Influence of size on the sources of energy consumed by overwintering walleye pollock (*Theragra chalcogramma*)

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ABSTRACT

The critical size hypothesis proposes the risks of winter mortality are greatest for small individuals in fish populations. This results from size-dependent predation and starvation of wintering fishes. We extend this idea to walleye pollock (*Theragra chalcogramma*) and argue size-dependence leads to different wintering strategies among subadult life stages. We sampled fish quarterly, measured their size, growth and energy allocation. By comparing the contributions of endogenous energy sources (storage and structure) to metabolic demand in young-of-the-year (YOY) and juvenile pollock over winter we determined how length influenced their winter foraging requirement. From this we inferred the relative risks of starvation and predation for different sized fish. Young-of-the-year (≤170 mm) experienced high starvation risk and relied on foraging to meet routine metabolic cost. Consequently, they consumed relatively little storage or structural energy over winter. In contrast, juveniles (>170 mm and ≤270 mm) responded to the risk of predation by consuming significant amounts of protein and structural lipids while minimizing foraging. Consistent with these observations we found YOY maximized growth in fall while juveniles maximized energy storage. In spring, YOY resumed growth earlier than juveniles. These data indicate the critical size and period hypothesis can be extended to walleye pollock.

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1. Introduction

The critical size and period hypothesis proposes winter survival is more likely for juvenile fish that grow sufficiently large prior to winter (Beamish and Mahnken, 2001). Originally posed as an explanation for variation in salmon recruitment, the critical size hypothesis has been supported through studies of coho (*Oncorhynchus kisutch*) and pink salmon (*O. gorbuscha*) (Farley et al., 2007; Moss et al., 2005). However, demonstration of size dependent mortality among purely marine populations has been elusive (Sogard, 1997). The mechanisms leading to improved survival of large juveniles include physiological/ thermal tolerance, improved immune function, starvation and predation avoidance (Hurst, 2007). Starvation is an important factor because food supplies decrease in winter (e.g. Foy and Paul, 1999), which means fish must rely on their energy reserves in order to meet metabolic demand during winter. However, when these reserves reach critical values, fish must forage (Bull et al., 1996). Foraging results in increased exposure to predators (Scheuerell and Schindler, 2003). Consequently, juvenile fish must weigh the relative risks of starvation against predation in order to maximize survival over winter (Schindler, 1999). The smallest individuals in juvenile populations likely spend more time foraging because they have a lower

capacity for energy storage and higher mass-specific metabolic rates than larger juveniles (Schultz and Conover, 1999). This size dependent trade-off between foraging and predation risk is therefore an important element of the critical size hypothesis.

One approach to evaluating the trade-off between starvation and predation in the field is to build an energy budget that balances the cost associated with metabolic demand against the contributions from energy reserves. The difference represents the amount of energy that must be derived from foraging. In practice, fish often draw energy from both the storage and structural compartments in their bodies (Hurst and Conover, 2003). Energy derived from storage is drawn from lipids, while energy in the structural compartment derives primarily from proteins. Reductions in the protein content of fish can have important fitness impacts (Castellini and Rea, 1992). Assuming that structural catabolism incurs a fitness cost, then apportioning metabolic demand into storage and structural contributions can provide a measure of the relative importance of predation and starvation. In order to maximize fitness fish must either meet metabolic demand by catabolizing endogenous energy stores (storage or structural energy) or foraging in risky habitats (Abrahams and Dill, 1989). The decision to pursue one strategy over the other will be determined by the relative risks of the predation and starvation. A fish electing to catabolize structure in favor of foraging does so because the risk of predation has a greater fitness cost than the risk of starvation.

Walleye pollock (*Theragra chalcogramma*) is an ecologically important species that offers the opportunity to understand how

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subadult fish trade-off starvation and predation risk in winter. In the north Pacific, walleye pollock forage (Clausen, 1983) during winter but lose energy (Vollenweider, 2005). Moreover, subadult pollock are important prey to Steller sea lions and considerable effort has been put into determining the size of pollock consumed (Sigler et al., 2009). Currently, the effect of winter resource scarcity on pollock recruitment is unknown. A detailed analysis of the trade-off between starvation and predation in overwintering pollock offers the opportunity to develop a conceptual model for how winter influences their recruitment into adult populations. Given the economic and ecological importance of pollock to the north Pacific such a conceptual model should be of considerable interest.

In this study we hypothesized that young-of-the-year (YOY) and juvenile pollock have different growth strategies because the relative risks of starvation and predation depend on size. We tested this hypothesis by sampling YOY and juvenile pollock before and after winter and measuring their size, growth and energy allocation. These data are used to construct seasonal energy budgets and determine the amount of energy lost from storage and structural reserves over winter. These losses are combined with predictions of the metabolic cost of overwintering to estimate the contributions of storage, structure and foraging to winter metabolic costs. The resulting models describing the relation between size and the sources of energy used to meet winter energy needs provide an understanding of the relative risks of starvation and predation among different sized fish. The size and growth of YOY and juvenile pollock are subsequently discussed relative to the risks of starvation and predation.

2. Methods

2.1. Study area and sample collection

We sampled pollock during quarterly trawl surveys in Lynn Canal and Frederick Sound (Fig. 1) between September 2001 and May 2002. The fish were sampled in four seasons to determine the periods in which energy levels were most extreme. Detailed descriptions of the survey and collection methods can be found in Sigler and Csepp (2007) and Csepp et al. (Submitted). Pollock were found in discrete layers using hydroacoustics and sampled by mid-water rope trawl at a depth consistent with the layers. Randomly selected fish from each trawl sample were measured for forklength (Table 1) and a subsample of these were weighed and retained for chemical analysis (Table 2). Between 15 and 25 trawls were made in each area and time period depending on the intensity of echo sign. Individuals were classified as YOY or juvenile based on length frequency distributions constructed for each sampling period. Overall, YOY were ≤170 mm in length and juveniles were >170 mm and <270 mm. Conductivity, temperature and depth (CTD) measurements were made using a Seabird model SBE19+ CTD. Casts were made periodically along the survey track to characterize the vertical temperature profiles in each of the water bodies sampled (Fig. 1) allowing us to estimate the mean temperature of the water column where fish were recovered (Table 1). The depth of capture was determined from hydroacoustic data collected on the cruise. The hydroacoustic methods and estimates of biomass are reported elsewhere (Sigler and Csepp, 2007; Csepp et al., Submitted).

The retained fish were chemically analyzed to construct energy budgets and identify the proportion of energy allocated to structure or storage. Fish retained for chemical analysis were flash frozen in liquid nitrogen (−196 °C) and vacuum sealed immediately after obtaining their lengths and weights. Following the cruise, all samples were stored at −80 °C until chemical analysis, which occurred within three months. Chemical analyses included determination of the lipid, water, ash, and total protein, lipid class composition and RNA/DNA ratios. Carbohydrate content was considered negligible. All analyses were performed on individual whole fish, homogenized following the
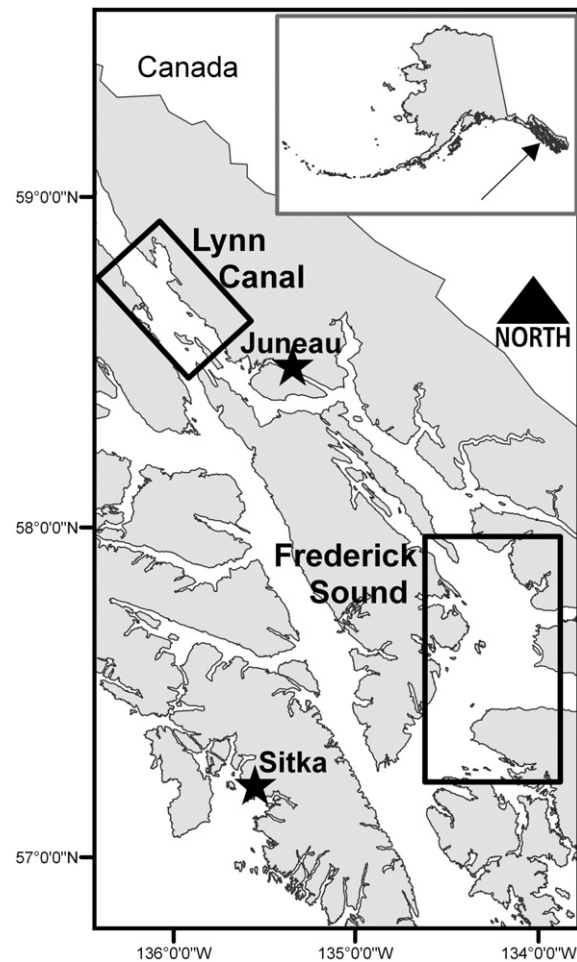

Fig. 1. Study areas in southeastern Alaska. The center of the Lynn Canal sampling area is approximately 58 ° 31′ 33″ N, 134° 59′ 12″ W. The center of the Frederick Sound area is approximately 57 ° 21′ 32″ N, 133° 41′ 23″ W.

procedures outlined in Vollenweider (2005). Stomachs were not removed prior to analysis.

2.2. Chemical analysis

Details of mass specific measurements of lipid, water, ash, protein and energy for these fish have been previously reported (Vollenweider,

Table 1
Sampling dates, sample size (*n*), average (± 1 s.e.) length (mm), depth (m), and temperature (°C) at capture depth between 2001 and 2002. All lengths were significantly greater than that of the preceding period (*P*<0.05).

		Young-of-the-year	Juveniles
5–15 September 2001	Length	94.0 ± 0.3	213.4 ± 0.9
	n	1570	369
	Depth	87 ± 33	87 ± 34
	Temperature	6.5 ± 0.3	6.6 ± 0.3
28 November–6 December 2001	Length	117.3 ± 0.4	220.4 ± 0.8
	n	868	588
	Depth	83 ± 25	97 ± 16
	Temperature	5.5 ± 0.5	5.7 ± 0.8
27 March–6 April 2002	Length	136.4 ± 0.8	231.4 ± 1.5
	n	236	203
	Depth	116 ± 31	73 ± 51
	Temperature	5.4 ± 0.1	5.3 ± 0.1
23 May–1 June 2002	Length	156.1 ± 0.5	250.2 ± 0.9
	n	507	742
	Depth	59 ± 13	86 ± 34
	Temperature	6.4 ± 0.3	6.3 ± 0.2

Table 2
Average (±1 s.e.) composition of pollock used in this study. Lipid, protein and ash are presented on a wet mass basis, lipid class values are percentages of total lipid classes. Abbreviations: PC phosphatidylcholines; PE phosphatidylethanolamines.

	September 2001	December 2001	March 2002	May 2002
YOY				
n	10	12	19	14
% Lipid	2.25 ± 0.28	3.71 ± 0.27	1.99 ± 0.12	2.77 ± 0.24
% Protein	15.10 ± 0.44	14.70 ± 0.38	13.98 ± 0.13	14.72 ± 0.06
% Moisture	79.97 ± 0.33	78.94 ± 0.49	81.01 ± 0.21	80.28 ± 0.27
% Ash	2.68 ± 0.08	2.82 ± 0.08	2.78 ± 0.06	2.64 ± 0.05
% Wax esters	0.95 ± 0.45	1.42 ± 0.24	0.55 ± 0.10	0.85 ± 0.15
% Triacylglycerols	1.70 ± 1.14	7.27 ± 1.80	2.01 ± 0.65	4.65 ± 1.15
% Sterols	1.97 ± 0.50	6.90 ± 1.10	2.66 ± 0.21	3.20 ± 0.30
% Monoacylglycerols	0.41 ± 0.41	0.31 ± 0.06	0.01 ± 0.01	0.02 ± 0.02
% Free fatty acids	6.79 ± 0.67	6.01 ± 0.53	5.04 ± 0.27	7.38 ± 1.48
% PE	1.38 ± 0.51	0.67 ± 0.08	1.34 ± 0.05	1.39 ± 0.07
% PC	1.87 ± 0.46	1.50 ± 0.21	2.97 ± 0.13	4.17 ± 0.25
Juveniles				
n	11	14	10	15
% Lipid	2.74 ± 0.35	4.97 ± 0.39	2.10 ± 0.25	2.02 ± 0.16
% Protein	16.86 ± 0.54	15.52 ± 0.18	14.27 ± 0.23	14.96 ± 0.11
% Moisture	77.42 ± 0.67	77.56 ± 0.33	80.69 ± 0.35	80.45 ± 0.14
% Ash	2.79 ± 0.26	2.67 ± 0.17	3.03 ± 0.30	2.78 ± 0.09
% Wax esters	1.15 ± 0.27	2.58 ± 0.33	1.53 ± 0.83	0.59 ± 0.08
% Triacylglycerols	2.73 ± 0.85	18.38 ± 2.63	3.74 ± 1.18	2.54 ± 0.54
% Sterols	2.26 ± 0.34	7.70 ± 0.91	2.53 ± 0.27	2.59 ± 0.22
% Monoacylglycerols	0.21 ± 0.10	0.28 ± 0.07	0.00 ± 0.00	0.19 ± 0.06
% Free fatty acids	6.03 ± 0.46	6.94 ± 0.35	3.33 ± 0.51	8.50 ± 1.00
% PE	0.71 ± 0.08	0.65 ± 0.05	1.23 ± 0.05	1.08 ± 0.10
% PC	1.01 ± 0.11	1.16 ± 0.13	3.32 ± 0.23	3.69 ± 0.24

2005). Briefly, lipid was extracted from ~1 g of wet sample homogenate using a modification of Folch's method outlined by Christie (1982). Lipid, moisture and ash content were measured gravimetrically. Protein content was estimated from the total nitrogen content as determined by the Dumas method (Association of Official Analytical Chemists, 2002).

Lipid was fractionated to determine the proportions allocated to structure, metabolic intermediates and storage using high-pressure liquid chromatography. The method followed Heintz et al. (2004). Calibration standards include a wax ester (myristyl myristate), cholesterol, triacylglycerol (triolein), monoacylglycerol (mono-olein), free fatty acid (heneicosanoic acid), bovine phosphatidylcholine and bovine phosphatidylethanolamine. Wax esters and triacylglycerols were identified as storage lipids, structural lipids included phosphatidylcholine, cholesterol and phosphatidyethanolamine. The free fatty acids and monoacylglycerols were considered metabolic intermediates.

Increases in the average lengths of YOY and juveniles could arise from growth, size dependent mortality or size selective migration. We assumed we could identify the cause of size changes by combining observations of energy content with a measure of instantaneous growth, RNA/DNA. Growth-related increases in the average length would require simultaneous increases or maintenance of energy and RNA/DNA levels. Size dependent mortality would be characterized by lost energy and the appearance of an RNA/DNA minimum some time during the period. RNA/DNA integrates RNA production relative to DNA over a period of approximately one week (Weber et al., 2003), so it is an imperfect measure of growth over time. Here we use RNA/DNA as an index of instantaneous growth and interpret changes between seasons as an indicator of the direction of change in growth. We determined RNA/DNA ratios spectrophotometrically following methods outlined in Heintz (2009).

2.3. Statistical analysis of size, growth and energy content

The average size and growth of YOY and juveniles were compared among seasons. The mean lengths of fish in a given age class (i.e. YOY or juvenile) were compared by one-way ANOVA with sampling period

as the main factor. Lengths were subsequently compared between adjacent periods using Student's *t* test. Comparison of lengths in this manner only revealed apparent growth over each of the three intervals: fall (September to December), winter (December to March) and spring (March to May). Therefore we also examined the RNA/DNA ratios to index instantaneous growth at the time of capture (Buckley et al., 1999). Using a one-way ANOVA for each age class, post-hoc comparisons were made to identify differences between adjacent seasons using Tukey HSD methods.

Seasonal energy budgets were constructed for YOY and juveniles separately. The total energy content of each fish was estimated from the wet mass, percent lipid, protein and their calorific equivalents; 36.43 kJ/g and 20.10 kJ/g for lipid and protein, respectively (Brett 1995). Similarly, the energy allocated to structure (protein, phosphatidylcholine, cholesterol and phosphatidylethanolamine), storage (wax esters and triacylglycerols) and metabolic intermediates (free fatty acids, monoacylglycerols) was determined from the same calorific equivalents. Fish lengths and estimates of their energy (kJoules) were transformed to their logarithms (base 10) and analyzed by ANCOVA. Lengths were a covariate and sampling period was the main fixed factor and slopes were assumed constant across periods. Differences among periods were examined post-hoc using Tukey HSD tests. Prior to the analysis the assumptions of normality (Anderson's test), homogeneity of variance (Cochran's Q) and common slope were examined and found to not influence our conclusions. The common slope assumption was evaluated by initially performing the analysis with an interaction between length and sampling period present. In all cases the interaction term was found to be not significant ($P > 0.331$).

2.4. Contributions of energy sources to routine metabolic cost

The amount of energy lost from the storage and structural compartments over winter were compared with the routine metabolic demand over the same period. We estimated the routine metabolic demand from a previously published model that accounts for mass and water temperature (Paul 1986). The model is:

$$D = 99.958 + 4.393\,w \tag{1}$$

Where D is metabolic demand in calories per day at 5.5 °C and w is the wet mass in grams. We chose this model over others because it was the only one that offered estimates of metabolic cost in calories. Comparison of results described here with those derived from the model described by Cianelli et al. (1998) did not differ substantially.

Respiratory energy demand for fasting fish was predicted over the 118 days between our median December and March sampling dates. We used separate length weight regressions for YOY and juveniles in December and March to estimate the geometric mean weights of fish in each of 11 length classes over winter. We subsequently estimated the routine metabolic cost for each length class based on their geometric mean weight. The length classes spanned 10 mm beginning with 110 mm and ending with 250 mm. The following relation was used to estimate the proportion of this metabolic cost fueled by catabolism of storage energy:

$$C_i = \frac{E_{storage-Dec_i} - E_{storage-March_i}}{118D} \tag{2}$$

Where C_i is the daily contribution of storage energy for the *i*th size class, $E_{storage-Dec}$ is the average storage energy for a fish in the *i*th size class in December and $E_{storage-March}$ is the average storage energy found in fish from the *i*th size class in March. The value of D in the denominator was calculated with $\bar{w}_i$, the geometric mean weight of fish in the *i*th age class over the 118 days between December and

March. These proportions were plotted against the midpoint of each length class. A similar approach was employed for structural energy.

Models relating the size of fish to the contributions of storage and structural energy were used to see if fish of different sizes vary in their contributions of storage and structural energy to metabolic demands. Such differences would indicate variable reliance on forage and indicate the relative risks of starvation and predation vary with size. We had no a priori information regarding the shape of the relations. Therefore we sequentially fit linear, exponential, logarithmic, lognormal, parabolic and Gaussian functions to the observed relationships between size and the proportional contribution to routine metabolic cost. The best fitting curve was identified as that with the lowest second-order Akaike information criterion (AIC_c). The best-fit curves were used to sum the contributions of storage and structure to routine metabolic cost. The difference between the sum and the estimated routine metabolic cost was considered to be the amount of energy obtained by foraging.

3. Results

3.1. YOY size, growth and energy allocation

During the fall (September to December) of 2001 YOY pollock increased in size while maintaining a constant energy allocation strategy. YOY increased in length ($\pm$ s.e.) from 94 ± 1 mm to 117 ± 1 mm ($t = 44.66$; $P < 0.001$) (Fig. 2). However, RNA/DNA ratios were lower in December ($t = 6.95$; $P < 0.001$) (Fig. 3) indicating lower instantaneous growth rates in December. Parameter estimates and associated statistics for the ANCOVAs are given in Table 3, least square means for representative fish are given in Table 4. The total energy of fish at a given length did not change in fall ($t = 0.495$; $P = 0.960$) (Table 4). Hence, the allocation of energy between structure (protein, phospholipids and sterols), storage (waxes and triacylglycerols) and metabolic intermediates (free fatty acids, monoacylglycerols) remained constant ($t > 0.212$; $P > 0.821$) (Table 4). Energy allocated to structure accounted for 84% of the total energy in September and 81% in December. Energy stores accounted for 6% and 10% of total energy in September and December, respectively. The energy found as metabolic intermediates accounted for 8% of the total energy in both September and December.

In contrast to the fall, YOY pollock lost energy over winter (December to March) while simultaneously increasing in length. Energy levels in March were the lowest observed during the year (Table 4). Mean length increased over winter from 117 ± 1 mm to 136 ± 1 mm ($t = 21.03$; $P < 0.001$). Average RNA/DNA ratios increased slightly ($t = 3.179$; $P = 0.015$), indicating that instantaneous

Fig. 3. RNA/DNA ratios of YOY and juvenile pollock sampled from southeastern Alaska in 2001 and 2002. Asterisks show periods that differ significantly ($P < 0.035$) from the previous period.

growth rates had reached some minimum level during winter. Also, fish lost approximately 19% of their total energy ($t = 3.122$; $P = 0.013$) (Table 4). Losses of structure and storage were disproportionate with their relative contributions to total energy in December. Structural losses were estimated to account for 41% of the energy loss even though no change was detected ($t > 1.62$; $P = 0.380$). Losses in the amount of energy allocated to storage ($t = 5.54$; $P < 0.001$) accounted for 47% of the total energy loss, despite representing 10% of the December total. The amount of energy found as metabolic intermediates also declined during this period, accounting for approximately 12% of the total energy loss, but this decrease was not statistically significant ($t = 2.057$; $P = 0.181$).

In spring (March to May) YOY pollock resumed growing and recovered the energy they lost in late winter. During spring pollock lengths increased significantly from 136 ± 1 mm to 156 ± 1 mm ($t = 21.53$; $P < 0.001$). RNA/DNA ratios simultaneously increased ($t = 3.18$; $P = 0.015$) indicating a substantial increase in growth. Energy content increased by 22% in spring ($t = 2.81$; $P = 0.035$) returning fish to their pre-winter levels. This increase was allocated approximately in proportion to body composition in March. In March 90% of the energy was allocated to structure, 1% was found in storage and 7% was identified as metabolic intermediates. In May, 87% was in structure, 2% in storage and 8% was in metabolic flux. None of these changes were statistically significant ($t < 2.49$; $P > 0.073$).

3.2. Juvenile size, growth and energy allocation

In fall juveniles exhibited little evidence of structural increases but increased their energy reserves. Juvenile lengths increased slightly from 213 ± 1 mm to 220 ± 1 mm (Fig. 2) during this period ($t = 5.78$; $P < 0.001$) and instantaneous growth rates did not change between September and December as indicated by constant RNA/DNA ratios ($t = 1.60$; $P = 0.375$) (Fig. 3). Nor was there any detectable change in energy content of fish ($t = 0.19$; $P = 0.997$). Parameter estimates and associated statistics for the ANCOVAs are given in Table 3, least square means for representative fish are given in Table 4. Despite the constancy of total energy there was some evidence of a change in energy allocation between structure and storage. Structural energy accounted for 85% and 73% of the total energy in September and December, respectively. However these amounts were not statistically different ($t = 2.44$; $P = 0.084$). Conversely storage energy increased ($t = 2.61$; $P = 0.057$) from 5% to 17% of the total energy. Metabolic intermediates accounted for 10% and 7% of the total energy in September and December, respectively but these values did not differ ($t = 1.94$; $P = 0.227$).

Juvenile pollock lost significant amounts of energy over winter while increasing in length. In March energy levels fell to the lowest levels
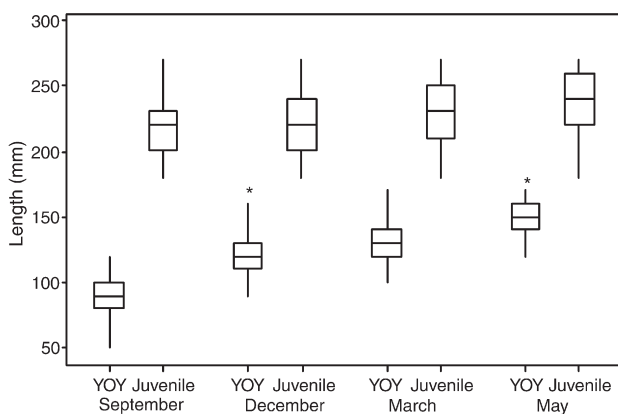
Fig. 2. Boxplots showing quartiles of lengths of YOY and juvenile pollock sampled from southeastern Alaska in 2001 and 2002. Within each age class (YOY and juveniles), mean lengths identified with an asterisk are significantly different from the previous sampling period ($P < 0.01$). Sample sizes are given in Table 1.
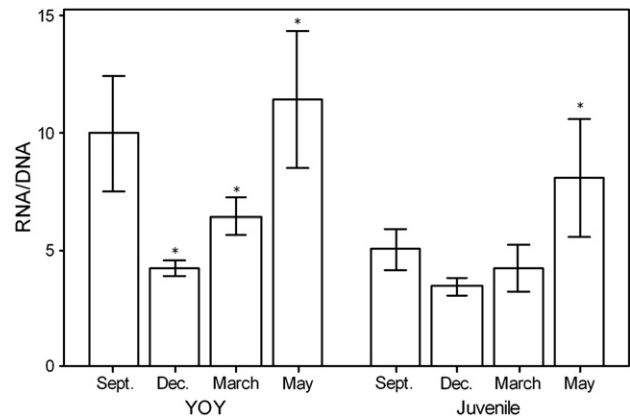
Table 3
Result of ANCOVA's used to estimate length specific energy content of YOY and juvenile pollock. Models were of the form Response (kJ) = β_{period}Length$^{\beta 1}$. Column labeled P displays α for the sampling period effect. All coefficients shown were significantly different from zero ($P < 0.001$), except for the slope for juvenile storage energy ($P = 0.235$).

Response	β_1	β_{Sep01}	β_{Dec01}	β_{Mar02}	β_{May02}	R^2	P
YOY ANCOVA results							
Total E	2.816	6.63E−05	6.92E−05	5.62E−05	6.85E−05	0.903	0.003
Structural E	2.733	8.33E−05	8.37E−05	7.56E−05	8.91E−05	0.909	0.050
Storage E	6.209	3.21E−13	5.23E−13	5.76E−14	1.13E−13	0.495	<0.001
Metabolic E	2.208	1.08E−04	1.07E−04	7.68E−05	1.11E−04	0.486	0.050
Juvenile ANCOVA results							
Total E	3.063	2.58E−05	2.61E−05	1.69E−05	1.94E−05	0.858	<0.001
Structural E	3.060	2.23E−05	1.95E−05	1.54E−05	1.75E−05	0.894	<0.001
Storage E	1.988	4.05E−04	1.51E−03	1.80E−04	1.47E−04	0.354	<0.001
Metabolic E	2.647	2.36E−05	1.79E−05	6.70E−06	1.57E−05	0.697	<0.001

Table 4
Length adjusted energy (kJ) content and wet weight (g) of subadult pollock at four different sampling times. Values reflect estimates (± 1 s.e.) determined from results of ANCOVAs whose parameters are given in Table 2. Values marked with an "*" differ significantly from that of the preceding period ($P < 0.05$).

Period	Number sampled	Wet weight	Total energy	Structural energy	Storage energy	Metabolic intermediate energy
YOY (125 mm)						
September	10	15.36 ± 0.35	54.08 ± 4.72	45.39 ± 3.72	3.46 ± 2.47	4.65 ± 1.04
December	12	13.60 ± 0.30	56.49 ± 2.99	45.60 ± 2.27	5.64 ± 2.04	4.63 ± 0.62
March	19	12.52 ± 0.26	45.81 ± 1.92*	41.21 ± 1.62	0.62 ± 0.17*	3.31 ± 0.35
May	14	13.41 ± 0.29	55.85 ± 3.65*	48.53 ± 2.98	1.22 ± 0.54	4.76 ± 0.79
Juveniles (232 mm)						
September	11	104.1 ± 4.1	453.9 ± 24.99	384.6 ± 17.4	20.46 ± 10.06	42.95 ± 5.09
December	14	92.2 ± 3.5	460.3 ± 19.69	335.7 ± 11.8	76.49 ± 28.78	32.51 ± 3.14
March	10	84.8 ± 3.2	297.2 ± 15.22*	264.9 ± 11.1*	9.10 ± 4.22*	12.19 ± 1.42*
May	15	90.9 ± 3.5	342.0 ± 16.7	302.0 ± 12.1	7.44 ± 3.05	28.58 ± 3.01*

observed during the year (Table 4).The average length of juveniles increased from 220 ± 1 mm to 231 ± 2 mm over winter ($t = 6.49$; $P < 0.001$). However, instantaneous growth rates did not change during the period as indicated by RNA/DNA ratios ($t = 0.81$; $P = 0.848$). Total energy for fish of fixed length decreased by approximately 35% ($t = 6.74$; $P < 0.001$), nearly twice the loss of YOY. As in the YOY, contributions of storage and structure were disproportionate with initial body composition. Approximately 42% of the loss was accounted for by losses in storage energy ($t = 4.31$; $P < 0.001$) even though storage only accounted for 17% of the total energy in December. Losses of structural energy ($t = 4.46$; $P < 0.001$) accounted for another 44% of the total loss. Decreases in the amount of metabolic intermediates ($t = 6.88$; $P < 0.001$) accounted for 13% of the remaining lost energy.

In spring, pollock started to recover the energy they lost over winter while increasing in size. In spring the average length of juvenile pollock increased from 231 ± 2 mm to 250 ± 1 mm ($t = 10.82$; $P < 0.001$). The growth increment over this period was equal to that of YOY, approximately 20 mm. Similarly, RNA/DNA ratios increased over the levels observed in the previous periods ($t = 4.87$; $P < 0.001$). In contrast there was no change in energy content. The average content increased by approximately 13%, but this difference was not statistically significant ($t = 0.214$; $P = 0.997$). The relative contributions of structure and storage to total energy remained constant over this period (Table 4). Approximately 82% of this increase was the result of an increase in structural energy, but this change was not statistically significant ($t = 2.21$; $P = 0.137$). Similarly, the decrease in storage energy during this period was not statistically significant ($t = 0.381$; $P = 0.981$), accounting for −3.7% of the total energy gain. In contrast, metabolic intermediates increased significantly during this period ($t = 5.56$; $P < 0.001$). This increase accounted for 37% of the increase in total energy.

3.3. Contributions of energy sources to routine metabolic cost

At the beginning of winter YOY had insufficient reserves to meet the impending metabolic demand. Routine metabolic cost over the

118 days between the December and March sampling periods exceeded the total energy content of the average sized YOY (Fig. 4). Only those individuals greater than 158 mm in December had energy contents in excess of their routine metabolic cost. For example a 125 mm fish had an estimated total energy content of ~56 kJ in December (Table 4) and a routine metabolic cost of ~78 kJ (Fig. 4) over the winter. Consequently energy loss in these fish accounted for relatively little of routine metabolic cost. Fish this size experienced a net energy loss of 10.7 kJ (Table 4), which accounted for less than 14% of routine metabolic cost. In contrast, individuals averaging 232 mm experienced a 163 kJ net energy loss (Table 4), which accounted for 74% of their routine metabolic cost (Fig. 4).
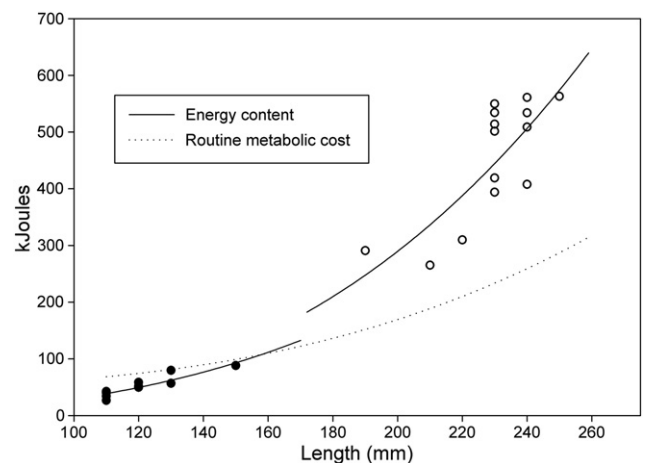

Fig. 4. Estimated routine metabolic cost (total kJ) for different sized pollock over the 118 days between the December and March and their estimated energy content (kJ) in December (dotted line). Routine metabolic costs reflect values predicted from Eq. (1). Energy content (solid line) shows the allometric relationships between total energy and length in December for YOY (filled symbols) and juveniles (open symbols). The allometries are described in Table 3.

Table 5
Functions are relating length (Lth) and the contribution of structural energy to routine metabolic cost over winter. Coefficient values marked with an "*" are significantly different from 0 ($P<0.05$). Values <0.05 in the column labeled "P" indicate the model accounts for a significant amount of error. AIC_c is the value for the associated Akaike information criterion.

Type	Function	β_0	β_1	β_2	R^2	AIC_c	P
Exponential	$\beta_0+\beta_1(1-e^{\beta_2 Lth})$	−514	552	0.022	0.569	45.57	0.082
Linear	$\beta_0+\beta_1 Lth$	−27.8	0.266*	–	0.508	41.07	0.044
Logarithmic	$\beta_0+\beta_1\times Ln(Lth)$	−232.4*	49.04*	–	0.573	40.07	0.030
Lognormal	$\dfrac{\beta_0 e^{-0.5\times\left(\frac{Ln\left(\frac{Lth}{\beta_1}\right)}{\beta_2}\right)^2}}{Lth}$	10613*	217.1*	0.165*	0.807	39.93	0.016
Parabolic	$\beta_0+\beta_1 Lth+\beta_2 Lth^2$	−161.5*	1.911*	−0.005	0.677	43.56	0.046
Gaussian	$\beta_0 e^{-0.5\times\left(\frac{Lth-\beta_1}{\beta_2}\right)^2}$	50.34*	214.1*	34.1	0.832	39.00	0.013

YOY pollock conserved their structural energy during winter despite facing metabolic demands that outstripped their reserves. The relationship between length and the contribution of structural energy to routine metabolic cost was explained best by the logarithmic, lognormal and Gaussian functions (Table 5) ($P<0.03$; $R^2>0.573$). The lowest AIC_c was observed for the Gaussian model (shown in Fig. 5) and AIC_c for the other two differed (Δi) by less than 1.08. The other models differed by more than 2.06. Losses of structural energy did not account for more than 5% of routine metabolic cost until fish length exceeded 140 mm and peaked at a size (213 mm) near the mean length of juvenile pollock in December. Contributions of structural energy to routine metabolic cost decreased rapidly thereafter, accounting for virtually none of the routine metabolic cost in individuals greater than 300 mm long.

The storage energy mobilized during winter was of most value to the largest juveniles. The linear and logarithmic models had lower AIC_c values than any of the other models (Table 6). The linear model had the lowest AIC_c, differing from the logarithmic model by 0.43. All of the other models differed from the linear model by at least 2.05. The linear model is shown in Fig. 5 ($P=0.002$; $R^2=0.862$). YOY needed to exceed 105 mm in length before storage offered any relief to routine metabolic cost. In contrast, the model predicts that a 464 mm individual would have met 100% of their metabolic demand with storage energy. Coincidently, 90% of 450 mm pollock were sexually mature in the Bering Sea in 2002 and 2003 (Stahl and Kruse, 2008).
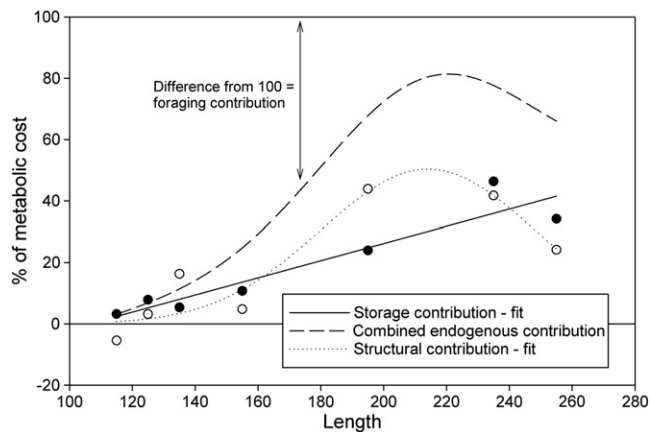
The portion of the metabolic cost met by foraging can be inferred from the sum of the storage and structural contributions. This suggests that an average YOY (119 mm) relied on foraging for more than 95% of routine metabolic cost over winter, while the largest YOY (e.g. 170 mm) foraged to meet 60% of their metabolic cost. In contrast, juveniles of average length (220 mm) relied on foraging to meet less than 20% of their routine metabolic cost over winter. Fish that exceeded 240 mm in December relied more on storage than structure to meet routine metabolic cost and also increased their reliance on exogenous energy sources. By time fish averaged 255 mm foraging accounted for 34% of routine metabolic cost, while the majority of endogenous energy came from storage.

4. Discussion

Analysis of the relationship between size and the sources of energy used in winter supports our hypothesis that the relative risks of starvation and predation are size dependent. The smallest pollock could not contribute any endogenous resources to meet routine metabolic cost, hence they relied on foraging. This is consistent with laboratory observations of hunger-induced risk taking by YOY pollock (Sogard and Olla, 1997) and increased starvation rates among relatively small YOY pollock under laboratory conditions (Sogard and Olla, 2000). These data suggest YOY were primarily motivated by starvation risk during winter. The conclusion that the smallest fish must forage also accounts for the apparent inverse relationship between size and energy density among pollock sampled in Prince William Sound during March 1996 (i.e. Fig. 5e in Paul et al., 1998). In contrast, larger juveniles derived as much as 80% of their routine metabolic cost from endogenous sources. Thus, proportional losses in energy for juveniles exceeded the losses for YOY in this study and YOY in the central Gulf of Alaska as reported by Buchheister et al. (2006). However, reduced foraging was not without a fitness cost as approximately 50% of the endogenous supplies derived from structural components. Coincidently, free fatty acid levels in juveniles dropped significantly in March suggesting entry into stage III starvation (Castellini and Rea, 1992). These data suggest that the fitness cost associated with lost structural energy was lower than that associated with foraging.

The apparent failure of juveniles to forage could be accounted for by prey densities that were too low to warrant foraging or the presence of predators reduced the benefit of foraging below that of catabolizing structure. The former seems unlikely given YOY were able to find food and maintain energy levels and YOY and juveniles forage on the same prey (Clausen, 1983). The presence of sea lions in the survey areas supports the latter. Between May 2001 and March 2004 juvenile pollock were found in 76.5% of the sea lion scats examined from Frederick Sound and they represented 22% of the total biomass sea lions ingested (Sigler et al., 2009). In contrast, YOY pollock represented only 2.4% of the ingested biomass. Size reconstructions indicated that the average size of pollock consumed by sea lions was consistent with that of juvenile pollock (Sigler et al., 2009;

Fig. 5. Observed and estimated contributions of structural (proteins, sterols, and phospholipids), storage (wax esters and triacylglycerols) and foraged energy to the routine metabolic cost in pollock. Routine metabolic cost for each size class was calculated for the 118 days between the December and March samples using Eq. (1). Symbols show the contributions from structure (open symbols) and storage (filled symbols) observed in different size classes. The lines show the fit for models with the lowest AIC_c values. The dashed line shows the total endogenous contribution calculated as the sum of the structural and storage contributions. The difference between 100 and the total endogenous contribution is the percentage derived from foraging.

Table 6
Functions relating length (Lth) and the contribution of storage energy to routine metabolic cost over winter. Coefficient values marked with "*" are significantly different from 0 ($P<0.05$). Values <0.05 in the column labeled "P" indicate the model accounts for a significant amount of error. AIC_c is the associated value for the Akaike information criterion.

Type	Function	β_0	β_1	β_2	R^2	AIC_c	P
Exponential	$\beta_0 + \beta_1(1-e^{\beta_2 Lth})$	−37.4	233.8	0.002	0.830	40.95	0.013
Linear	$\beta_0 + \beta_1 Lth$	−29.69*	0.279*	—	0.862	29.97	0.002
Logarithmic	$\beta_0 + \beta_1 \times Ln(Lth)$	−232.2*	49.0*	—	0.854	30.40	0.002
Lognormal	$\dfrac{\beta_0 e^{-0.5\times\left(\frac{Ln\left(\frac{Lth}{\beta_3}\right)}{\beta_2}\right)^2}}{Lth}$	5736	16097	−0.000	0.677	58.61	1.00
Parabolic	$\beta_0 + \beta_1 Lth + \beta_2 Lth^2$	−39.4	.394	−.0003	0.830	36.89	0.012
Gaussian	$\beta_0 e^{-0.5\times\left(\frac{Lth-\beta_1}{\beta_2}\right)^2}$	40.42*	236.5*	49.5*	0.916	32.01	0.003

Womble and Sigler, 2006). Moreover, the average maximum daily dive depth of juvenile sea lions in Frederick Sound averaged 85 m, (Sigler et al., 2009), approximately 10 m shallower than the average depth at which juveniles were captured.

The inverse relationship between size and winter foraging indicates that size dependent mortality should be evident if foraging increases predation risk. Size dependent mortality accounts for our observation of increased average length of YOY over winter, but diminished energy. In addition, instantaneous growth rates indicated by RNA/DNA ratios suggested fish grew at minimal rates during the winter. Finally, the coefficient of variation for length decreased from 11.2% to 8.9% between December and March. Steller sea lions focused their consumption of pollock on YOY in December 2001 after those fish moved into offshore habitats (Sigler et al., 2009). Sea lions are not the only predator of YOY pollock. Cannibalism of YOY pollock in the Bering Sea is size dependent (Livingston, 1989). Also, the smallest pollock disappeared from samples collected between October and March 1996 in Prince William Sound (Paul et al., 1998).

Reliance on endogenous reserves over winter is likely to impose a different set of fitness costs. Much of the energy consumed over winter came from catabolism of structural substrates, consistent with energy loss patterns in other reports (Hurst and Conover, 2003). However, prolonged starvation loss can lead to reduced swimming speeds in cod (Gadus morhua) as a result of diminished glycolytic enzyme activity (Martinez et al., 2003). Additional fitness costs associated with structural catabolism may be incurred through compensatory growth the following spring. Johnsson and Bohlin (2006) reported increased mortality among brown trout (Salmo trutta) undergoing compensatory growth in a natural stream.

4.1. Growth strategies of YOY and juvenile pollock

The differences in energy loss observed in YOY and juveniles were presaged by differences in the way they allocated energy in fall. YOY substantially increased in length between September and December while maintaining constant body composition. During the same period instantaneous growth rates slowed. This increase in length was accompanied by a slowing of instantaneous growth rates. In contrast, instantaneous growth among juveniles was constant during fall, but they altered their body composition by increasing energy stores. This latter behavior of pre-winter fattening has been described for other marine species in the Gulf of Alaska including adult sand lance (Ammodytes hexapterus) (Robards et al., 1999), Pacific herring (Clupea pallasi) and Pacific hake (Merluccius productus) (Vollenweider, 2005).

A significant increase in RNA/DNA ratios in March indicated growth of YOY recovered from winter minima faster than juveniles. In contrast, juveniles did not increase growth until May. By that time YOY had recovered their pre-winter energy while juveniles were just beginning to recover. This difference is consistent with observations relating the foraging behavior of Atlantic salmon (Salmo salar) to their nutritional state and the number of days left in winter (Bull et al.,

1996). By delaying foraging, juveniles may have less time to recover the lost structural energy in spring.

4.2. Potential for bias

We combined observations from Lynn Canal and Frederick Sound based on the assumption that location effects on energy would be negligible relative to season. It was based on initial comparisons that revealed seasonal changes accounted for most of the variation observed in the energy content of pollock from these areas. However, location effects on mass specific energy content of YOY have been identified within season when locations had different temperature profiles (Ciannelli et al., 2002). In addition, length adjusted mass and otolith growth increments have been found to vary among YOY pollock sampled in different bays near Kodiak, Alaska (Wilson et al., 2005). These reports of spatial variation in energy content suggest starvation risk for YOY is likely to vary spatially.

The influence of temperature on the energetic trade-offs identified here is unknown. These samples were collected in a single year and there can be significant inter-annual variability in food availability and temperature. Inter-annual variation in the energy content of YOY pollock has been reported for the Bering Sea (Ciannelli et al., 2002) as have fluctuating temperatures (Hunt and Stabeno, 2002). Assuming an abundance of prey, warm temperatures during the growing season should increase pollock growth rates and hence size prior to winter. Kooka et al. (2007) compared the growth of pollock at different temperatures and found optimal growth occurs near 12 °C. However, rapid growth is consistent with decreased energy density (Kooka et al., 2007). In contrast, increasing winter temperatures would increase routine metabolic cost. A 2 °C increase in winter temperature would increase routine metabolic cost by 14% over values used here (Cianelli et al., 1998). Consequently, predictions of how starvation and predation risk will trade-off depend on summer and winter temperatures and likely vary annually.

A more important bias derives from the use of routine metabolic cost to determine the contributions of foraging and endogenous sources. Fishes residing at high latitudes normally experience food shortages in winter suggesting the opportunity for adaptation. Castellini and Rea (1992) found that while the biochemical pattern associated with fasting and starvation is the same in most animals some species have adapted mechanisms that allow for prolonged periods of food deprivation. Among those include reductions in routine metabolic rate as described by Beamish (1964). This would serve to decrease the reliance on foraging and the observed endogenous contributions would become proportionately greater. Thus, our conclusion that YOY rely on foraging to a greater extent than juveniles would remain unchanged.

In this study the fitness cost associated with catabolism of endogenous reserves is unknown. Juveniles lost significant amounts of structural energy over winter, but a small amount of protein catabolism is necessary in fasting organisms to supply the nervous system with glucose. Note that protein accounted for the majority of

the structural energy and losses of total body protein amounted to less than 10% in juveniles. Atlantic cod had diminished swimming performance when starvation led to a 15% decrease in white muscle protein (Martinez et al., 2003). These values are much lower than the 30–50% loss normally considered a signal of entry into Stage III starvation (Castellini and Rea, 1992). However, free fatty acids decreased dramatically over the same period, suggesting that lipid catabolism was diminished, a signal that Stage II starvation was nearing the end. Indeed, lipid levels in both juveniles and YOY in March were near 10% (dry mass), approaching the threshold level (7%) required for starving pollock to stay alive (Sogard and Olla, 2000). While the fitness cost of structural catabolism is unknown, the differences between YOY and juveniles suggests differential responses to the conflicting risks of predation and starvation.

4.3. Pollock and the critical size and period hypothesis

The critical size and period hypothesis proposes that winter survival of juvenile fish depends on their growth in late summer and fall (Beamish and Mahnken, 2001). We found that increased size in subadult pollock diminishes starvation risk, which then reduces the amount of time that must be spent foraging. For the smallest fish, foraging can never really cease. For larger and older fish the risk of starvation becomes devalued and they can afford to avoid foraging and concomitant exposure to predators. This translates to a growth maximization strategy for YOY. However, larval development in spring and early summer constrains the amount of time available for somatic growth until late summer and fall. Consequently, growth in fall when the YOY are most capable of storing energy is a likely an important determinant of winter survival. Pollock therefore represent a marine species whose winter survival is likely described by the critical size and period hypothesis. **[ST]**

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