



## Regional, interannual and size-related variation of age 0 year walleye pollock whole body energy content around the Pribilof Islands, Bering Sea

L. CIANNELLI\*§, A. J. PAUL† AND R. D. BRODEUR‡

\*School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98105, U.S.A., †University of Alaska, Institute of Marine Sciences, Seward Marine Center, Seward, AK 99664, U.S.A. and ‡Northwest Fisheries Science Center, NOAA, Newport, OR 97365, U.S.A.

(Received 20 August 2001, Accepted 27 March 2002)

Mean whole energy content ( $E_{wb}$ ) of age 0 year walleye pollock *Theragra chalcogramma* was 19.928 KJ g<sup>-1</sup> dry mass in 3943 fish collected from different habitats around the Pribilof Islands frontal structure, south-east Bering Sea, during September 1994–1996 and 1999. It varied, however, with habitat type. Fish residing offshore had higher  $E_{wb}$  than fish residing inshore of the frontal regions. Age 0 year walleye pollock  $E_{wb}$  changed in a non-linear fashion with fish size, with larger juveniles typically having higher  $E_{wb}$ . Size thresholds were identified at which the relationship between age 0 year walleye pollock  $E_{wb}$  and  $L_S$  changed. One such threshold was found at 46 mm where  $E_{wb}$  reached a local minimum. Another threshold was found at 80 mm beyond which  $E_{wb}$  tended to remain constant with size. Overall mass-length and  $E_{wb}$ -length residuals were highly correlated with each other ( $r=0.73$ ,  $P\ll 0.0001$ ). The slope of the regression, however, was higher for smaller fish. Possible mechanisms are proposed to explain the observed ontogenetic variation in nutritional status and the role of age 0 year walleye pollock late summer  $E_{wb}$  on survival over their first critical winter of life.

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Key words: age 0 pollock; energetics; Pribilof Islands; Bering Sea.

### INTRODUCTION

The age 0 year stage of walleye pollock *Theragra chalcogramma* (Pallas) in the south-east Bering Sea, is an important component of the pelagic food web (Livingston, 1993; Springer, 1992). Age 0 year walleye pollock is an important prey for a variety of demersal fishes (Brodeur & Livingston, 1988; Lang *et al.*, 2000) marine mammals (Sinclair *et al.*, 1994; Antonelis *et al.*, 1997) and seabirds (Decker *et al.*, 1995; Decker & Hunt, 1996). Due to their high abundance and diet (Brodeur *et al.*, in press), age 0 year walleye pollock are a primary consumer of zooplankton (Brodeur & Wilson, 1999).

Juvenile walleye pollock reside in high numbers around the Pribilof Islands (Traynor & Smith, 1996; Brodeur *et al.*, 1997, in press), where they can find higher prey abundance compared to other Bering Sea shelf areas (Flint *et al.*, in

§Author to whom correspondence should be addressed. Present address: NOAA/AFSC/RACE, 7600 Sand Point Way NE, Seattle, WA 98115, U.S.A. Tel.: +1 206 526 4315; fax: +1 206 526 6723; email: Lorenzo.Ciannelli@noaa.gov

press). Each summer tidal mixing forms a structural thermal front around the islands. The front separates a well-mixed inshore region, from a thermally stratified offshore region (Stabeno *et al.*, 1999). The length of the frontal region changes annually and ranges from *c.* 5 to >20 km, depending mainly on the strength of water column stratification (Stabeno *et al.*, 1999). In general, oceanographic fronts generate enhanced feeding conditions due to mechanical aggregation of particles and to replenishment of water column nutrients (LeFèvre, 1986; Franks, 1992; Sournia, 1994).

The nutritional status of fishes is reflected in the amount of energy stored in their tissue. The somatic energy content of juvenile walleye pollock during late summer is thought to affect their survival probability during their first winter (Sogard & Olla, 2000). In turn, winter mortality is one of the principal mechanisms regulating recruitment variability of fish species residing in highly seasonal systems (Sogard, 1997; Hurst & Conover, 1998; Paul & Paul, 1998; Schultz *et al.*, 1998; Foy & Paul, 1999).

Spatial and annual variability of the physical environment around the islands has the potential to affect the nutritional status of age 0 year walleye pollock (Ciannelli, *in press*) and could ultimately affect their somatic energy content. Another factor that could potentially affect age 0 year walleye pollock whole body energy content ( $E_{wb}$ ) is their size. In general, during early life stages of fishes the amount of storage lipids tends to increase with age (Norton *et al.*, 2001), resulting in large individuals having higher energy content than smaller individuals. In some species, however, additional source of size-related variation of energy content can also be caused by different ecological habits between larger and smaller fish. For example, the standard length ( $L_S$ ) of age 0 year walleye pollock collected around the Pribilof Islands can range from 20 mm to >90 mm (Brodeur *et al.*, 1997). In several studies it was reported that juvenile walleye pollock diet changes with size (Merati & Brodeur, 1996; Brodeur, 1998; Schabetsberger *et al.*, 2000). Larger juveniles walleye pollock (>50 mm  $L_S$ ) feed primarily on large copepods (>2 mm prosome length, *Neocalanus* spp., *Calanus marshallae*) and euphausiids (*Thysanoessa* spp.), while juveniles <50 mm feed primarily on small copepods (<2 mm prosome length, *Oithona*, *Acartia*, *Pseudocalanus*). Thus, juvenile walleye pollock of slightly different sizes feed on different prey and can therefore experience different degrees of food availability and nutritional status at a single site.

The purpose of the present study was to investigate the  $E_{wb}$  of juvenile walleye pollock in relation to factors that can influence it, including space, time and fish size. Age 0 year walleye pollock of different sizes collected around the Pribilof Islands in different years and hydrographic habitats were analysed for  $E_{wb}$ . Because most of the size variation of the sampled age 0 year walleye pollock population was thought to be due to age rather than growth (Brodeur *et al.*, *in press*), it was assumed that the analysis of  $E_{wb}$  and size was also indicative of ontogenetic changes in age 0 year walleye pollock energy storage. The correlation between mass –  $L_S$  residuals with  $E_{wb}$  –  $L_S$  residuals obtained from the same fish was also examined, with the intent of understanding whether these two independent measures of fish nutritional status were in agreement.

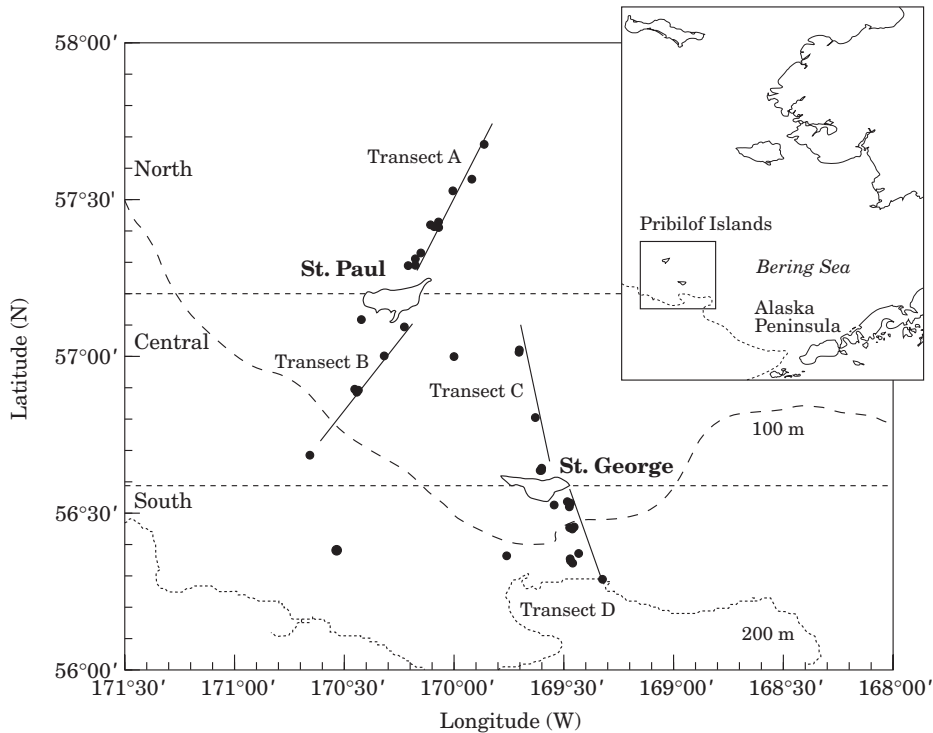


FIG. 1. Study area and locations of regions (North, Central, South) and frontal transects (A–D) where age 0 year walleye pollock sampling stations were localized (●). Field sampling occurred in mid September of 1994–96 and 1999.

## MATERIALS AND METHODS

### FISH COLLECTION AND MEASUREMENTS OF SOMATIC ENERGY

Age 0 year walleye pollock were collected during four years, 1994–96 and 1999, from 44 stations in different hydrographic habitats around the Pribilof Islands (Fig. 1). In each year data were collected during the first half of September along four transects: A, north of St Paul, B, south of St Paul, C, north of St George, and D, south of St George (Fig. 1). Within each transect, samples were collected over three hydrographic habitats: inshore, front and offshore. Habitat separation was based on temperature profiles following the criteria set by Stabeno *et al.* (1999). The inshore region had a totally mixed vertical profile, the frontal region was weakly stratified, and the offshore region was strongly stratified. The specific boundary between the front and offshore habitat was set where the temperature profile showed a twofold increase in temperature between the surface waters and below the thermocline. The rate of change in bathymetry around the Pribilof Islands varies according to the region examined. North of St Paul, toward the Bering Sea shelf, the bathymetry slowly descends to 60–70 m and remains constant for a large portion of the shelf. South of St Paul, the bottom depth reaches over 100 m, and remains constant toward the south-east. Finally south of St George, the bottom depth abruptly increases to >300 m as it descends the Bering Sea slope. The different bathymetry of these three regions can also affect the local hydrography and ultimately the feeding success of age 0 year walleye pollock. Hence, the analysis of age 0 year walleye pollock  $E_{wb}$  was also done according to region, as well as transect and habitat. The three regional levels were: (1) North, including the area north of St Paul (north of 57°12' N), (2) Central, including the area between St Paul and St George (between 56°36'–57°12' N), and (3) South, including the area south of St George (south of 56°36' N) (Fig. 1).

TABLE I. Number of stations sampled for age 0 year walleye pollock analysis of  $E_{wb}$ . Stations were partitioned by region, transect, hydrographic habitat and year of collection

Region	Transect	Habitat	1994	1995	1996	1999
North	A	Inshore	1	1	—	1
		Front	2	1	2	2
		Offshore	1	1	—	1
Central	B	Inshore	—	1	2	—
		Front	—	—	2	—
		Offshore	1	1	2	—
	C	Inshore	—	—	2	—
		Front	—	—	2	—
		Offshore	—	—	3	—
South	D	Inshore	—	1	1	2
		Front	—	—	1	3
		Offshore	1	1	1	4

Fish were sampled in midwater using a 140 m<sup>2</sup> anchovy trawl with a 3 mm mesh codend (Wilson *et al.*, 1996). The net was fished to target on vertical layers of acoustic scatter believed to be age 0 year walleye pollock (Brodeur *et al.*, 1997). Upon collection a random sample of at least 50 fish from each station was frozen for later  $E_{wb}$  analysis.

In the laboratory the fish were partially thawed and then measured for  $L_S$  to the nearest mm. To avoid loss of body tissue and lipid, fish samples were not completely thawed and gut content was not removed from the stomach. The gut content may have influenced the results of the analysis. The error caused by loss of tissues and lipids during surgical operation, however, could have been greater than the error caused by processing the entire sample. Individual fish wet masses were not taken because the samples had been frozen and some desiccation might have occurred. Walleye pollock were freeze-dried whole and then placed in a convection oven at 60° C until they appeared to reach a constant mass. The drying process at 60° C may have caused some loss of volatile lipids. Individuals were weighed to the nearest 0.1 g to get whole body dry mass. Whole dried fish were ground in a mill and measurements of caloric content made by bomb calorimetry using a Parr Adiabatic Calorimeter Series 1240. All calorimetric samples were weighed to the nearest 0.0001 g with a single 0.5–1.0 g sample burned per fish. Whole body energy content was expressed as KJ g<sup>-1</sup> dry mass.

#### DATA ANALYSIS

Measures of  $E_{wb}$  were obtained from a total of 3943 individual juvenile walleye pollock. A multi-factor ANOVA was used to examine spatial and inter-annual variation of  $E_{wb}$ . When significant effects were found, a Tukey multiple comparisons test was used to identify group differences within each factor. The statistical analysis presented several challenges. First, spatial and temporal sampling coverage was unbalanced (Table I). A further complication was that within the region or transect and year, there was high station-to-station variation. Therefore station had to be included as a nested factor. The nested design limited analysis to the few instances in which there was more than one station per each combination of year and spatial level. Therefore, not all effects could be tested at once; rather, several tests were implemented on different combinations of the data as follows. To test for region and year effect, all of 1995 and 1996 data were used (Table I). To test for transect and habitat effect, all data from transect B and C during 1996 only were used (Table I). Also, since  $E_{wb}$  changed non-linearly with  $L_S$ ,  $L_S$  was included as a covariate of the statistical model. Moreover, variance around  $E_{wb}$  v.  $L_S$  was not homogeneous; therefore, data were log-transformed to reduce the non-linearity of  $L_S$  v.  $E_{wb}$  and homogenize the variance. Finally, because of the high sample size of fish analysed (c. 4000), any factor that was interacted with  $L_S$  turned out to be statistically

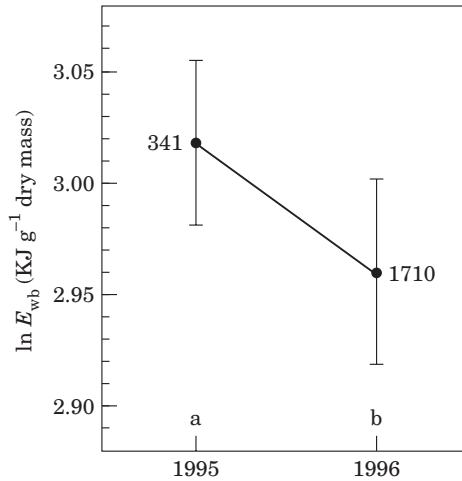


FIG. 2. Least square adjusted mean ( $\pm 1$  s.d.) of  $\ln E_{wb}$  by year. Numbers indicate sample size. Data shown include only samples from 1995 and 1996. Different letters indicate significant differences between means.

significant, a situation which was considered to convey little information. Thus, any interactions with length were excluded from the models. Exclusions of  $L_S$  interaction terms did not change the results of the main factors.

The relationship between age 0 year walleye pollock  $L_S$  and  $E_{wb}$  was investigated by using a non-parametric general additive model (GAM) on all data points available. GAM analysis makes no assumption on the shape of the relationship between independent and dependent variables. The relationship between mass -  $L_S$  residuals ( $R_W$ , independent variable) and  $E_{wb} - L_S$  residuals ( $R_E$ , dependent variable) was examined using linear regression analysis. Age 0 year walleye pollock  $L_S$  was included in the model, to control for possible interactions between fish  $L_S$  and  $R_W$ . The full linear regression model was:  $R_E = K + a_1 R_W + a_2 L_S + a_3 R_W L_S$ , where  $K$  is a constant and  $a_1$ ,  $a_2$  and  $a_3$ , are slope parameters. To avoid bias in residual estimates due to possible changes of the scaling coefficients between fish mass and  $E_{wb}$  over different fish sizes, both  $R_W$  and  $R_E$  were obtained by fitting a GAM model through the original set of data.

## RESULTS

The overall mean age 0 year walleye pollock  $E_{wb}$  was 19.928 KJ g<sup>-1</sup> dry mass. There was no regional effect ( $P=0.146$ ) nor interaction between the years and regions ( $P>0.5$ ) examined. There was, however, a significant year effect ( $F_{1,19}=6.620$ ,  $P=0.019$ ) (Fig. 2). There was no transect effect ( $P=0.20$ ) and no interaction of transect with habitat ( $P=0.123$ ). There was, however, a significant habitat effect ( $F_{2,7}=4.915$ ,  $P=0.046$ ) due to the fact that fish from the offshore region had significantly different  $E_{wb}$  from fish in the inshore region (Tukey multiple comparisons;  $P=0.049$ ) (Fig. 3).

Age 0 year walleye pollock  $E_{wb}$  significantly changed with  $L_S$  ( $F=214$ ,  $P\leq 0.0001$ ). The shape of the relation between  $E_{wb}$  and  $L_S$  was non-linear (Fig. 4), and in general larger specimens had higher  $E_{wb}$ . The GAM analysis performed in this study also indicated that there were apparent size thresholds at which the relationship between age 0 year walleye pollock  $E_{wb}$  and  $L_S$  changed. One size threshold was found at 46 mm where predicted  $E_{wb}$  reached a local

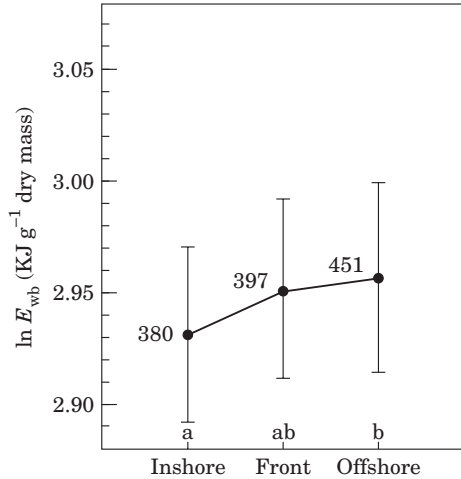


FIG. 3. Least square adjusted mean ( $\pm 1$  S.D.) of  $\ln E_{wb}$  by sampled hydrographic habitat. Numbers indicate sample size. Data shown include only samples collected during 1996 on transect B and C. Different letters indicate significant differences between means.

minimum ( $19.19 \text{ KJ g}^{-1}$  dry mass) (Fig. 4). Another size threshold was found at 80 mm ( $22.44 \text{ KJ g}^{-1}$  dry mass) beyond which  $E_{wb}$  remained rather constant with size (Fig. 4). The predicted maximum  $E_{wb}$  value was  $22.53 \text{ KJ g}^{-1}$  at the maximum  $L_S$  examined of 91 mm.

$R_W$  was significantly correlated with  $R_E$  ( $r=0.753$ ,  $P \ll 0.0001$ ) but  $L_S$  was not significantly correlated because the principal residuals are homogeneous around the predicted variables. The interaction of  $L_S$  and  $R_W$ , however, was significant ( $P \ll 0.0001$ ), suggesting that the slope of the relation between  $R_E$  and  $R_W$  ( $a_1$ ) changed with fish size. In particular,  $a_1$  values were higher (steeper relationship) for small juveniles and become progressively lower for large juveniles (Fig. 5).

## DISCUSSION

Age 0 year walleye pollock  $E_{wb}$  has been previously measured in other areas of the North Pacific. Paul *et al.* (1998a) measured an autumn  $E_{wb}$  of  $3.6 \text{ KJ g}^{-1}$  wet mass in age 0 year walleye pollock from Prince William Sound, which corresponds to  $18.7 \text{ KJ g}^{-1}$  dry mass assuming a 80.8% moisture content (A. J. Paul, pers. comm.). Van Pelt *et al.* (1997) and Anthony *et al.* (2000) measured a summer energy density of  $16.76$  and  $17.0 \text{ KJ g}^{-1}$  dry mass in two different locations along the Alaska Peninsula. Although these estimates of  $E_{wb}$  are within the range of values found in this study, a precise comparison could be tenuous due to the different methodology used in each study and to the effect of water content on measures of somatic energy content (Harris *et al.*, 1986). All of these studies, however, show that age 0 year walleye pollock have a lower  $E_{wb}$  than many other forage fish species (Van Pelt *et al.*, 1997; Paul *et al.*, 1998b; Lawson *et al.*, 1998; Payne *et al.*, 1999; Anthony *et al.*, 2000), most likely due to their low lipid content.

Interannual and spatial variation of age 0 year walleye pollock  $E_{wb}$  from around the Pribilof Islands may reflect variability in feeding success in different

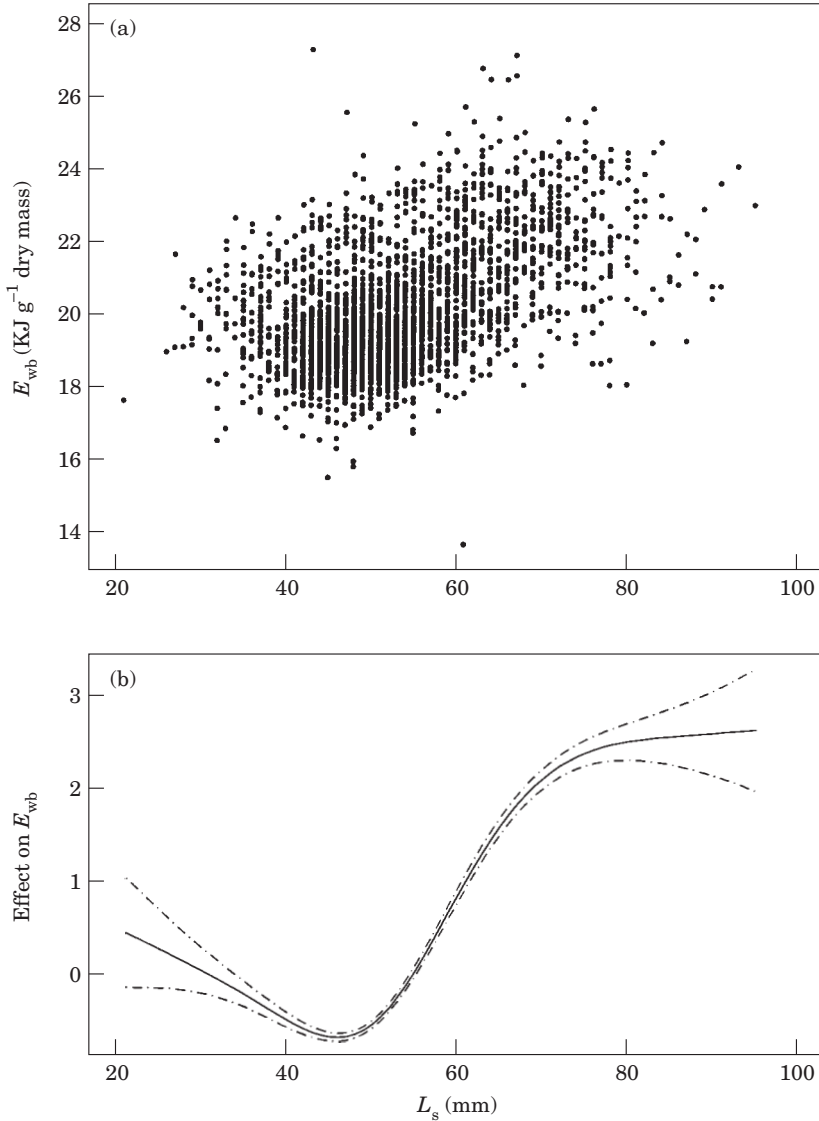


FIG. 4. (a). Scatterplot of all data available on age 0 year walleye pollock  $L_S$  (mm) and  $E_{wb}$ . (b) Generalized additive model (GAM) regression analysis showing the shape of the function relating  $L_S$  with  $E_{wb}$  ( $F_{1,3941}=214$ ,  $P \leq 0.0001$ ). — · —, s.e. boundary around the predicted shape.

years and in different hydrographic habitats of the study area. For example, age 0 year walleye pollock residing in the offshore hydrographic habitat tended to have higher  $E_{wb}$  than elsewhere. This finding is in agreement with other measures of age 0 year walleye pollock feeding success, such as potential growth (Ciannelli, in press) and length-specific mass (Brodeur *et al.*, 2000). Low  $E_{wb}$  was also found in age 0 year walleye pollock collected during 1996. This was a year in which mid-summer densities of age 0 year walleye pollock throughout the southeast Bering Sea were particularly high (R. D. Brodeur, unpubl. data). It was also a year when the fish had significantly lower size-specific mass than fish

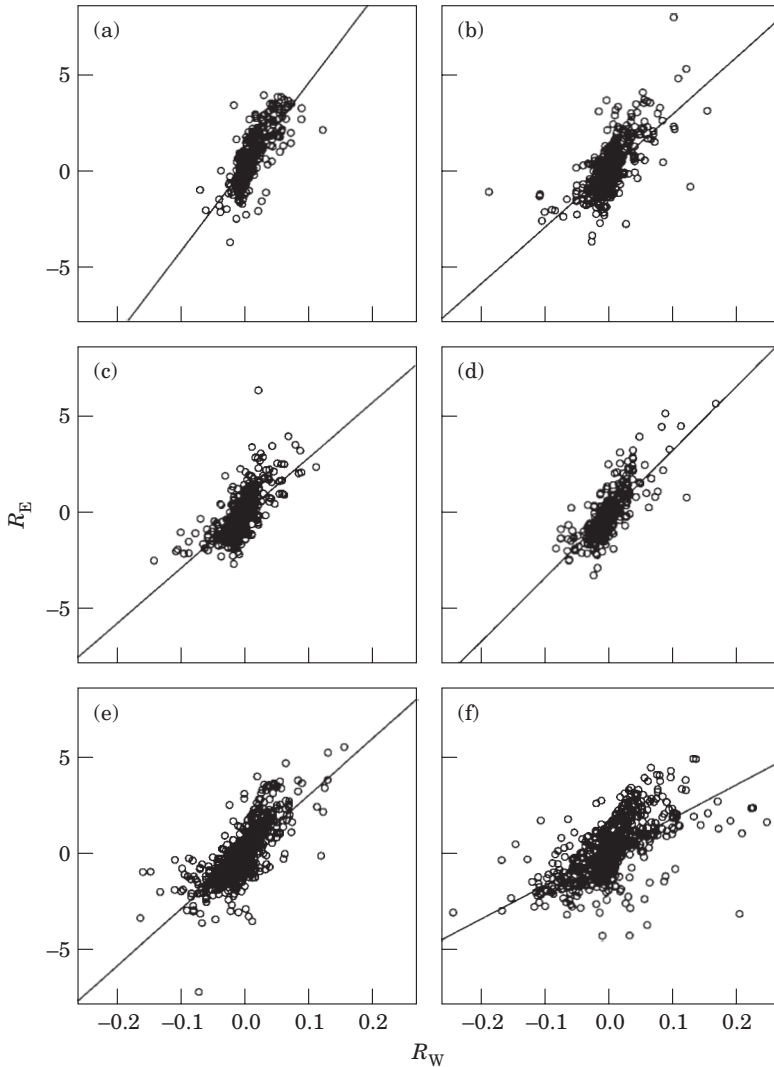


FIG. 5. Scatterplots of dry mass  $-L_S$  residuals ( $R_W$ ) v.  $E_{wb} - L_S$  residuals ( $R_E$ ) for (a) 21–42, (b) 42–46, (c) 46–49, (d) 49–51, (e) 51–60 and (f) 60–95 mm  $L_S$ .

collected in other years (Brodeur *et al.*, in press). In 1996 age 0 year walleye pollock diet was dominated by copepods <2 mm, even at size ranges in which they would usually be expected to feed on large copepods or euphausiids (Schabetsberger *et al.*, 2000). All of these conditions suggest that by the late summer of 1996, juvenile pollock may have been experiencing food limitation, and consequently low nutritional status.

Region did not affect age 0 year walleye pollock  $E_{wb}$ . This result indicates that within-region factors outweigh among-region factors. Within a region, different hydrography associated with frontal habitats may have influenced fish feeding success and subsequently  $E_{wb}$ . The predominance of habitat over region



dynamics, however, could not be proved in the analysis because there were not a sufficient number of stations to simultaneously test for a region and habitat effect (Table I).

The increase of  $E_{wb}$  with size found in this study is a common feature among juvenile fishes (Paul *et al.*, 1998a, b; Norton *et al.*, 2001). It indicates a tendency to allocate energy to body growth rather than storage during the earlier part of the juvenile stage, which could be a form of adaptation leading to higher survival. Presumably, with rapid growth comes faster swimming speed, so larger fishes have higher survival rate when size dependent predation mortality is high (Sogard, 1997). Moreover, storing energy in young fishes is curtailed somewhat because smaller fishes use more energy per unit mass than larger fishes (Paul, 1986). In contrast, large juveniles increase energy reserves, probably in preparation for over-wintering (Paul & Paul, 1998; Sogard & Olla, 2000). Because large fishes make a more optimal use of energy available to them, they also have increased chances of over-winter survival compared with small-bodied fishes at equally high energetic contents (Hurst & Conover, 1998; Gotceitas *et al.*, 1999; Schultz & Conover, 1999).

Two size thresholds were identified at which the shape of the relation between  $E_{wb}$  and  $L_S$  changed. The first size threshold was found at 46 mm, at which the relationship between age 0 year walleye pollock  $E_{wb}$  and  $L_S$  reached a local minimum (Fig. 4). This change in energy storage could have originated from a concurrent change in feeding habits. At a similar size range, juvenile walleye pollock change their diet from primarily small copepods to large copepods and euphausiids (Brodeur, 1998; Schabetsberger *et al.*, 2000), and switch from diurnal to nocturnal feeding (Brodeur *et al.*, 2000). Euphausiids in particular have a higher caloric content, in terms of dry mass, than most copepods (Davis *et al.*, 1998). The second threshold occurred at 80 mm, beyond which  $E_{wb}$  appeared to become asymptotic with size (Fig. 4). Two hypotheses could account for this relationship. First, the 80 mm size threshold could be generated because age 0 year walleye pollock exhaust their food resources by the time they reach that size (typically, autumn). Alternatively, at 80 mm  $L_S$  age 0 year walleye pollock reached a  $E_{wb}$  typical of adults. The first hypothesis implies that in the presence of abundant food resources, juvenile walleye pollock >80 mm still show an increase  $E_{wb}$  with size, while the opposite would hold if the second hypothesis was true. The second hypothesis, physiological maximum, seems more plausible because adult walleye pollock have similar  $E_{wb}$ , 16.3 to 18.4 KJ g<sup>-1</sup> dry mass (Smith *et al.*, 1986), to that observed in 80 mm fish.

A significant positive correlation was found between two different indicators of age 0 year walleye pollock nutritional status,  $R_E$  and  $R_W$ . Similar results were also reported by Harris *et al.* (1986) who showed that age 0 year walleye pollock condition index was positively correlated with  $E_{wb}$  and negatively correlated with water content. The fact that  $R_E$  was positively correlated with  $R_W$  indicated that a heavier than normal fish also had higher than normal  $E_{wb}$ . The slope of the regression between  $R_E$  and  $R_W$  was less acute (low  $a_1$ ) for larger fish than for smaller ones (Fig. 5), indicating that, once having fulfilled the growth requirements, smaller fish were more efficient than larger fish in converting surplus energy into nutritional reserves. Therefore, it is inferred that energy storage in small juveniles was still an important function, even though overall energy

storage tended to increase with fish size. It is possible that larger juveniles were progressively approaching their physiological maximum energy storage, which would explain the gentler slope observed in large fish. It is possible, however, that the steeper slope in smaller fish might reflect the effect of spatial or temporal variability originally associated with the  $E_{wb}$  data (habitat and year effects) that was not removed from the analysis used to estimate  $R_E$  due to the unbalanced nature of the sampling scheme.

One clear result of this study was that in late summer, age 0 year walleye pollock have low energy content compared to many other forage species (Van Pelt *et al.*, 1997; Lawson *et al.*, 1998; Paul *et al.*, 1998b). A question arises as to how age 0 year walleye pollock acquire enough energy to fulfil their metabolic needs throughout the winter. One possibility is by feeding, and another is by considerably lowering the metabolic rate, possibly by residing in cold pools. Paul *et al.* (1998a) found that age 0 year walleye pollock collected in Prince William Sound lost little energy throughout the winter, indicating the possibility that they continue to feed at this time. Winter conditions in the Bering Sea, however, are more severe than in Prince William Sound and age 0 year walleye pollock have less food available to them, which would suggest that in the Bering Sea they rely more on cold water adaptation. For example, the energy required for metabolism in a juvenile walleye pollock residing at 6° C (typical Prince William Sound winter temperature) is 112% greater than the energy required at 2° C (typical Bering Sea winter temperature) (Paul, 1986). Sogard & Olla (2000) found that simulated winter survival was increased in age 0 year walleye pollock remaining in cold temperatures. They also found that the recovery of food-deprived fish was almost immediate, even after >200 days of starvation. All of these indicate that age 0 year walleye pollock in the Bering Sea could survive mainly by cold water adaptation and occasionally on opportunistic feeding in winter. The lack of nutritional content data through the winter, however, makes it impossible to firmly conclude how they survive through the first critical winter in the Bering Sea.

We thank J. McDonald and P. Shoemaker for help in calorimetric estimation of  $E_{wb}$ , and to K. Mier for help with statistical analysis. We are grateful to the crew of the NOAA ship *Miller Freeman* for help provided in fish collection, and in particular to M. Wilson for directing the field sampling in 1999. Comments from S. Sogard, R. Schabetsberger, and two anonymous reviewers improved this manuscript. Laboratory facilities were provided by the University of Alaska Institute of Marine Science's Seward Marine Center Laboratory. This is contribution number 2696 from the Institute of Marine Science, University of Alaska. This research was sponsored by NOAA's Coastal Ocean Program through the Southeast Bering Sea Carrying Capacity Project and is contribution S416 to Fisheries-Oceanography Coordinated Investigations.

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