until they could be frozen. Temperature loggers (ONSET TidbiT v2) were deployed near the bay bottom at ~25 m below the surface for the duration of the study.

Additional samples from western Baranof Island were provided by commercial salmon fishermen, who observed unusually high numbers of pelagic age-0 sablefish in their purse seines in September 2018. These fish were caught in Deep Inlet and Crawfish Inlet, which are 40 and 60 km south of SJBB, respectively (Fig. 2). For a portion of our analysis, we acquired data from NMFS surveys conducted in 2016–2017. Pre-settlement age-0 sablefish were caught with surface trawl nets during August 2016 and July–August 2017 in the Gulf of Alaska, with sampling locations spanning from approximately 25 km west of Baranof Island in the east to near Kodiak Island in the west (Fig. 2). Finally, we used data from presumed age-1 sablefish retained from a NMFS rod and reel juvenile sablefish tagging survey in SJBB in July 2016.

## 2.2. Laboratory methods

Sablefish samples were prepared for bomb calorimetry (Craig et al. 1978, Siddon et al. 2013) to assess energy storage levels. Frozen fish were partially thawed, weighed (nearest 0.1 g), measured to fork length (nearest 1 mm), and otoliths and stomach contents were removed. Individual fish were homogenized and stored at  $-80^{\circ}\text{C}$  in vials capped with nitrogen gas to prevent oxidation. An aliquot was dried to a constant weight, crushed into powder, pressed into a pellet, and combusted using a PARR 6725 bomb calorimeter to determine energy density (ED;  $\text{kJ g}^{-1}$  dry mass). Calorimetry precision and accuracy were assured by 2 benzoic acid standards (error not exceeding 0.6%), one pollock tissue standard (error not exceeding 2.75%), and one sample replicate (CV not exceeding 1.5) every 2 d of instrument use, or approximately 30 samples.

Age of post-settlement sablefish was determined as the number of annuli in sagittal otoliths following the methods of the Committee of Age Reading Experts (2006). Otoliths were analyzed by staff at the Alaska Department of Fish and Game (ADF&G) Mark, Tag and Age Laboratory in Juneau, Alaska, or by the lead author. Pelagic juveniles from NMFS surveys in the Gulf of Alaska were assumed to be age-0 fish based on their lengths (see Fig. 3, see Table 1).

## 2.3. Data analysis

We used 2 indices of juvenile sablefish energy storage: ED and total energy (TE). ED measures the

amount of energy stored per unit mass of fish tissue and closely correlates with lipid content (Anthony et al. 2000, Siddon et al. 2013). We used ED in  $\text{kJ g}^{-1}$  on a dry mass basis to avoid the potential error caused by variable fish moisture contents in wet-mass-based ED measurements (Montevecchi & Piatt 1987, Van Pelt et al. 1997). TE is the amount of energy contained in the whole body of the fish ( $\text{kJ ind.}^{-1}$ ). We calculated TE by multiplying ED by fish dry weight. Dry weight is the product of fish percent dry mass and fish wet weight.

To address Objective 1, we analyzed overwinter energy storage of western Baranof Island fish from the 2018 year class only, as 2018 was the only cohort with late winter samples. October, March, and July fish were captured in SJBB; September fish were from nearby Deep and Crawfish inlets. We compared mean length, ED, and TE between successive seasons using Welch's 2 sample *t*-tests. We also calculated apparent growth rates ( $\text{mm d}^{-1}$ ) as the difference in mean length between subsequent seasons divided by the duration in days between the mid-points of successive sampling periods. We use the term 'apparent growth rates' because both somatic growth and size-selective mortality can lead to mean length increases in a population (Sogard 1997). To quantify seasonal changes in the relationships between energy storage and fish size, we performed ANCOVA on both ED and TE versus length and month; length and TE had a log-linear relationship so we applied a natural log transformation to both variables in the TE model (Faraway 2005). We compared slopes across months using post hoc pairwise Student's *t*-tests with Tukey's adjustment for multiple comparisons.

To address Objective 2, we analyzed a larger data set that included the 2017 and 2018 year classes from Western Baranof Island and fish collected in NMFS surveys from multiple years and additional seasons both earlier and later in ontogeny than available from 2018 year class. We separately modeled ED and log-transformed TE as a function of the potential predictors length, month, year class, and their 2-way interactions. Month was a categorical variable representing season. To differentiate age-0 and age-1 fish caught in the same month, we used capture month for age-0 fish and capture month plus 12 for age-1 individuals; for example, an age-0 fish in October would have a month of 10, and age-1 fish in October would have a month of 22. Residuals from all models were inspected for regression assumptions. One outlier with a residual 4 standard deviations above 0 and a Bonferroni *p*-value of  $7.9 \times 10^{-6}$  (Faraway 2005)

was removed from the ED model. Its removal did not change the top model or the overall conclusions.

Our set of candidate models included all possible combinations of predictor variables, and models were compared using the small-sample corrected Akaike's information criterion ( $\Delta\text{AICc}$ ), calculated as the difference between a given model's AICc score and the lowest AICc across all models. Models with  $\Delta\text{AICc} \leq 2$  were considered the set of best models (Burnham & Anderson 2002). Akaike weights were calculated to assess the relative strength of each model; weights range from 0–1 and are interpreted as the probability that a given model is the best among the set of candidate models (Burnham & Anderson 2002). Models were fit to the data and ranked using the 'dredge' function (Barton 2020) in R v.3.6.3 (R Core Team 2020).

### 3. RESULTS

#### 3.1. Overwinter energy allocation

Over the course of winter 2018–2019, ED of sablefish from the 2018 year class decreased while length and TE increased on average (Table 1, Fig. 3). Apparent growth was highest in September–October at  $1.18 \text{ mm d}^{-1}$ , whereas apparent growth between October and March was  $0.29 \text{ mm d}^{-1}$  and was  $0.25 \text{ mm d}^{-1}$  between March and July. Mean ( $\pm\text{SD}$ ) ED increased from  $20.9 \pm 0.6 \text{ kJ g}^{-1}$  in September to  $22 \pm 1.1 \text{ kJ g}^{-1}$  in October, then declined to  $21.3 \pm 1.4 \text{ kJ g}^{-1}$  in March, and declined further to  $20.4 \pm 1.1 \text{ kJ g}^{-1}$  in July (Table 1, Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m663p145\\_supp.pdf](http://www.int-res.com/articles/suppl/m663p145_supp.pdf)). Differences in mean ED between sequential sampling periods were relatively small ( $<8\%$ ) but statistically significant (Table S1). TE increased from a mean ( $\pm\text{SD}$ ) of  $349 \pm 74 \text{ kJ}$  in September to  $569 \pm 198 \text{ kJ}$  in October to  $785 \pm 276 \text{ kJ}$  in March to  $972 \pm 451 \text{ kJ}$  in July (Table 1). TE differences between successive months were also statistically significant (Table S1).

The slopes of relationships between energy storage (ED and TE) and length were higher in March than in other months, as indicated by significant interaction terms between length and month for ED and TE models ( $p < 0.05$ ; Table 2). ED slopes for September, October, and July were 0.019, 0.031, and 0.021, respectively (Fig. 4) and were not significantly different from each other ( $p > 0.65$ ; Table 3), while the March slope was 0.060 and differed non-significantly from September ( $p = 0.1$ ) and significantly from October and July ( $p < 0.05$ ; Table 3). The allometric slope

Table 1. Juvenile sablefish data sets. BS: Bering Sea; DIC1: Deep Inlet and Crawfish Inlet; GOA: Gulf of Alaska; SJBB: Saint John Baptist Bay; ED: energy density; TE: total energy; NMFS: National Marine Fisheries Service; UAF: University of Alaska Fairbanks

Year class	Catch year	Age and month	Area	N	Length mean (SD)	Length range	ED mean (SD)	TE mean (SD)	Source (survey or project)
2016	2016	Age-0 Aug	GOA	65	198 (22)	106–234	22.8 (0.9)	419 (153)	NMFS summer juvenile pollock <sup>a</sup>
	2017	Age-1 Jul	GOA	14	314 (17)	282–344	20.9 (0.5)	928 (253)	NMFS juvenile sablefish tag <sup>b</sup>
	2017	Age-1 Oct	SJBB	33	343 (34)	265–435	22.2 (1.5)	1749 (922)	UAF juvenile sablefish <sup>c</sup>
2017	2017	Age-0 Jul	GOA	6	66 (8)	56–73	20.4 (0.4)	10 (3)	NMFS summer juvenile pollock <sup>a</sup>
	2017	Age-0 Aug	GOA	14	152 (19)	118–195	21.8 (0.9)	165 (75)	NMFS summer juvenile pollock <sup>a</sup>
	2017	Age-0 Oct	SJBB	20	253 (20)	220–290	23.3 (0.9)	893 (249)	UAF juvenile sablefish <sup>c</sup>
	2018	Age-1 Jul	SJBB	34	333 (18)	271–371	22.5 (1.2)	1414 (365)	UAF juvenile sablefish <sup>c</sup>
2018	2018	Age-0 Sep	DIC1	18	201 (13)	180–225	20.9 (0.6)	349 (74)	Purse seine fishery <sup>d</sup>
	2018	Age-0 Oct	SJBB	34	239 (20)	200–278	22.2 (1.1)	569 (198)	UAF juvenile sablefish <sup>c</sup>
2019	2019	Age-1 Mar	SJBB	28	281 (20)	233–320	21.3 (1.4)	785 (276)	UAF juvenile sablefish <sup>c</sup>
	2019	Age-1 Jul	SJBB	40	311 (30)	257–374	20.4 (1.1)	972 (451)	UAF juvenile sablefish <sup>c</sup>

<sup>a</sup>Strasburger et al. (2018a,b); <sup>b</sup>Fenske et al. (2019); <sup>c</sup>Field collections for this study; <sup>d</sup>Samples obtained from purse seine fishery

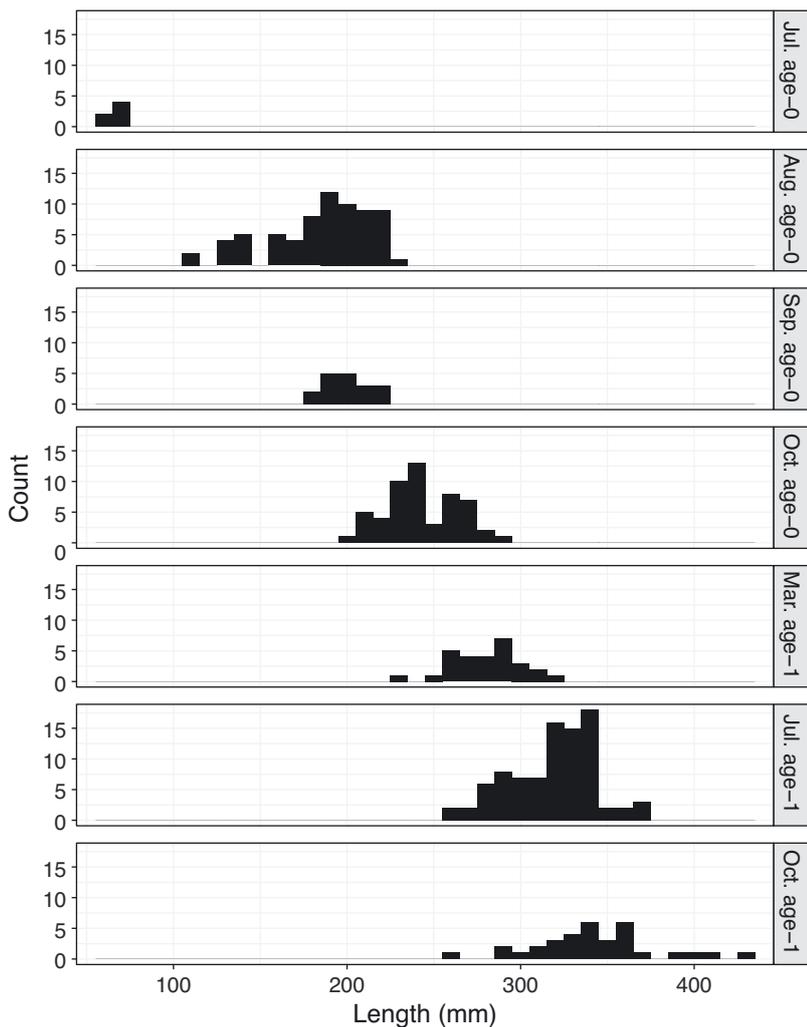


Fig. 3. Length–frequency histograms of sablefish analyzed for each sampling month. Years are pooled

for TE in March was 5.4 and was significantly higher than slopes in other months ( $p < 0.05$ ; Table 3), which ranged from 3.2 in September to 3.6 in October (Fig. 4). Slopes in September, October, and July did not differ from each other ( $p > 0.9$ ; Table 3). We did not catch any sablefish during our first late winter/early spring sampling effort (April–May 2018); therefore, we present overwinter energy allocation results for only the 2018 year class.

### 3.2. Size-based, seasonal, and annual variation in energy storage

Based on analyses of the full data set, sablefish ED and TE increased with length and varied by month and year class. The set of best models included a length  $\times$  month interaction (Table 4), suggesting that slopes of the ED–length and TE–length relationships varied with season, with the steepest slopes for both ED and TE occurring in March for age-1 fish (month 15) and the shallowest slopes for ED occurring in July for age-0 fish (month 7; Fig. S2, Table S2). The model with the lowest  $\Delta AICc$  for ED included a month  $\times$  year class interaction, and a similarly performing model ( $\Delta AICc = 1.59$ ) included a

Table 2. Model coefficients for sablefish length (length), months (monthx), and their interactions from ANCOVA models for 2018 year-class sablefish. ED: energy density; TE: total energy. TE and length are natural log transformed in the TE model

Parameter	ED				TE			
	Estimate	SE	<i>t</i>	<i>p</i>	Estimate	SE	<i>t</i>	<i>p</i>
Intercept	17.08	3.16	5.40	<0.01	-11.22	3.04	-3.69	<0.01
Length	0.02	0.02	1.21	0.23	3.21	0.57	5.60	<0.01
Month10	-2.26	3.60	-0.63	0.53	-2.19	3.49	-0.63	0.53
Month15	-12.52	3.90	-3.21	<0.01	-12.43	3.82	-3.26	<0.01
Month19	-3.28	3.46	-0.95	0.35	-2.39	3.38	-0.71	0.48
Length × month10	0.01	0.02	0.70	0.48	0.38	0.65	0.59	0.56
Length × month15	0.04	0.02	2.31	0.02	2.15	0.70	3.05	<0.01
Length × month19	0.00	0.02	0.14	0.89	0.34	0.63	0.55	0.58

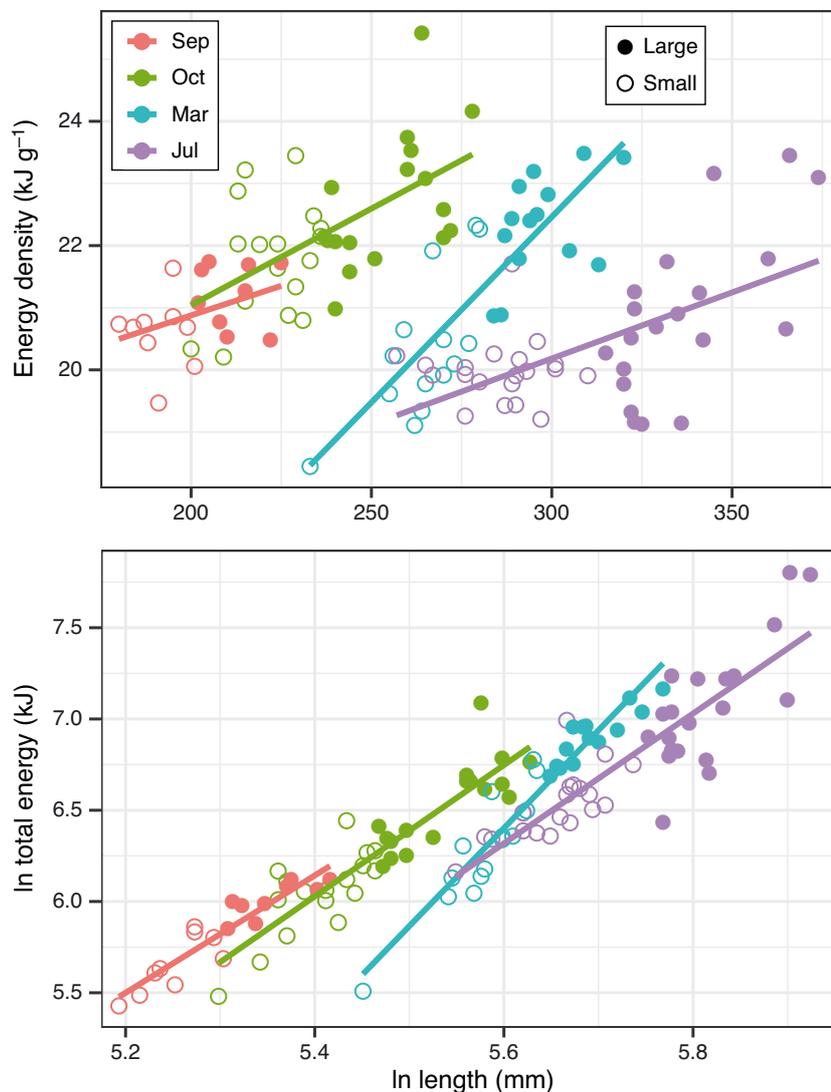


Fig. 4. Slopes of sablefish energy storage versus length relationships: energy density and total energy for the 2018 year class for each month sampled: September, October, March, and July. Fish are grouped as larger and smaller than seasonal median length

length × year class interaction (Table 4). The top TE model included all terms except a length × year class interaction (Table 4). The top models had  $R^2$  values of 0.63 and 0.97 for ED and TE, respectively. Sablefish of the 2017 year class stored more energy than the 2018 year class. An average-sized age-0 sablefish in October (244 mm) was predicted to have 0.7  $\text{kJ g}^{-1}$  higher ED and 180 kJ higher TE in 2017 than 2018. This difference persisted through July, when an average age-1 sablefish (320 mm) was predicted to have 1.5  $\text{kJ g}^{-1}$  higher ED and 147 kJ higher TE in 2017 than in 2019.

## 4. DISCUSSION

### 4.1. Energy allocation during winter

Winter affected fish of different sizes in strikingly different ways, consistent with the hypothesis illustrated in Fig. 1D, except that fish of all sizes grew during winter. Fish larger than the median size increased in length from October to March with minimal depletion of energy stores. Fish smaller than the median size also increased in length but depleted their energy stores. Mean TE for the 2018 cohort in March was higher than in October, but TE at a given length decreased. If we assume that fish grew but stayed in the same relative length quantile between October and March, a fish in the 80<sup>th</sup> percentile would grow 35 mm, accumulate 240 kJ in TE, and deplete its energy stores by 0.7  $\text{kJ g}^{-1}$ . Over the same period, a fish in the 20<sup>th</sup> percentile would increase 42 mm, gain only 111 kJ, and lose 1.4  $\text{kJ g}^{-1}$ . Relatively large fish at this life stage may prioritize energy storage, whereas relatively small fish continue to prioritize growth.

Table 3. Pairwise post hoc comparisons of the energy density (ED) versus length and total energy (TE) versus length slopes among seasons for the 2018 year class. Est.: estimated difference between slopes

Month	ED vs. length					TE vs. length				
	Est.	SE	df	t	p	Est.	SE	df	t	p
Sep–Oct	-0.01	0.02	112	-0.70	0.896	-0.38	0.65	112	-0.59	0.935
Sep–Mar	-0.04	0.02	112	-2.31	0.102	-2.15	0.70	112	-3.05	0.015
Sep–Jul	0.00	0.02	112	-0.14	0.999	-0.34	0.63	112	-0.55	0.947
Oct–Mar	-0.03	0.01	112	-2.64	0.046	-1.77	0.51	112	-3.44	0.004
Oct–Jul	0.01	0.01	112	1.16	0.652	0.04	0.40	112	0.10	1.000
Mar–Jul	0.04	0.01	112	4.14	<0.001	1.81	0.48	112	3.75	0.002

Size-based differences in energy allocation strategies may be advantageous. For example, small rainbow trout *Oncorhynchus mykiss* that focus energy into growth have a survival advantage over small trout that store more and grow less, whereas large rainbow trout that increase energy stores survive at higher rates than large trout that divert energy primarily towards growth (Post & Parkinson 2001).

The apparent growth rates we observed over the winter cannot be attributed solely to size-selective mortality. Size-selective mortality is common in marine fish during winter and tends to disproportionately remove the smallest individuals (Sogard 1997, Beamish et al. 2004, Hurst 2007). Size-selective mortality and somatic growth may coincide, which could potentially inflate the apparent growth rates in this study. However, in the absence of growth, a cohort of fish would have a narrower length range, higher mean length, and an unchanged maximum length after size-selective mortality (Sogard 1997). In contrast, our length range widened and maximum length increased in all subsequent seasons, including during winter, with March mean lengths exceeding the maximum length from the previous October. Size-dependent overwinter mortality can occur due to increased predation (Miranda & Hubbard 1994,

Sogard 1997), greater susceptibility to disease (Vollenweider et al. 2011), or from exhaustion of energy stores in small fish (Schultz & Conover 1999, Norcross et al. 2001, Hurst 2007). Hungry sablefish are more likely to endure unfavorable temperatures in pursuit of food (Sogard & Olla 1998), and hungry fish assume greater predation risk while actively foraging (Sogard & Olla 1997). These sources of mortality may compound each other in

small fish if they deplete their energy reserves before large fish.

Steepening relationships between energy storage and length (Figs. 1D & 4) can occur when fish are in periods of energy loss. Large fish tend to have greater energy stores and have lower mass-specific metabolic rates, an advantageous combination to minimize energy depletion. Greater retention of energy stores in large individuals during starvation experiments has been demonstrated for walleye pollock *Gadus chalcogrammus* (Sogard & Olla 2000), Atlantic silverside *Menidia menidia* (Schultz & Conover 1999), and yellow perch *Perca flavescens* (Post & Evans 1989). For energy depletion to explain our results, sablefish would have grown and gained energy between fall and early winter and then failed to meet metabolic demands during mid-winter. Growth and energy deposition after October in fish that lose energy over the winter is plausible. Age-0 and age-1 pollock increase in length and percent lipid between September and December (Heintz & Vollenweider 2010), and age-1 Pacific herring *Clupea pallasii* ED increases in October–November before declining into winter (Foy & Paul 1999). Continuous growth throughout winter is realistic given environmental conditions. In laboratory experiments,

Table 4. The 95% confidence set of models, based on Akaike weights, describing variation in energy density (ED) and total energy (TE) in sablefish.  $\Delta$ AICc is the AICc for each model minus the lowest AICc across all candidate models

Model parameters	R <sup>2</sup>	$\Delta$ AICc	Weight
<b>ED</b>			
month + length + year class + length $\times$ month + month $\times$ year class	0.65	0	0.572
month + length + year class + length $\times$ month + length $\times$ year class	0.65	1.59	0.26
month + length + year class + length $\times$ month + month $\times$ year class + length $\times$ year class	0.65	4.14	0.073
month + length + year class + month $\times$ year class	0.63	4.44	0.062
<b>TE</b>			
month + log(length) + year class + log(length) $\times$ month + month $\times$ year class	0.98	0	0.742
month + log(length) + year class + log(length) $\times$ month + month $\times$ year class + log(length) $\times$ year class	0.98	2.27	0.238

post-settlement age-0 sablefish eating ad libitum rations grew  $0.41 \text{ mm d}^{-1}$  in  $5^\circ\text{C}$  (Krieger et al. 2019) compared to an apparent growth rate of  $0.29 \text{ mm d}^{-1}$  in this study at a minimum SJBB bottom temperature of  $6.2^\circ\text{C}$  in winter 2018–2019. Improved foraging success for large sablefish compared to small ones could also explain the steep allometric slope in March. In a separate analysis of the same fish we collected from SJBB, sablefish carbon and nitrogen isotope ratios were both positively correlated with length in March (M. W. Callahan et al. unpubl. data), indicating size-based differences in foraging habits. Sablefish sampled in March were also observed to feed on squid that were large relative to sablefish size (M. W. Callahan et al. unpubl. data). Large predators likely have better foraging success (Juanes & Conover 1994, Scharf et al. 2000), and if bigger sablefish more effectively capitalized on large, high-energy prey, they could better retain lipid over the winter. Large juvenile striped bass *Morone saxatilis* in a Virginia reservoir had higher quality diets than smaller individuals, and this size-based diet difference contributed to greater retention of lipid reserves in large striped bass through winter (Fig. 1D; Sutton & Ney 2001).

Smaller sablefish losing relatively more energy over winter compared to larger individuals differs from seasonal shifts observed in juveniles of other Northeast Pacific fish species. Larger fish commonly experience greater energy loss than smaller individuals (Fig. 1C). For example, Southeast Alaskan age-1 pollock lost 35% of their TE overwinter, whereas age-0 pollock lost only 19% (Heintz & Vollenweider 2010). These differences are attributed to age-0 fish foraging at higher rates while age-1 fish rely much more heavily on endogenous stores, a strategy that reduces predation risk.

## 4.2. Temporal variation in energy allocation

Between their first summer and autumn, age-0 sablefish grow rapidly while increasing energy stores. The high apparent growth rates we observed between September and October 2018 are consistent with values previously reported in the literature. Post-settlement age-0 sablefish grew  $1.16 \text{ mm d}^{-1}$  at  $12^\circ\text{C}$  in laboratory experiments (Krieger et al. 2019), and Sigler et al. (2001) found an average growth of  $1.2 \text{ mm d}^{-1}$  for Gulf of Alaska age-0 juveniles during summer. Age-0 sablefish in July had higher ED than previously reported for similar sized fish in the Gulf of Alaska (Van Pelt et al. 1997), but our July age-0

samples consisted of only 6 individuals of a narrow size range, and size-based patterns of energy storage during this period of rapid growth should receive further examination.

Annual variation in energy storage levels is common in juvenile fish (e.g. Heintz et al. 2013). While we found strong evidence for variability in ED and TE across years, there was little evidence for annual differences in the allometric slope of energy storage. Similarly, allometric slopes of striped bass lipid content did not differ by year in a 5 yr field study (Hurst & Conover 2003). Annual variation in allometric slope is plausible, as laboratory experiments have demonstrated that energy storage allometries may vary by fish size and by temperature (Schultz & Conover 1999, Post & Parkinson 2001). Temperature changes have the potential to shift relative advantages of small and large fish. With low food availability, cold winters disproportionately decreased energy stores of small steelhead *O. mykiss*, while warm winters disproportionately depleted large steelhead energy reserves (Connolly & Petersen 2003). Future research on juvenile sablefish could test whether the observed steep allometric pattern in winter persists under different prey and temperature scenarios.

Age-0 sablefish were smaller and had lower ED in October 2018 compared to October 2017, which could have resulted from density-dependent reductions in growth in 2018 (the 2018 sablefish year class appears larger than the 2017 year class based on juvenile abundance; Hanselman et al. 2019) or from different environmental conditions. Differences in temperature and prey abundance and quality prior to October sampling could also have influenced growth. Gulf of Alaska summer sea surface temperatures were warmer in 2018 than in 2017 (Zador & Yasumiishi 2018), which could have led to faster growth given sufficient food; however, pink salmon *Oncorhynchus gorbuscha*—an important food source for juvenile sablefish in early fall (Coutré et al. 2015)—were more abundant in 2017 than 2018 (Zador & Yasumiishi 2018). Differences in pre-winter sizes and energy stores between 2017 and 2018 year class fish were maintained through the following summer. Larger pre-winter size along with cooler temperatures during winter 2017–2018 (Fig. S3) may have led to less winter energy depletion in 2017 year class fish.

## 4.3. Conclusions

Our results are consistent with the hypothesis that more frequent warm years may benefit sablefish.

Since age-0 sablefish heavily prioritize growth and grow faster in warm water (Sogard & Olla 2001, Krieger et al. 2019), they are more likely to enter winter at large sizes and with higher energy stores in warm years, assuming access to sufficient food (Sogard & Spencer 2004). We found that large fish have energy reserve advantages during winter, suggesting that faster growth before winter could lead to improved overwinter survival and eventual recruitment to the commercial fishery. Recent warm years have already coincided with high recruitment, and increased frequency of large sablefish year classes carry economic and ecological implications. The unusual scaling relationship between sablefish energy stores and size during winter might contribute to sablefish thriving in warm regimes.

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