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The Influence of Sampling Location, Timing, and Hatching Origin on the Prediction of Energy Density in Juvenile Pink Salmon

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U.S. DEPARTMENT OF COMMERCE
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ABSTRACT

Accurate estimation of energy density of fish is important for biogenetic models. Our objectives for this study were to determine which variables could be used to predict energy density instead of estimating energy density directly with bomb calorimetry. Secondly, we examined the variability in energy density relative to the sampling location within the Gulf of Alaska, the stock of origin, and the year the fish was sampled. Juvenile pink salmon *Oncorhynchus gorbuscha* were collected from the Gulf of Alaska during July 2001 and 2002. Energy density (J/g of wet weight) was estimated using bomb calorimetry. Hatchery stocks were identified from otolith thermal marks, and non-thermally marked fish were assumed to be wild. Energy density differed significantly by transect ($P < 0.000$), year ($P < 0.000$) hatchery stock ($P = 0.001$), and the interaction of origin and transect ($P = 0.018$). Body size was not related to energy density. However, % dry weight (dry weight/wet weight) was related to energy density ($R^2 = 0.93$) and thus can be used in regressions to estimate energy density. We used energy densities predicted from a regression with % dry weight in bioenergetic modeling simulations. Error associated with energy density predictions affected bioenergetic models of body growth by up to 7-8% over a 30-day period. This error increased as the water content of fish increased and as the energy density decreased. Biological factors should be considered when predicting energy densities so that errors are minimized.

CONTENTS

INTRODUCTION

Bioenergetic models have become so widespread that model parameters have been described for almost 40 fish species (i.e., reviewed in Hanson et al. 1997, Zhou et al. 2005). Bioenergetic models help fisheries biologists answer questions about multiple ecological processes, including fish growth as it relates to temperature (Walker et al. 2000), habitat quality (Nislow et al. 2000), energy costs (Holker and Breckling 2002), responses to varying rations of food (Walker et al. 2000; Paukert et al. 2003), and fish response to contaminants (Solvana and Roberto 2001. Trudel and Rasmussen 2001). Energy densities of predators and prey are key inputs of bioenergetic models. Sensitivity analyses have shown that bioenergetic models can be prone to errors in energy density when fish growth or growth-related parameters (Stewart et al. 1983, Bartel et al. 1986). To generate accurate estimates from bioenergetic models, energy density values for predators and prey must reflect fluctuations from ontogeny, location, season in the environment. Because accurate estimates of energy density are difficult to obtain, published values are often used from closely related species (Hartman and Brandt 1995). These values can be misrepresentative of the actual energy content.

There are several methods available for estimating energy density. The first method uses the proximate constituents of water, ash, lipids, carbohydrates, and proteins to estimate the total energy content. Because 98% of the constituents of fish are lipid and protein (Higgs et al. 1995), the energy equivalent of these tissues are used to calculate the total energy. Several energy equivalent values have been used for lipids and protein, but they may not provide accurate estimates of total energy (Craig et al. 1978), and the method is time-consuming and expensive. Lipid content is the primary determinant of energy density because protein remains fairly stable whereas lipids tend to fluctuate (Anthony et al. 2000). Because water content is a good

approximation of the amount of lipids and protein in the body (Groves 1970), the relationship between water content and energy density has been modeled with linear regressions to estimate energy density for many fish species (Brett et al. 1969, Hartman and Brandt 1995, Trudel et al. 2005, Wuenschel et al. 2006). For this method to be successful, the relationship between energy density and the body water content must be established with direct measurements of energy density. The most accurate and time consuming method of obtaining energy density is to directly measure it with bomb calorimetry.

Energy density is dynamic and can vary in marine fish species by season, ontogeny, and size class (Jansgaard 1974, Robards et al. 1999, Anthony et al. 2000, Vollenweider 2005, Wuenschel et al. 2006). Boldt and Haldorson (2004) found that pink salmon energy density varied by location within Prince William Sound, Alaska, which likely reflects differences in prey availability (Boldt and Haldorson 2002, 2004). Their results indicate that energy content, and therefore growth conditions, were location specific. Pink salmon (*Oncorhynchus gorbuscha*) have only one year at sea to grow so they must devote much of their energy toward body growth and not energy storage. The fast growth rate of pink salmon may make it more difficult to reserve calories for lipid storage than in other salmon species. So, above average energy densities, reflecting higher lipid concentrations, may dictate the survival of pink salmon more so than in other salmon species. Differences in energy density like those observed by Boldt and Haldorson (2004) should be included in bioenergetic models of pink salmon ecology because the differences may have large impacts on the growth and over-winter survival of pink salmon. However, because bomb calorimetry is time consuming and expensive, it is desirable to use the less time intensive and inexpensive method of predicting energy density from the relationship between energy density and percent dry weight.

Our first objective for this study was to examine the relationships between energy density, estimated directly with bomb calorimetry, and length, weight, condition, and % dry weight (water content) of juvenile pink salmon to determine which variables could be used to predict energy density. Our second objective was to examine the variability in energy density relative to the sampling location within the Gulf of Alaska, the stock of origin, and the year the fish was sampled. Finally, we estimated the error in the prediction of energy density from the relationship of % dry weight and energy density. We did this by examining the sensitivity of 30-day bioenergetic models of growth to the errors in energy density prediction. In the case of pink salmon, small differences in body growth and the proportions of proximate constituents may have significant impacts on the prediction of energy density from water content.

METHODS

Sampling and Laboratory Methods

In July of 2001 and 2002, cruises were conducted in the central Gulf of Alaska on board the FV *Great Pacific*, a 38-m long stern-trawling vessel. Although a more rigorous sampling of the entire Gulf of Alaska was conducted (Farley et al. 2001, Cokelet et al. 2002), samples from three transects were used for this study (Fig. 1). Juvenile salmon were collected with a 198-m long midwater rope trawl, which had a spread of 52 m horizontally and 18 m vertically, towed for 30 minutes. Fork length (to the nearest millimeter) and weight (to the hundredths of a gram) of juvenile age-0 pink salmon were recorded and otoliths were removed and examined for thermally induced markings to determine the hatchery of origin (either Armin F. Koernig [AFK], Wally Noerenberg [WN], or Solomon Gulch [SG]). Because thermal marks are added to otoliths in the hatchery to signify the hatchery or origin and the year of release, we assumed that fish

lacking thermal marks were of wild stock. Fish were frozen onboard until they were prepared for bomb calorimetry in the lab.

We removed the stomachs contents from each juvenile pink salmon (n = 452) and then dried fish in a gravity convection oven for 2-7 days at 55-60 °C. We measured the weight of each fish every 24 hours until they lost less than 0.1 g of weight per day. Percent dry weight was calculated by dividing the final dry weight by the wet weight (excluding stomach contents and otoliths) × 100. We homogenized the dried fish into a fine powder using a Waring pulverizer and a mortar and pestle and then pressed a subsample of the powder into 0.15 g pellets. We stored the pellets in a desiccator cabinet to prevent reabsorption of water before they were bombed in the calorimeter. Energy density in cal/g of dry weight was estimated using a Parr 1425 Semimicro Bomb Calorimeter (Parr Instrument Co. 1991). We then converted these values to J/g wet weight for use in a bioenergetic model. Additionally, multiple calorimetry runs were performed on 10 pink salmon sampled in 2001 to determine if there was intra-fish variability that could be attributed to the bomb calorimeter, user error, or irregularities in the pellet composition. The calorimeter was calibrated for each user by performing a standardization run on a benzoic acid pellet of a known energy density. The bomb calorimeter calculates a correction factor for each user that is then used for the energy density estimation of future samples (Parr Instrument Co. 1991).

Analysis

ANCOVA

Of the 452 pink salmon samples bombed in the calorimeter, 312 were collected in 2001 and 140 in 2002. Samples from all transects (Fig. 1) and all hatcheries of origin were represented in the 2001 and 2002 samples. We used an analysis of covariance (ANCOVA; Sall et al. 2005) to

test for differences in the energy densities of the pink salmon by origin (O_k [AFK, WN, or SG hatcheries, or wild]), year sampled (A_i), survey transect (T_j), and % dry weight (D_l) using the following full model:

$$Y_{ijklm} = \mu + A_i + T_j + O_k + \beta_0(D_l - \overline{D}) + A_i \times T_j + A_i \times O_k + A_i \times \beta_1(D_l - \overline{D}) + T_j \times O_k + T_j \times \beta_2(D_l - \overline{D}) + O_k \times \beta_3(D_l - \overline{D}) + A_i \times T_j \times O_k + A_i \times T_j \times \beta_4(D_l - \overline{D}) + T_j \times O_k \times \beta_5(D_l - \overline{D}) + A_i \times T_j \times O_k \times \beta_6(D_l - \overline{D}) + e_{ijklm}, \quad \text{Eq. 1}$$

where Y_{ijklm} is the energy density from bomb calorimetry, μ is the theoretical population mean, $\overline{D}$ is the mean % dry weight for all individuals, $\beta_{0\text{-}6}$ are the regression coefficients for the covariate term *D*, and e_{ijklm} is the normally distributed random error. The main effects were year, origin, and transect, while % dry weight was treated as a continuous covariate. All possible interactions were included in the full model. For significant interactions ($\alpha = 0.05$), we performed separate ANOVA models for each level of the significant effect and used a Tukey Kramer honestly significant different (HSD) test to compare levels within the ANOVA (Engqvist 2005, Sall et al. 2005). In these ANOVA models, significant effects from the full model were also included.

Regressions

We examined the correlations of energy density (directly estimated with bomb calorimetry) with more easily measured variables (length, weight, condition factor, and % dry weight [dry weight/wet weight]) to determine if linear regressions could be used to predict

energy density. The standard deviation of the residuals of the regression between % dry weight and energy density was then used in bioenergetic models to assess the sensitivity of these models to errors in energy density predictions.

Bioenergetic Model

We used the predicted energy densities from the regression (Fig. 2) in Wisconsin bioenergetic modeling simulations (Hanson et al. 1997) to quantify the difference in growth estimates from directly estimated energy densities and predicted energy densities. We first used predicted values from the regression at fixed % dry weights as the consumer energy densities. In other simulations, we used the same predicted energy density at each % dry weight plus/minus two standard deviations of the residuals of the regression (Fig. 2). This measured the sensitivity of the bioenergetic model to prediction error associated with estimating the energy densities from a regression. The Wisconsin model calculates the consumption of prey required to satisfy the observed growth over a given time interval, or the growth rate that should result from a specified amount of consumption, and is based on the energy-balance equation:

$$C = G + M + W, \qquad \text{Eq. 2}$$

where C is the total energy consumed, G is the growth, M is metabolic costs (e.g., respiration, activity, and specific dynamic action), and W is waste (excretion and egestion). Physiological parameters used to represent juvenile pink salmon were taken from the pink/sockeye parameter set (Beauchamp et al. 1989). Bioenergetic model simulations were run for a 30-day time period using data collected on all stations of the Seward line transect (Transect No. 2, Fig. 1) during the 2001 survey. Model input data from the transect included average 10-m surface temperature,

average pink salmon body size (wild and hatchery combined, 19.2 g), and literature energy density values for prey items (Davis et al. 1998). Consumer end weight was fit to a constant proportion of daily maximum consumption (0.80). Previous studies have shown that juvenile pink salmon in the Gulf of Alaska feed at 90-95% of their maximum daily ration (Cross et al. 2005); therefore, we believed a constant proportion of 0.80 was a conservative estimate.

RESULTS

Intra-fish Variability

Three calorimetry runs were conducted on 10 fish, and the intra-fish variability of energy density ranged from 0.12 - 0.99% ($\bar{x}$ = 0.60%), which was 5.7 - 0.7 J/g wet weight ($\bar{x}$ = 28.1 J/g wet weight; Fig. 3). This variability can be attributed to slight differences in the subsample composition, and error from the bomb calorimetry unit. The calorimeter has a margin or error of 0.5% (Parr Instrument Co. 1991), so the variability we observed seemed reasonable.

ANCOVA

All origins were present at all transects in both years (Table 1). A series of models were run with one non-significant variable ($\alpha = 0.05$) excluded each time until all variables left were significant. In all models, year, % dry weight, transect, origin, and the interaction of origin and transect all accounted for a significant amount of the variation in energy densities (Table 2).

Separate ANOVA were run for each origin and for each transect in order to test for pair-wise differences among hatcheries of origin within each transect and among transects within each origin (Tukey Kramer HSD test, $\alpha = 0.05$, Sall et al. 2005). For example, because hatchery × transect was a significant interaction, we performed one ANOVA for transect one in which the explanatory variables were % dry weight, year, and hatchery. Within this ANOVA we compared

all origins to each other using a Tukey Kramer HSD test, which tests for pair-wise differences. Additionally, we ran similar ANOVA for each transect and then for each hatchery. For AFK hatchery fish, there were significant differences in energy density between Transect numbers 1 and 3, and between Transect numbers 1 and 2. Wild fish were significantly different between Transect numbers 1 and 2 and Transect numbers 3 and 2. SG energy densities were not significantly different between transects, while WN hatchery energy densities were significantly different between Transect numbers 1 and 3 and between Transect numbers 3 and 2. Overall there were no patterns, except that both AFK and WN hatchery energy densities differed between Transect numbers 1 and 3. Because there were many significant pair-wise differences due to transect, it appears that location is an important factor in determining a fishes' energy density.

Pair-wise differences were also found between hatcheries at each transect. At Transect number 1, WN and wild fish had significantly different energy densities. At Transect number 2, there were no significant differences between origins, and AFK and wild fish were significantly different at Transect number 3. There was no pattern to the pair-wise differences between origins nor between transects. However, there were fewer significant differences between origins within a transect than there were transects within hatcheries. This may indicate that location has a stronger effect on energy density than origin.

Regressions

No strong relationships existed between length, weight, or condition factor and energy density (range of R^2 = 0.07-0.14; Fig. 4). Therefore, the size of the fish is not a good predictor of caloric density. The coefficient of determination of the relationship of % dry weight and energy density was very high (R^2 = 0.93; Fig. 2). We subtracted each energy density measured directly

from the predicted value to get a residual (Fig. 2). The residuals had a standard deviation of 112 J/g of wet weight (two standard deviations = 224) and the largest residual was 607. A difference of up to about 25 J/g of wet weight (0.5%) is the acceptable margin of error of the bomb calorimeter (Parr Instrument Co. 1991, Trudel et al. 2005); however, 84 % of the residuals were over 25 J/g of wet weight.

Bioenergetic Model Simulations

In the bioenergetic models, low % dry weights yielded higher variability in growth estimates. The difference in end weight at two standard deviations from the predicted energy density was 6 g, which is an error of 8% (Fig. 5). This error decreased as % dry weight increased (Fig. 5). The largest residual of the pooled regression (607 J/g wet weight) would have a much greater error than what we observed in this simulation.

DISCUSSION

The condition factor, length, and weight of juvenile pink salmon were not highly correlated with energy density (Fig. 4). Body size and energy density were also poorly correlated in recently out-migrated pink salmon from Prince William Sound, Alaska (Boldt and Haldorson 2004) and in coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*) (Trudel et al. 2005). Additionally, coho salmon and Chinook salmon energy densities are not correlated with condition (Madenjain et al. 2000), nor with protein content (Trudel et al. 2005). However, we found a strong correlation between % dry weight and energy density, which has also been documented in coho and Chinook salmon (Trudel et al. 2005), and other groups of fish including, clupeids, pleuronectids, cyprinids, and osmerids (reviewed in Hartman and Brandt 1995).

We found that the energy density of pink salmon differed significantly by the transect, year, origin, and the interaction of origin and transect (ANCOVA; Table 2). Two hatcheries (AFK and WN) had significantly different energy densities at Transect numbers 1 and 3. There were other significant pair-wise comparisons, but no other patterns were present. The number of significant differences between transects within hatcheries was higher than the number of significant differences among hatcheries within a transect. This may indicate that location has a stronger effect on energy density than origin. Boldt and Haldorson (2004) also found that location had a significant effect on energy density of juvenile pink salmon.

Other studies have also found significant effects of area, season, and species on energy density. White crappie (*Pomoxis annularis*) energy density varied among reservoirs in Ohio (McCollum et al. 2003). Wuenschel et al. (2006) found an effect of ontogeny on the relationship of % dry weight and energy density in juvenile grey snapper (*Lutjanus griseus*) and spotted seatrout (*Cynoscion nebulosus*). Trudel et al. (2005) suggested that seasonal, species, and area differences should be considered when using regressions to estimate energy density. In a study of the energy density of eight North Sea fish species, the energy density of all species studied differed significantly by season (Pederson and Hislop 2001). The energy density can change in response to seasonal feeding changes including starvation (Oliver et al. 1979, Pangle and Sutton 2004), increases in rations (Hayes and Taylor 1994, Pangle and Sutton 2004), prey switching (Breck 1998), reproductive status (Anthony et al. 2000), or season (Anthony et al. 2000; Vollenweider 2005). Conversely, some studies have found little variation in energy density, and concluded that related species be pooled by taxonomic group for energy density prediction from regressions with % dry weight (Hartman and Brandt 1995; Pederson and Hislop 2001).

Variability in the regression is caused by fluctuations in the proportions of lipids and protein that can not be explained by water content. Although the ANCOVA did not detect

significant effects of year, transect, or stock on the slope of the % dry weight and energy density relationship, they still are affecting the slope in a biologically significant way, as seen by the differences in end weight after 30-days in the bioenergetic model. At a fixed % dry weight, the discrepancy in the actual energy densities can be attributed to differing proportions of lipids and protein in an individual fish. Even small changes in the proportion of constituents can cause a marked increase in energy density because lipids have almost double the energy content as protein (Brett 1995). Year, location, origin, and possibly other variables, are contributing to the variability in the relationship between energy density and % dry weight, or in other words affecting the proportion of lipids and proteins. Because these variables affect the relationship of % dry weight and energy density, the regression systematically biases estimates of energy density. Some of the variability between the regression lines at 16% dry weight can be attributed to a small sample size (Fig. 2); however, there is a strong increasing trend in variability as % dry weight decreases which is independent of sample size (Fig. 5). The increase in variability at low % dry weight means that the proportion of lipids and proteins is more variable when water content is high. Wuenschel et al. (2006) also found variability in regressions of % dry weight and energy density that was attributed to ontogeny. This variability caused estimates in energy density to be overestimated by up to 25%.

The trend of increasing variability in energy density was apparent for fish with low % dry weights (Fig. 5) and smaller fish (Fig. 6). This may be because the smaller, less energy-dense fish have high water content, are under energetic stress, and are starting to use protein reserves as well as lipid reserves. Age-0 pollock, *Theragra chalcogramma*, and capelin, *Mallotus villotus*, use a greater proportion of protein than lipids when energetically stressed, whereas age-1 fish used lipids before protein (Ron Heintz, NMFS-ABL, pers. commun.). So it is possible that the

age-0 juvenile pinks in this study are using protein reserves as well as lipids, and are therefore experiencing fluctuations in the ratio of protein and lipids as they become less energy dense.

The error in end weight after 30 days from the bioenergetic model is likely biologically significant and may be large enough to warrant concern. It has been hypothesized that juvenile salmon must reach a critical size to meet minimum metabolic requirements before the end of the first growing season in order to survive the winter at sea (Mortensen et al. 1999, Beamish and Mahnken 2001). Moss et al. (2005) examined pink salmon scales from Prince William Sound, Alaska and found that fish that survived to adulthood were comparatively larger and faster growing than juvenile fish sampled at sea. They concluded that size-selective mortality occurs during the winter at sea after the fish have the opportunity to reach a critical size during the first summer. Differences in end weight, like we saw in our bioenergetic model (Fig. 5), may be large enough to draw false conclusions about the over-winter survival of pink salmon. The error we saw in our bioenergetic models is systematically biased by the factors we examined (year, transect, origin), so any growth and survival predictions will also be systematically biased.

There are a few options to consider when deciding how many samples should be bombed in a calorimeter and how many should be predicted with the dry weight method. The first option, which is the most accurate and most expensive, is to perform calorimetry on all of the samples. The second approach is to perform calorimetry on a sample of the fish, and save resources by predicting the energy densities of a portion of the fish. If there is a reason to believe that there may be other factors affecting energy density, such as maturation, prey switching, or seasonal growth patterns, then several regressions can be used to capture this variability. Using exploratory analyses like these can be helpful in deciding how many samples should be bombed in a calorimeter and what sources of variation should be accounted for when using regressions for prediction.

When energy densities are going to be used for purposes other than bioenergetic models that are sensitive to energy density, more error in the estimates may be acceptable. In these cases, performing calorimetry on fewer samples would make sense. Estimating a portion of the samples may be adequate for bioenergetic models that are less sensitive to energy densities, such as consumption rate models (Stewart et al. 1983). This method may also be appropriate when energy density is used as an index of health (McCollum et al. 2003, Boldt and Haldorson 2004). For example, it may be a valuable parameter for models of population dynamics, such as spawner-recruit relationships. Climate variables often are used to help the predictive power of these models, but the addition of a direct index of health may help fisheries scientists to formulate more accurate models (Shotwell and Adkison 2004).

When predicting energy density values with a regression of % dry weight and energy density, it is important to dry a large number of fish at the same time and then decide which fish samples should be bombed. For a robust regression with minimal error, it is necessary to have samples that represent a variety of % dry weights, thus providing contrast in the data. To get the best possible estimates of energy density, the bomb calorimeter should be used on fish that have % dry weights that are uncommon. This will help with prediction error due to small sample sizes at rare % dry weights. If there is increasing error at certain % dry weights like we observed at low % dry weight (Figs. 5, 6), these should also be bombed instead of estimated. It is helpful to examine the predicted and actual energy density values throughout the process to interpret the residuals of the regression and decide how many more and which samples should be run in the calorimeter.

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Table 1. -- Mean energy density ($\bar{x}$, J/g wet weight), standard error (SE), and number of samples (n), of juvenile pink salmon sampled from the Gulf of Alaska. Summary statistics are stratified by year (2001 and 2002), transect number (1-3), and stock (one of three hatcheries: Armin F. Koernig (AFK), Wally Noerenberg (WN), or Solomon Gulch (SG), or wild). Energy density was estimated using bomb calorimetry.

Year	Transect	Origin	$\bar{x}$	SE	n
2001	1				
		AFK	4,275	234	7
		SG	4,205	86	18
		WN	4,391	95	12
		Wild	4,247	91	22
	2				
		AFK	4,188	63	35
		SG	4,038	45	41
		WN	4,169	60	29
		Wild	4,082	66	31
	3				
		AFK	4,294	86	25
		SG	4,418	70	27
		WN	4,501	48	32
		Wild	4,556	58	33
2002	1				
		AFK	4,081	192	7
		SG	4,334	127	25
		WN	4,534	94	14
		Wild	4,601	142	21
	2				
		AFK	4,272	143	20
		SG	4,379	85	13
		WN	4,476	110	9
		Wild	4,059	215	6
	3				
		AFK	4,570	447	3
		SG	4,697	179	10
		WN	4,814	164	8
		Wild	4,935	118	4

Table 2. -- ANOVA F-test of factors affecting the energy density of juvenile pink salmon. df denotes the degrees of freedom, F-ratio is the F-test statistic used for hypothesis testing, and P is the significance of the test.

Effect	df	F-ratio	P
Origin	3,434	5.38	0.001
Year	1,434	106.09	< 0.000
Transect	2,434	14.42	< 0.000
% dry weight	1,434	7754.51	< 0.000
Origin×Transect	6,434	2.59	0.018

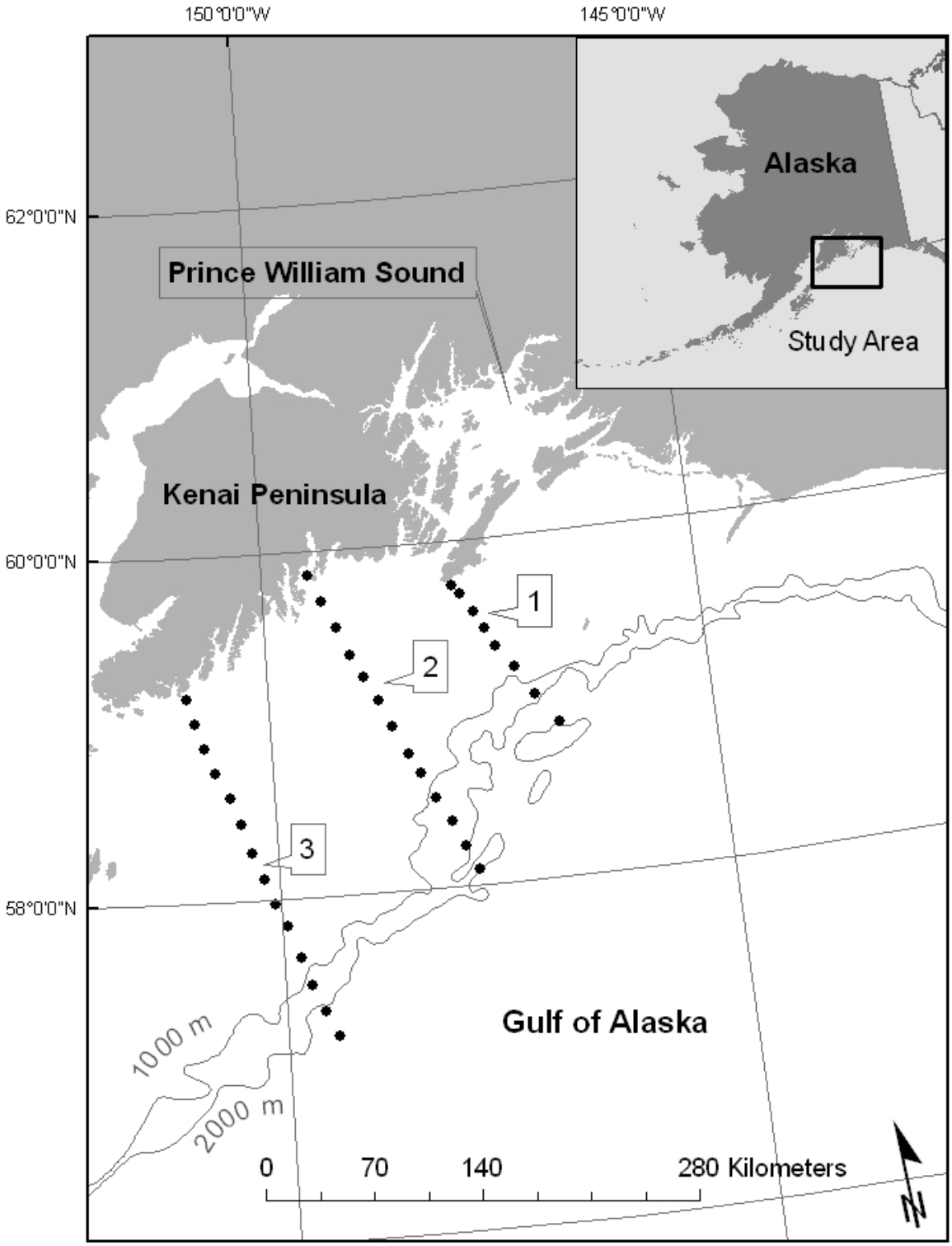

Figure 1. -- Transects and sample locations for juvenile pink salmon on research cruises in July of 2001-2002.

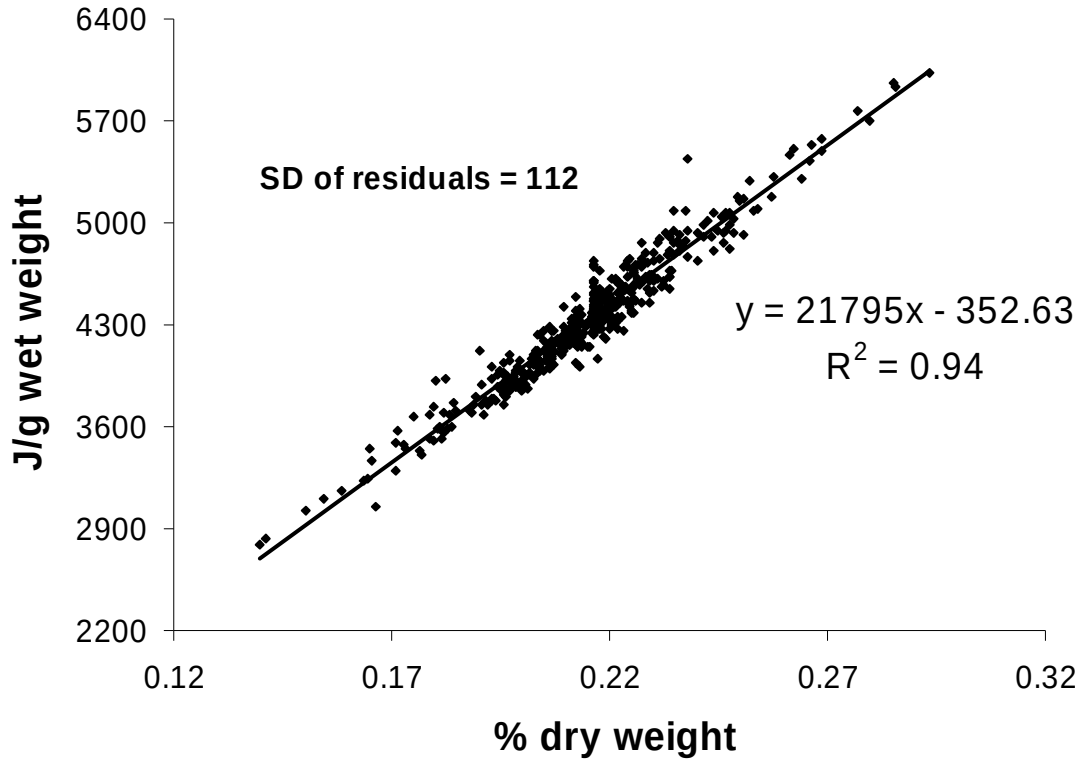

Figure 2. -- Linear regression of energy density and % dry weight of juvenile pink salmon. The formula is presented with the coefficient of determination (R^2), as well as the standard deviation (SD) of the residuals (| observed – predicted |).

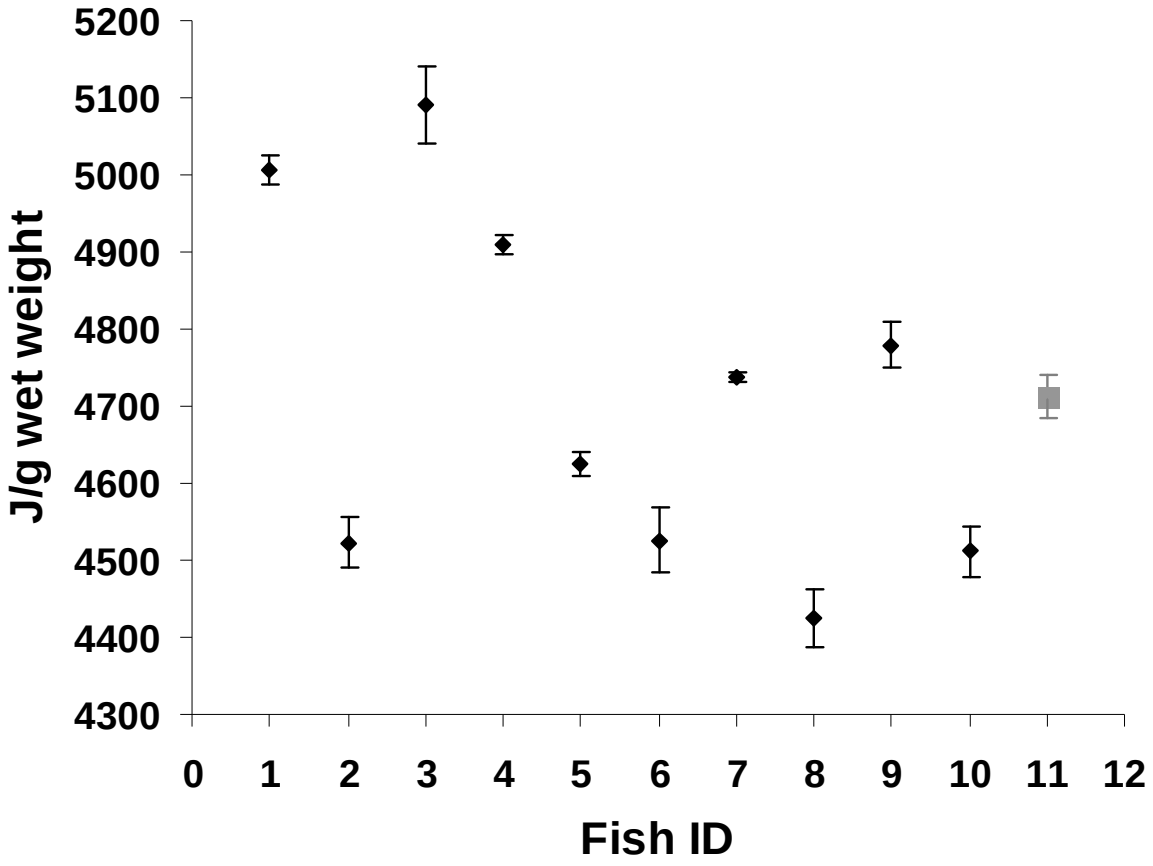

Figure 3. -- Intra-fish variability in energy density measured using bomb calorimetry. Error bars represent 95% confidence intervals. Three energy density values were obtained for each of the 10 juvenile pink salmon. The mean of all 10 fish and the mean of all the error bars are in grey.

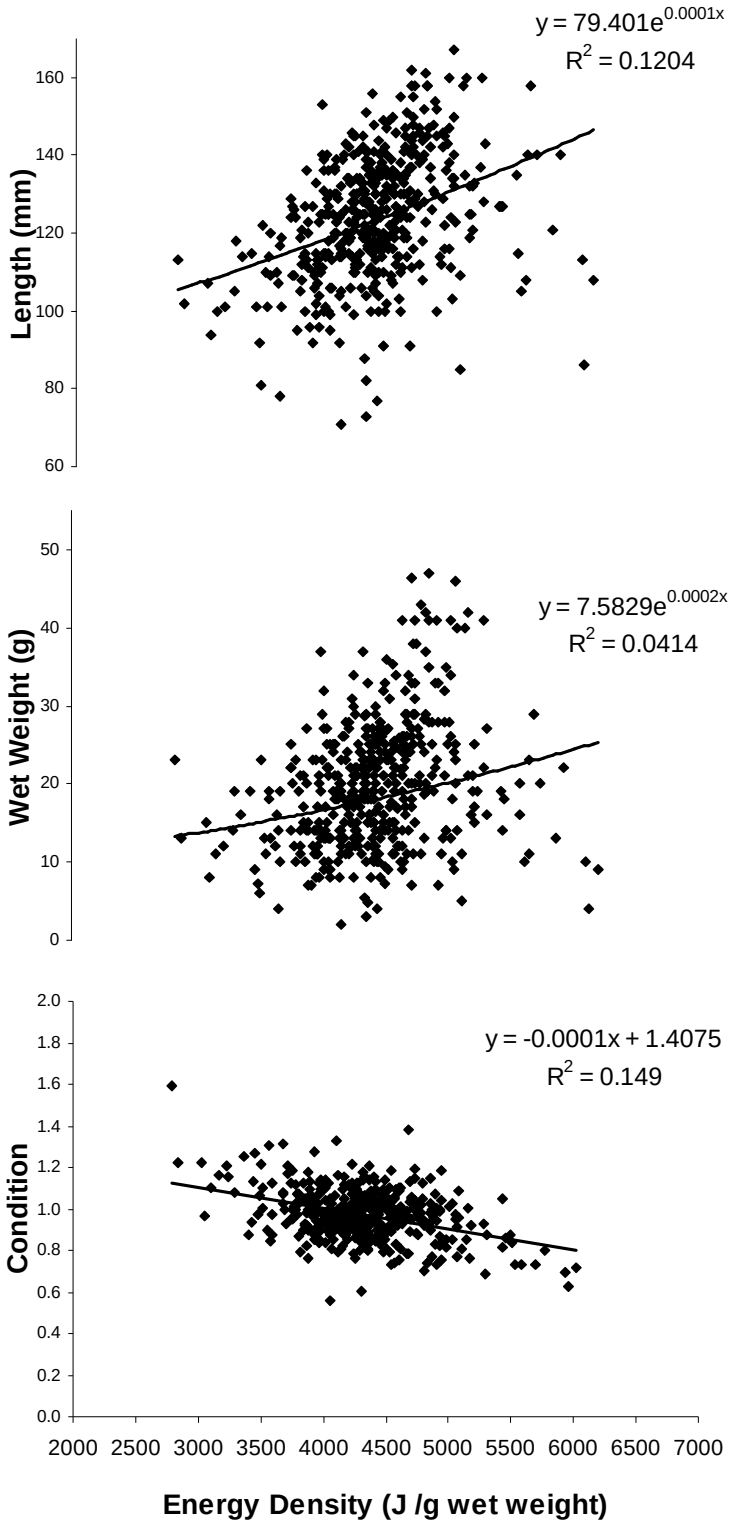

Figure 4. -- Regressions of condition factor, length, and wet weight versus the energy density of juvenile pink salmon. A linear formula is presented with its coefficient of determination (R^2). Exponential models are presented for length and weight.

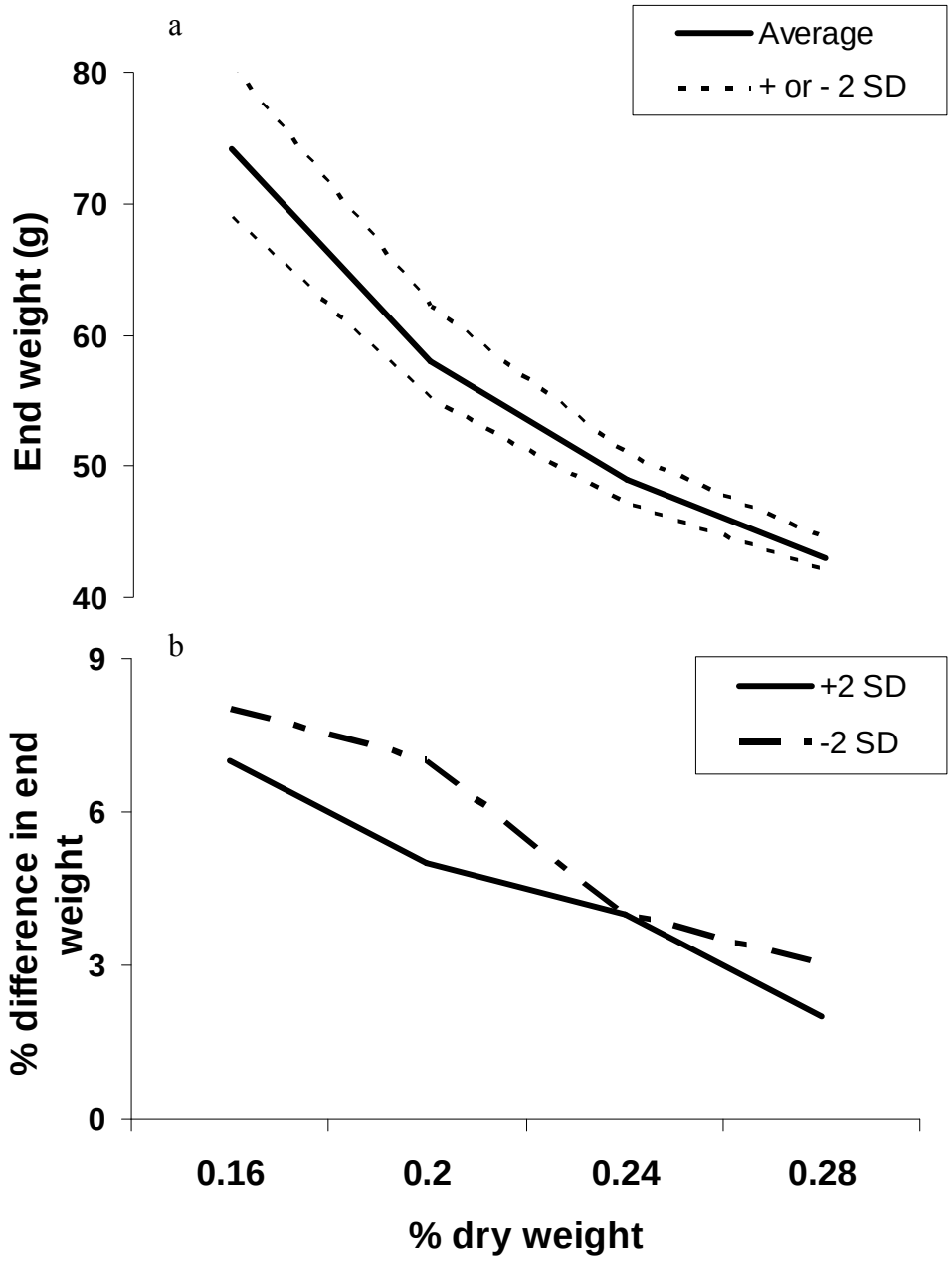

Figure 5. -- Bioenergetic model simulation of weight after 30 days, when all variables are held constant except energy density. (a) The solid line is the estimated growth when energy density is predicted from a regression with dry weight. The large dashed line represents estimated growth when the predicted energy density +/- 2 standard deviations (SD) of the residuals is used in the model. (b) The % difference in end weight between the growth estimated from predicted energy, and the growth estimated when energy density is -2 (long dash) and +2 standard deviations of the residuals (solid black) from the predicted energy density. The % difference describes the error in growth estimates that can be attributed to using predicted energy densities instead of using energy densities directly measured with bomb calorimetry.

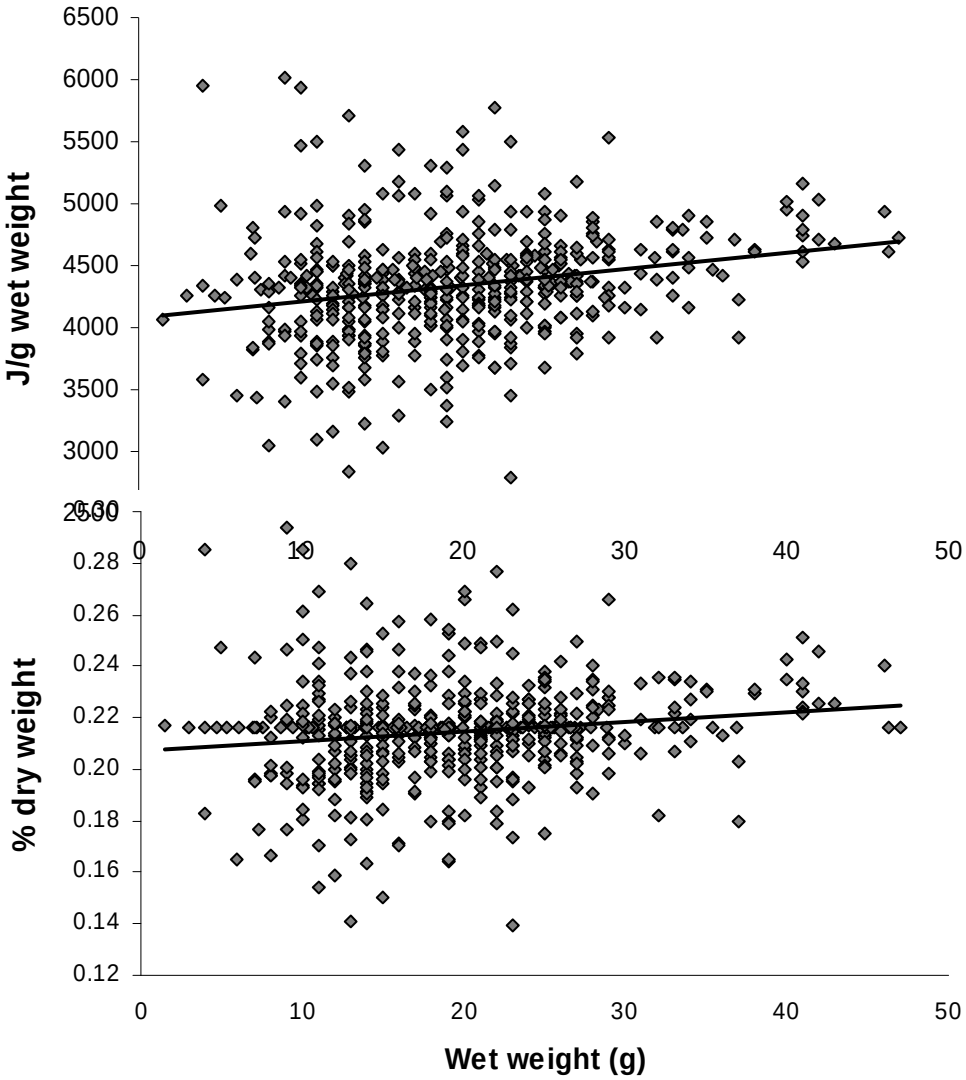

Figure 6. -- Energy density measured with bomb calorimetry and % dry weight of juvenile pink salmon from the Gulf of Alaska, plotted against the wet weight. The linear regression is also shown in black to demonstrate the trend.

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