Seasonal Variation in Energy Allocation Strategies of Walleye Pollock

by
Ron Heintz and Johanna J. Vollenweider

Multiple age groups of pollock utilize the study region, including young-of-the-year, juveniles, and mature fish. Distinct age groups of pollock are stratified predominantly by depth as well as habitat type. Photo by Johanna J. Vollenweider.

Understanding how fish allocate energy is key to understanding the processes underlying their recruitment. The allocation strategies used by juvenile fish have important implications for survival, while strategies employed by adults influence reproductive success. Decreasing water temperatures can lead to a reduction or cessation in feeding rates among many fish species, forcing individuals to rely on energy reserves to survive winter. These reserves are most critical for small-sized fish, which have higher metabolic rates than larger members of their cohort. In addition, small fish are more likely to be preyed upon. Consequently, rapid growth prior to winter reduces both the metabolic cost of overwintering and the risk of predation. However, individuals that channel all of their energy to growth do so at the cost of their energy reserves, suggesting the existence of an optimal allocation between growth and storage. Adults may be able to switch to piscivory in winter to offset winter energy costs, but they still must allocate energy to gametic growth and provisioning. Adult marine fish often time their reproduction so that their offspring can maximize use of spring zooplankton blooms. In the absence of winter foraging, adult energy reserves must therefore be obtained some time during the year prior to reproduction. Thus, evaluation of energy allocation strategies can be of value in understanding both the fitness and survival of individuals and populations.

Evaluations of energy allocation in juvenile fish have demonstrated the influence of season and size on strategies, the trade-off between growth and storage on predation risk, and the effect of fish size on energy depletion during winter. Allocation strategies in wild populations are often studied by evaluating the way in which lipid mass scales with fish size. This is similar to estimating the condition factor, whereby the slope between mass and length is examined to determine if mass is increasing proportionately with length. Fish are assumed to be actively storing lipid when lipid mass is found to increase disproportionately more than length. Most of these analyses have focused on juvenile fish residing in fresh water and the general idea that the extent of size-dependent mortality over winter is related to the size and energy stores attained by a cohort prior to the onset of winter.

We applied the lessons learned from previous energy allocation studies to examine seasonal variation in the energy allocation patterns in walleye pollock (*Theragra chalcogramma*) at different developmental stages. In contrast to previous studies, we chose to measure energy allocation and growth directly rather than measuring the allometry between lipid and

size. To measure energy allocation we observed the proximate and lipid class composition of young-of-the-year (YOY), juvenile, and adult pollock collected quarterly in southeastern Alaska. The proximate composition provided estimates of the water, ash, protein, and lipid content of the fish and hence their total energy content. The lipid class analysis allowed us to determine the proportion of lipid allocated to storage versus structural moieties, because fish store energy as triacylglycerols, while phospholipids and cholesterol are the main structural components of cell membranes. Thus, we could directly measure which proportion of the total energy in each fish was allocated to structural and storage molecules. To estimate growth, we recorded the ratios of the RNA and DNA content of each fish based on the idea that increased amounts of RNA relative to DNA indicate increased rates of protein synthesis. We subsequently contrasted these measures to test the hypothesis that energy allocation between storage and growth varies seasonally and ontogenically in walleye pollock.

The data presented in this article are part of the work we have been doing to examine the seasonal changes in energy and nutritional content of forage fish species in the eastern Gulf of Alaska and Bering Sea. These data can provide scientists at the Alaska Fisheries Science Center (AFSC) with detailed information on the energetic requirements of forage fish species and the value of forage fish as prey. In addition, our development of fatty acid libraries describing forage fish species and their prey will allow us to better understand forage fish trophic dependencies. The location of the Auke Bay Laboratory (ABL) in southeastern Alaska provides easy access to forage species year-round, which has facilitated our development of energy allocation models for other species such as Pacific herring, capelin, Pacific cod, Pacific hake, eulachon, arrowtooth flounder, Pacific halibut, and sablefish. Those data are currently being published in other reports. By partnering with other AFSC groups we have been able to describe the amount of energy available to foraging Steller sea lions and sources of energy that sea lions consume. In upcoming reports we will be describing the vertical distribution of energy in the near and offshore waters of the eastern Bering Sea.

MATERIALS AND METHODS

Pollock were collected quarterly from two locations in southeastern Alaska during 2001 and 2002.

The length and weight of each fish were recorded and fish were immediately frozen. Individuals were categorized into life stages by length. Young-of-the-year (YOY) were identified as those individuals less than or equal to 170 mm fork length (FL), juveniles as 180 mm to 270 mm FL, and adults as greater than 280 mm FL.

Fish were homogenized in ABL's Nutritional Ecology Laboratory, where we also performed the proximate, lipid class, and fatty acid analyses. All chemistries were performed on whole fish homogenates. Ratios of RNA/DNA were determined using a spectrophotometric method at the University of Southern Mississippi. Moisture and ash content were determined using a Leco Thermogravimetric analyzer and total nitrogen content was determined using the Dumas method adjusted for our Leco FP528 nitrogen analyzer. Protein content was determined by multiplying the total nitrogen content by 6.25. We determined the lipid content gravimetrically from an aliquot of lipid extracted from the homogenate following an adaptation of Folch's method. We assumed carbohydrate levels were negligible and estimated the total energy content as the sum of the energetic equivalents for the lipid (36.43 kJ/g) and protein (20.10 kJ/g) mass in the whole fish.

To understand how the energy was partitioned between structure and storage, we examined the composition of the lipid using high performance liquid chromatography. This method allowed quantification of the amount of lipid found in storage depots (wax esters and triacylglycerols), cell membranes (phosphatidylethanolamines, phosphatidylcholines, and cholesterol), and in metabolic flux (free fatty acids and monoacyl- and diacylglycerols). The energy allocated to storage was estimated as the summed energy equivalents for the observed mass of triacylglycerols (TAG) and wax esters in fish tissue divided by the dry mass of the fish. Structural energy was estimated as the summed energy equivalents for the phospholipids, cholesterol, and protein divided by the dry mass of the fish. The energy equivalents for all lipid classes were assumed to be 36.43 kJ/g.

RESULTS

Energy Allocation in YOY Pollock

Young-of-the-year pollock in our sample increased in length between September and December and between March and May, but no growth was apparent between December and March (Table 1).

Table 1. Average lengths, weights, and RNA/DNA ratios (±1 SD) of walleye pollock collected at different times of year in southeastern Alaska between September 2001 and May 2002.

Adult walleye pollock				
	September	December	March	May
N	29	22	24	24
Length (mm)	411.0±78.71	469.1±80.05	457.9±92.17	412.1±86.63
Mass (g)	606.28±356.81	874.18±404.53	894.25±585.34	549.33±309.12
RNA/DNA	4.010±1.483	4.077±1.904	4.558±2.833	6.181±3.793

Juvenile walleye pollock				
	September	December	March	May
N	11	14	9	13
Length (mm)	212.7±19.02	229.3±14.92	221.1±32.57	233.8±29.59
Mass (g)	82.73±21.27	91.71±17.31	75.56±37.87	99.38±34.55
RNA/DNA	5.005±1.299	3.406±0.698	4.194±1.340	8.060±3.769

YOY walleye pollock				
	September	December	March	May
N	10	12	19	12
Length (mm)	96.0±10.75	120.0±12.06	131.1±13.70	147.5±13.57
Mass (g)	6.80±2.15	12.00±3.81	15.05±4.82	23.00±7.36
RNA/DNA	9.966±3.195	4.220±0.516	6.418±1.597	11.430±1.841

Table 2. Seasonal changes in the average proximate composition (±1 SD) of walleye pollock in southeastern Alaska from September 2001 to May 2002.

Adult walleye pollock				
	September	December	March	May
N	29	22	24	24
Moisture (% wet mass)	77.04±2.103	78.45±2.103	78.36±1.66	80.22±1.175
Lipid (% dry mass)	14.84±7.087	15.96±7.087	14.73±5.183	10.36±5.043
Ash (% dry mass)	13.30±3.187	14.79±3.187	13.97±2.558	17.06±3.671
Protein (% dry mass)	71.64±6.236	69.56±6.236	69.72±4.864	74.69±4.514
Energy (kJ/g dry mass)	19.88±1.757	19.79±1.757	19.38±1.426	18.79±1.439

Juvenile walleye pollock				
	September	December	March	May
N	11	14	9	13
Moisture (% wet mass)	77.42±2.236	77.56±1.218	80.78±1.140	80.4±0.541
Lipid (% dry mass)	11.96±4.333	21.93±5.784	10.39±3.710	10.45±3.030
Ash (% dry mass)	12.61±3.580	11.92±2.808	16.12±4.792	13.97±1.637
Protein (% dry mass)	76.12±5.133	69.29±3.693	74.07±2.458	76.23±2.546
Energy (kJ/g dry mass)	19.41±0.985	21.92±1.608	18.67±1.167	19.18±0.864

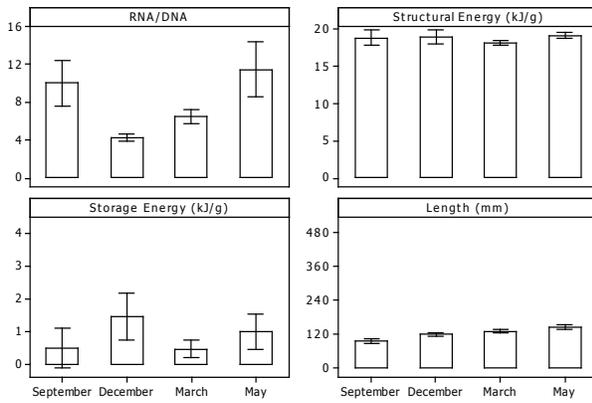| YOY walleye pollock				
	September	December	March	May
N	10	12	19	12
Moisture (% wet mass)	79.97±1.054	78.94±1.697	81.01±0.932	80.3±1.000
Lipid (% dry mass)	11.33±4.682	17.48±3.550	10.42±2.292	13.94±4.142
Ash (% dry mass)	13.35±0.953	13.45±1.619	14.68±1.381	13.46±1.128
Protein (% dry mass)	75.32±4.375	69.84±4.202	73.65±2.382	74.71±3.381
Energy (kJ/g dry mass)	19.27±0.862	20.41±0.956	18.6±0.588	20.09±1.022

Figure 1. Energy allocation and growth in YOY pollock between September 2001 and May 2002. Structural and Storage energy scales are in kJ/g dry mass. Error bars depict 95% confidence intervals.
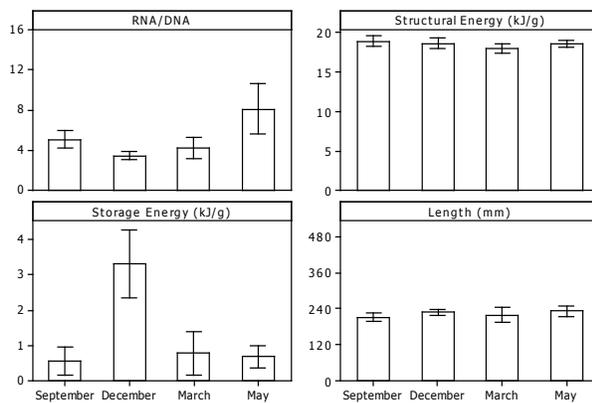

Figure 2. Energy allocation and growth in juvenile pollock between September 2001 and May 2002. Structural and Storage energy scales are in kJ/g dry mass. Error bars depict 95% confidence intervals.
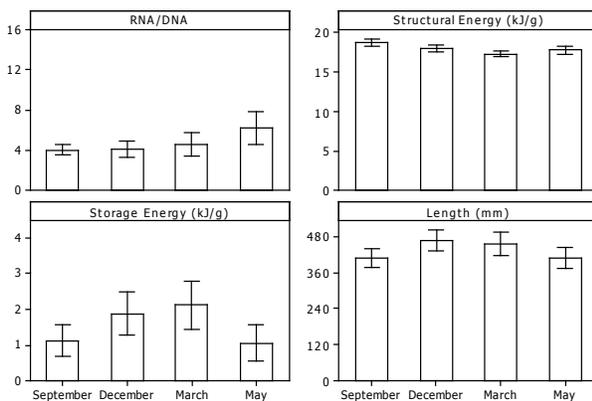

Figure 3. Energy allocation and growth in adult pollock between September 2001 and May 2002. Structural and Storage energy scales are in kJ/g dry mass. Error bars depict 95% confidence intervals.

Consistent with increased size between September and December, RNA/DNA ratios were highest in May and September (Fig. 1). Conversely, RNA/DNA ratios were at a minimum in December, consistent with the observation of little growth over winter. Increasing RNA/DNA ratios in March and May suggest that following the spring plankton bloom, YOY pollock initiated a period of relatively high growth rates.

When RNA/DNA levels decreased, energy stores were at their maximum so that allocations to storage varied out of phase with RNA/DNA ratios. At the same time, structural energy decreased insignificantly. This suggests that stored energy supplied a signficant amount of energy during winter relative to the structural elements. In December, allocations of energy to storage reached a maximum and growth was at its lowest level. At this point YOY pollock averaged 1.46 kJ of stored energy per gram of dry tissue. In contrast, energy allocated to structure was more than tenfold higher (Fig. 1). Between December and March, YOY pollock lost more than two-thirds of their stored energy, while losing less than 5% of their structural energy. This translated to a small loss in overall energy from 20.4 kJ/g to 18.6 kJ/g, despite the dramatic decline in energy stores (Table 2). By March all of the energy stored between September and December had been lost as storage levels fell to 0.5 kJ/g, representing a 66% decrease in energy stores. In contrast, the amount of energy allocated to structural components was relatively constant throughout the year.

Energy Allocation in Juvenile Pollock

Juvenile pollock also demonstrated a coupling of energy allocations to growth and storage. Like the YOY fish, juveniles decreased their protein synthesis rates between September and December and resumed increasing them in spring following the plankton bloom (Fig. 2). However, while YOY pollock increased their RNA/DNA ratios significantly between December and March, juveniles maintained low levels of protein synthesis through March and only increased synthesis rates afterwards. In addition, juveniles generally had much lower rates of protein synthesis than YOY pollock (Table 1), as indicated by generally lower RNA/DNA ratios and reduced variation in RNA/DNA ratios throughout the year.

Juvenile pollock differed from YOY pollock in the magnitude with which they were able to pro-

vision their storage depots. Like YOY fish, juveniles began provisioning their energy depots after September. However, peak storage levels in juvenile pollock averaged 3.3 kJ/g tissue, more than twice that seen in YOY. This improved storage capacity resulted, in part, from decreased costs associated with protein synthesis relative to YOY. As winter progressed, juveniles lost most of the energy they had stored, decreasing their reserves to 0.8 kJ/g in March and 0.7 kJ/g in May. This represented a loss of 75% of their energy reserves during the period between December and March, and the consumption all of the energy they had acquired between September and December. As with YOY, juveniles consumed less than 5% of their structural energy so that total energy only declined from 21.9 to 18.7 kJ/g (Table 2) .

Energy Allocation in Adult Pollock

Adult pollock demonstrated comparatively little relationship between growth and energy storage (Table 1; Fig. 3). Ratios of RNA/DNA indicated that protein synthesis rates were highest during May, suggesting peak tissue production occurred after May. This is consistent with the other life stages and the observation that peak energy allocation to structural components was in September. During most of the year, RNA/DNA ratios remained constant at approximately 4.2, a value consistent with the lowest values observed in the juvenile (3.4) and YOY pollock (4.2). Thus, RNA/DNA ratios near 4.2 likely represent protein synthesis rates associated with regulation and maintenance of existing protein. In contrast to YOY and juveniles, adult pollock increased their energy reserves throughout the winter. Adults apparently began provisioning their depots after September, reaching a peak level of 2.1 kJ/g tissue in March. Between March and May adult pollock lost approximately 50% of this energy and energy stores dropped to levels below those observed in September. Pollock in Lynn Canal are known to spawn between March and May, suggesting that the energetic costs associated with reproduction are covered by energy acquired the previous fall and winter (Table 2).

DISCUSSION

These data demonstrate that walleye pollock at all developmental stages change their energy allocation strategies seasonally and the strategies are tuned to life history demands. Young-of-the-year and juveniles balance the need to grow and store energy over winter in order to maximize survival, while adults reduce growth and maximize allocation to storage to prepare for spawning. Viewed together these data indicate that as pollock increase in age, the conflicting demands of growth and energy storage diminish. Thus, pollock life history can be viewed as a process by which the constraints imposed by the need for growth diminish to the point that eventually all the energy surplus to routine metabolism can be focused on reproduction. The ability of large adult pollock to allocate most of their energy to reproduction suggests a mechanism by which older and larger pollock can produce higher quality gametes.

In contrast to adults, YOY pollock must maintain growth even in winter as demonstrated by their relatively high RNA/DNA ratios. Protein synthesis is the most energetically consumptive process in living organisms, and YOY pollock synthesized protein at the highest rate on all sampling occasions. The elevated costs associated with protein synthesis account for the diminished capacity of YOY pollock to store energy prior to winter. Rapid growth benefits YOY pollock by allowing them to obtain larger prey, reduce predation risk, and minimize metabolic costs. However, the associated reduction in storage capacity imposes a greater need to forage throughout the winter, presenting YOY pollock with a choice between increased risk of starvation or predation.

The constraints of growth were less severe for juvenile pollock, which had reduced growth rates relative to YOY pollock at all times of the year. The RNA/DNA ratios of juveniles in December were equivalent to those of the adults, suggesting protein synthesis levels for juveniles were apparently at the maintenance levels at this time. This reduced cost allowed juveniles to store the greatest amounts of energy prior to winter and presumably minimize their foraging costs and exposure to predation over winter.

Costs of Overwintering

Despite dramatic energy losses during the winter, juvenile pollock remained above their energetic limits to survival in March. Anorexia between December and March is evident from the amount of energy lost. The estimated maintenance ration for a juvenile pollock at 3°C is 0.023 kJ/g per day, suggesting

Clockwise, from upper left. *Trawling*: Midwater trawling is used to ground-truth species identification for hydroacoustic surveys, to estimate size frequencies by species, and to collect samples for nutritional analysis. *Deck full of pollock*: A large catch of juvenile walleye pollock is deposited on the deck of a trawler. Catches are sorted, subsampled, and morphometric features of individual fish are recorded. Samples representative of the catch are retained for nutritional analysis. *Sorting the catch*: A catch of small forage species from the midwater trawl is sorted prior to morphometric processing. A 1-inch mesh cod-end liner retains small species, including myctophids, shrimp, eulachon, capelin, and northern smoothtongue. *Full cod-end:* The cod-end of a small, midwater sampling net is brought aboard for sample processing. *Basket of pollock*: A representative sample of predominantly juvenile walleye pollock caught by midwater trawl. Photos by Johanna J. Vollenweider.

that maintenance cost for a 50-g juvenile over 120 days at 3°C is on the order of 138 kJ. We observed an average loss of 2.5 kJ/g between December and March. For a 50-g individual, this represents a loss of 127 kJ from stored energy. Thus, there was little need for feeding among juvenile pollock during this period. Moreover, lipid levels dropped to approximately 10% of the dry mass, above the 7% limit to starvation described in the literature. A regression (r^2 = 0.75) between TAG and lipid content in juvenile pollock indicates that when TAG is completely depleted the lipid content drops to 6.7%, the level reportedly associated with starvation.

Young-of-the-year pollock from Prince William Sound, Alaska, used similar amounts of energy over winter as pollock in southeastern Alaska. Measurements of total energy indicated that YOY pollock lost little or no energy over winter in Prince William Sound between October and March, while our data indicate that pollock in southeastern Alaska lost less than 5% over the same period. The observations in Prince William Sound led the authors of that report to conclude that YOY pollock must have foraged during winter. That is consistent with our observation of increased energy stores between September and December. However, the energy acquired between September and December was lost completely by March, begging the question of whether foraging occurred during this later period. Assuming the same maintenance requirement as that for juveniles, the cost for a 12-g pollock to survive for 120 days at 3°C is found to be approximately 33 kJ. Losses from YOY energy stores account for 22 kJ of the required 33 kJ, indicating that the remaining 11 kJ must have been supplied by feeding. Therefore, YOY pollock in Prince William Sound and southeastern Alaska depend on exogenous energy sources throughout the year.

Adult pollock in the Bering Sea in 1998 and 1999 followed the same pattern of diminished energy content during reproduction, but overall had higher energy levels than the pollock described here. These differences in energy content derive primarily from relatively large amounts of lipid in Bering Sea pollock. For example, in September the Bering Sea pollock had lipid levels 50% greater than those we observed in pollock from southeastern Alaska. These higher lipid levels may have resulted from a greater demand for energy storage by adult pollock in the Bering Sea. The Bering Sea pollock lost 1.05 kJ/g tissue between September and March, while the southeastern Alaska pollock lost only half that amount. Moreover, we observed increases in energy content between September and December, while the authors of the Bering Sea study reported a loss. Thus, adult pollock from southeastern Alaska may acquire energy later into the fall than Bering Sea pollock and ultimately may require lower levels of energy. Interannual variability in the availability of energy might also account for these differences. The Bering Sea pollock were collected in 1998-99 while those described here were collected in 2001-02. Researchers from ABL have observed interannual variation in the timing and magnitude of peak energy content for eastern Gulf of Alaska herring consistent with the type of differences we have described for pollock. This suggests that differences in the timing and magnitude of peak energy content between pollock in the Bering Sea and the eastern Gulf of Alaska may indicate interannual differences in foraging success. Therefore, monitoring of annual variation in energy levels may prove useful for predicting the future productivity of pollock stocks.

The Nutritional Ecology Laboratory at ABL has been operating since 2001, examining the energy allocation strategies of forage fish species including capelin, eulachon, Pacific herring, sand lance, Pacific cod, Pacific hake, and various myctophids, bathypelagics, and flatfish; we have also cataloged the fatty acid compositions of these species. Currently we are focused on identifying the fatty acid compositions of Bering Sea and eastern Gulf of Alaska forage fish and their prey, to better understand the sources of energy consumed by forage fish. By coupling the seasonal diet data with the energetic constraints on forage fish we can begin to understand how fluctuations in prey availability impact different phases of forage fish life history. Simultaneously, the data describing the nutritional value and fatty acid compositions of forage fish allow us to understand the relative value of the diets of species that prey on forage fish. For example, we have shown how energy sources consumed by Steller sea lions in Lynn Canal vary seasonally and how those changes correlate with changes in the energy available in the local prey field. Thus, by understanding how forage fish acquire and allocate energy, the Nutritional Ecology Laboratory serves the AFSC as a valuable resource for understanding the flow of energy in the Gulf of Alaska and Bering Sea.