Variability in the energy density of prey and its consequences for growth in juvenile Chinook Salmon

by

Jacob Daniel Cole Weil
BSc, University of Victoria, 2015

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Abstract

Understanding how energy flows through ecosystems reveals underlying ecological patterns that can drive processes such as growth and survival of organisms. To understand how energy is transferred through organisms, the energy content or energy density (ED) of both consumers and prey must be determined. To facilitate the ease of ED measurement across taxa, I developed a model to estimate the ED of organisms using percent ash-free dry weight (AFDW). Using data obtained from 11 studies with broad taxonomic, temporal and spatial coverage, I compared common predictors of ED using linear models. AFDW was determined to be the superior predictor of ED relative to previous metrics and was predictive for a broad range of taxonomic groups including aquatic invertebrates, aquatic vertebrates, aquatic plants and terrestrial invertebrates. This AFDW model enables measurement of ED with minimal cost and time investment, which allows ED to be more readily determined for diverse taxa. Next, I applied the AFDW method to the diet of a pelagic consumer, juvenile Chinook Salmon, to determine the effect of variable prey ED on growth. In 2017, I collected monthly zooplankton and fish samples of known importance in the diet of juvenile Chinook Salmon to look for fine-scale taxonomic, temporal and spatial differences in ED. Decapod zoeae and megalopae differed significantly from each other and showed family level variability in ED. Amphipods also showed significant species-level variability in ED. Temporal differences were observed, but did not reveal a consistent pattern among groups. Spatial variability was not significant. Using bioenergetics models, growth of juvenile Chinook Salmon was predicted to be greater when using fine-scale ED estimates. This difference was not substantial on average, but in some cases represented more than a two-fold difference in growth between coarse- and fine-scale estimates. These results suggest the need for higher resolution diet ED data when determining growth projections for juvenile Chinook Salmon. With the aid of the AFDW model presented in this thesis, the effort required to obtain these data is greatly reduced.

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Acknowledgments

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Chapter 1 – Introduction

1.1 General Introduction

The growth and survival of organisms depends to a large extent on energy flow. Understanding how energy flows through an ecosystem can reveal underlying ecological patterns that drive processes such as growth and food web dynamics (Brown et al. 2002, Cohen et al. 2003). An organism's ability to obtain enough energy to surpass metabolic demands and allocate excess energy to growth and reproduction is essential for survival (Karasov & Martínez del Rio 2007). The availability of energy to higher trophic levels depends on the content and transfer efficiency of energy from lower levels (Lindeman 1942). Understanding the pathways through which energy flows in an ecosystem can allow us to link processes at the molecular scale, such as energetic needs, all the way to individual and population level dynamics (Nisbet et al. 2000).

Optimal foraging theory (OFT) predicts that an organism will attempt to forage in a manner that maximizes energy acquired, while limiting energetic costs (Pyke 1984). This theory predicts feeding strategies, movement and the behaviour of organisms based on the goal of acquiring an optimal diet for growth (Pulliam 1974). OFT decisions are typically balanced against conflict with competitors (Svanbäck & Bolnick 2007) as well as predators (Brown 1999). In order to make accurate predictions regarding prey choice via OFT, information regarding the quality of prey is required (Pulliam 1974). Historically, prey quality was inferred from prey size (Werner & Hall 1974), however more recent studies have used a direct measure of energy content to describe patterns of optimal foraging (Bowen et al. 1995).

The energetic content of individuals is typically quantified as the amount of energy contained in a specific unit of mass (energy density (ED)), and is most accurately measured using bomb calorimetry (Cummins & Wuycheck 1971). Alternatively, ED can be mathematically derived from the composition of lipids and proteins in an organism using energetic equivalents (e.g. Logerwell & Schaufler 2005). This process, however, can introduce further variability, as equivalents for macromolecules often vary significantly (see Brett 1995), which can lead to deviation in these estimates from those that are empirically derived (Craig 1977). Bomb calorimetry, however, also has limitations. It is time-consuming and can be costly for large sample sizes and thus inference methods have been developed as an alternative (e.g. Hartman & Brandt 1995, Ciancio et al. 2007, James et al. 2012). These alternative models estimate ED from percent-dry mass, making use of the observed inverse relationship between percent fat and protein with moisture content (Flath & Diana 1985). The introduction of these models has vastly improved our ability to derive ED values for use in studies of diet and energy transfer (Johnson et al. 2017).

In aquatic systems, trophic structure controls the amount of energy transferred to each trophic level (Hairston & Hairston 1993). Small, numerically abundant phytoplankton make up the base of these food webs, transferring energy to larger and rarer species at higher trophic levels (Cohen et al., 2003). Efficiently assimilating energy from lower trophic levels into somatic growth and reproduction requires sufficient availability of prey (Welker et al. 1994). However, as there is such a wide variability in the energetic content of organisms (Cummins & Wuycheck 1971), feeding on different kinds of prey also has important consequences for growth (Rosen & Trites 2000, Spitz et al. 2010). Information about both the quality and quantity of prey are required in order to understand how feeding ecology affects growth in marine predators (Kitchell et al. 1977).

Acquiring energy during early life-history stages has long been understood as an important factor affecting survival in marine fish (Hjort 1914). The timing and availability of prey during the early period is tied to growth and ultimately survival (Cushing 1990). Larval and juvenile fishes typically increase the size spectrum of prey that they consume over the course of ontogeny (Ghan & Sprules 1993, Arrhenius 1996, Mittelbach & Persson 1998), likely due to a release from gape-limitation (Schael et al. 1991). In salmonids, the early marine period has been extensively studied for its role in growth and survival (Beamish et al. 2004, Moss et al. 2005, Farley et al. 2007, Duffy & Beauchamp 2011). A great diversity of life histories has been characterized for these species and significant variability in feeding ecology exists (Quinn 2018). The diet of juvenile Pacific Salmon varies from highly zooplanktivorous to mainly piscivorous depending on species (Brodeur & Pearcy 1990): Pink (*O. gorbuscha*), Chum (*O. keta*) and Sockeye (*O. nerka*) salmon overlap in trophic position, sharing a similar zooplankton resource base, whereas Chinook (*O. tshawytscha*) and Coho (*O. kisutch*) salmon tend to feed on higher trophic level species (Brodeur & Pearcy 1990, Johnson & Schindler 2012). Juvenile Chinook and Coho Salmon typically undergo an ontogenetic shift in feeding mode to piscivory during their first marine summer (Brodeur, 1991) and the timing of this shift has been linked to survival (Daly et al. 2009, Litz et al. 2017). Thus, understanding the energetic factors that drive variability in growth during the early marine period for juvenile Salmon should ultimately help us predict the marine survival for adults.

1.2 Thesis Overview

The overall goal of this thesis is to examine the energetic role that organisms have within a food-web and, by using juvenile Chinook Salmon as an example, determine how variability in prey type can ultimately affect growth and survival. To achieve this goal, I first develop a new method to assess the energy density (ED) of organisms to facilitate the classification of prey by energetic value. I then employ this method on a field-collected dataset of prey for juvenile Chinook Salmon to describe fine-scale variability between similar species. By applying these estimates of ED to a growth model, I assess how variability in the ED of prey organisms affects the growth of juvenile Chinook Salmon.

In Chapter 2, I describe a new method for estimating the energy density of aquatic organisms, plants and terrestrial invertebrates. Earlier methods either measured ED directly, or inferred it from models using dry-weight or proximate components as a proxy. These models were often species-specific and occasionally generalized for broader taxonomic groups, yet no previous model allowed for the accurate estimation of ED for invertebrates, vertebrates and plants with a single equation. By summarizing data from 11 studies broad in taxonomic, temporal and spatial scope, I compare common predictors of ED using linear models. Model selection reveals that percent ash-free dry weight (AFDW) was a superior predictor of ED compared to previous metrics. I explore the possibility of expanding this model to include terrestrial vertebrates and its broader application as a tool to quickly and accurately estimate ED in diet and food web studies.

In Chapter 3, I apply the method from the previous chapter to invertebrate and vertebrate prey of juvenile Chinook Salmon to examine variability in ED and its effect on growth. Specifically, I seek to determine if fine-scale taxonomic, temporal or spatial variability in ED exists between prey of known importance to juvenile Chinook Salmon. I describe significant variability in ED between decapod megalopae and zoeae, including several family-level differences. Amphipods also varied significantly by species. Temporal trends remained sporadic and species-specific, while spatial variability on a localized scale was not significant. Using bioenergetics models, I show that differences in the composite ED of the diet may significantly alter estimations of growth in juvenile Chinook Salmon. This thesis highlights the general need to refine the resolution with which we assess the diet of juvenile Chinook Salmon specifically and aquatic predators more generally.

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Chapter 2 – Percent ash-free dry weight as a robust method to estimate energy density across taxa

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2.1 Introduction

Tracing energy flow through ecosystems has been used since Lindeman (1942) as a tool to answer questions about growth, species interactions and community dynamics. An assessment of energy fluxes in ecosystems requires not only the quantification of the diet of consumers (Nielsen et al., 2018), but also a determination of the energy density (ED) of both the prey and consumers (Cummins & Wuycheck, 1971). ED is a commonly used currency in ecology to ask questions related to growth, energy budgets, waste metabolism and foraging behaviour across a diversity of species (Rodgers & Sinclair, 1997; Chen, Thompson, & Dickman, 2004; Litzow et al., 2004; Herrera, Osorio, & Mancina, 2011; Peckham et al., 2011). It is a key parameter in a wide variety of bioenergetics and growth models (e.g. Benoit-Bird, 2004; Maino & Kearney, 2015; Deslauriers, Heironimus, & Chipps, 2016) but can be quite sensitive to error (Bartell et al., 1986). This error remains an important source of variability as somatic energy content and composition can vary substantially depending on spatial context (Schultz & Conover, 1997; Ruck, Steinberg, & Canuel, 2014; Dessier et al., 2018), season sampled (Pederson & Hislop, 2001; Chen, Thompson, & Dickman, 2004), or ontogenetic stage (Woodland, Hall, & Calder, 1968; Lawson et al., 2018). Thus, accurate measurements of ED are imperative to the validity of predictions made from these models.

Bomb calorimetry is the most direct approach for measuring ED, though it is also time consuming, costly and can have sample requirements that are challenging for estimating ED of smaller species (typically at least 25 mg of dry sample is required (Cummins & Wuycheck, 1971)). When bomb calorimetry is not feasible, ED values are often borrowed from the literature or estimated using alternative methods. Proximate analysis makes use of conversion factors for major body constituents such as lipid and protein and converts them into gross energy content (e.g. Logerwell, & Schaufler, 2005; Battam et al., 2010). While proximate analysis is regularly employed in lieu of direct measurement, it entails greater time and cost requirements than bomb calorimetry. In addition, lipid and protein extractions involve intricate methods than can introduce further error into estimates. There are also no standardized conversion factors for proximate constituents, even among a single class such as fishes (values can range from 17.2-23.9 kJ/g for protein and 34.7-39.8 kJ/g for lipid; Brett 1995). As a result, ED estimates from proximate analysis can differ substantially from those obtained from bomb calorimetry (Craig, 1977).

Other inference methods have been developed based on observed relationships between organic components and ED. The most common alternative to infer ED for bioenergetics studies is through the relationship between energy content and percent dry-matter. In aquatic organisms, this relationship exists due to the negative association between percent fat and protein with water content (Craig, 1977; Flath & Diana, 1985). A predictive model to estimate ED based on these assumptions was first developed for fish by Hartman and Brandt (1995). Several such relationships have since been developed in the aquatic realm for individual species or locations (e.g. Trudel et al., 2005; Ciancio et al., 2007) as well as more generally for fish (Hartman & Brandt 1995) and terrestrial and aquatic invertebrates (James et al., 2012). The most obvious advantage of employing these models is that they greatly reduce time and cost requirements, allowing researchers to obtain quick and easy estimates of ED for a large number of samples since all that is required is drying and weighing samples.

Models used to estimate ED from dry-weight (DW) commonly assume that DW reflects the digestible energy or organic content of an organism and should thus be directly associated with ED. However, variability in inorganic material such as bone (Cameron, 1985), salt (Arai, 1997) or calcium carbonate shells (Lalli & Gilmer, 1989) between invertebrates and vertebrates as well as aquatic and terrestrial organisms may introduce error into models that predict ED, and may preclude the development of a general relationship to predict ED from DW across both aquatic and terrestrial organisms. This material typically comprises the indigestible ash-weight of organisms and can be removed from the DW fraction to represent total organic content (Lucas, 1994) or ash-free dry weight (AFDW). Hence, AFDW may provide a more accurate estimate of digestible energy across a wide range of taxa.

A second assumption made by models that estimate ED from dry-matter is that a negative relationship exists between lipid and water content (Flath & Diana, 1985). While this may be true for animals, plants and algae rely much more heavily on carbohydrates for storage as well as structure in their cell walls. As carbohydrates have a lower ED than high-energy constituents like lipids, one would expect a lower estimate of ED in these organisms for the same value of AFDW. A novel model to estimate ED from AFDW would remove the error associated with variability in inorganic matter and provide a more accurate estimate of ED while remaining economical with respect to both time and cost. This model however, would likely need to incorporate expected taxonomic differences between groups that vary greatly in proximate composition.

The current study will investigate a novel, predictive model for estimating ED using AFDW across a wide range of aquatic and terrestrial organisms. Other common predictors, including percent dry-weight, percent-protein and percent-lipid content will also be examined to compare their predictive power in estimating ED. We expect that AFDW will be a superior predictor of ED relative to DW, percent-protein and percent-lipid content. Across taxonomic groups, we also expect to observe a lower value for ED in plants than for animals at the same value of DW or AFDW due to a higher reliance on low-energy carbohydrates by algae and plants for storage and cell structure. Using AFDW would allow for the standardization among individuals with a variable component of inorganic matter that does not contribute to digestible energy for predators. AFDW also does not suffer from time and cost restraints and allows for the accurate estimation of ED values for very small organisms.

2.2 Materials & Methods

2.2.1 Data Collection

To determine the predictive power of percent ash-free dry weight in estimating the ED of both aquatic and terrestrial organisms, data were obtained from the literature that met the following selection criteria: ED was directly measured via bomb calorimetry, AFDW was measured and at least one other predictor variable was measured (either dry weight, percent protein or percent lipid content). Using the Web of Science database, the search terms “energy content”, “somatic energy”, “energy density”, “energetic value”, “caloric content”, “ash-weight”, “dry weight” and “ash-free dry weight” were used to select studies that met our criteria. Originally, all taxonomic groups were to be included. However, only two papers were found that included data for AFDW and ED in terrestrial vertebrates (20 observations; Myrcha & Pinowski, 1970; Holmes, 1976) and these records represented very low taxonomic coverage (only passerine birds). As such, we excluded terrestrial vertebrates from our analyses. Generally, papers that contained AFDW data also contained DW information, however very few also listed percent protein and percent lipid content. Thus, data were subset into two groups that contained 1) only DW and AFDW measurements and 2) DW and AFDW measurements as well as percent protein and lipid content. The two datasets were analyzed separately and all data are available in Appendix A.

2.2.2 Linear models

A series of linear models were developed for each of the two datasets. ED values (kJ/g wet weight) were plotted against predictor variables (DW, AFDW, percent protein and percent lipid) for each subset. All the data were $\log_{10}$ transformed prior to performing the analyses. Dummy variables (a value of 0 or 1) were assigned to each data point corresponding to the broad taxonomic grouping of the organism. Broad taxonomic groups included aquatic invertebrates (AI), aquatic vertebrates (AV), terrestrial invertebrates (TI) and aquatic plants and algae (APA). Dataset two did not contain any TI data. APA organisms were used in the base model and were therefore assumed as zeroes. Two other dummy variable groups were included to determine if significant differences in model predictions exist between aquatic animals (AA) and terrestrial animals, and between animals (AN) and plants. Candidate models included a single continuous predictor (AFDW, DW, percent protein or percent lipid) and a subset of non-overlapping dummy variables (e.g. AA and AI would not be included in the same model), resulting in 22 candidate models for dataset one (for AFDW and DW) and 20 candidate models per predictor for dataset two (including all predictor variables). Candidate models were limited to one continuous predictor per model due to significant co-linearity among predictors. Both model sets were compared independently using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002). Candidate models were ranked based on their AICc scores and log-likelihood (Log*L*), R^2 adjusted for number of predictors, cumulative Akaike weights (w_i) and the difference between the given and best-fitting model (Δ_i) were calculated for each model (Burnham & Anderson, 2002). The best-fitting model was determined by the lowest AICc score (a Δ_i value of 0.0), however a Δ_i of less than 2 was also considered to have substantial support (Burnham & Anderson, 2002). Any model with a Δ_i between 4 and 7 was considered to have considerably less support, and Δ_i values greater than 10 were assumed to have essentially no support. The w_i score is considered analogous to the probability that a candidate model is the best supported of the given set of models. The standardization of continuous variables to a mean of zero and standard deviation of one is recommended when interpreting the effect of dummy variables (Legendre & Legendre, 1998). However, the continuous predictors were left unstandardized as no differences in results were observed after standardization. Leaving data in this format allowed for the simpler application of models in predicting ED. All statistical analyses were conducted using R statistical software (R Core Team, 2017).

2.3 Results

2.3.1 Literature summary

Eleven publications were found that met the criteria for dataset one (publications that measured both DW and AFDW), of which 200 organisms, ontogenetic stages or seasonal records were tabulated (Appendix A). Broad taxonomic coverage included 107 records of aquatic invertebrates, 30 of aquatic vertebrates, 43 of aquatic plants and algae and 20 of terrestrial invertebrates. Spatial coverage included oceanic waters from the North and South Atlantic as well as the Pacific Ocean, freshwater data from Europe and terrestrial sources from North America and Australia. Terrestrial insects reared in the lab were also included as a source in the model (Woodland, Hall, & Calder, 1968). The temporal extent of sampling occurred in every season across a five-decade span (1962 to 2007). Three publications met our criteria for the direct measurement of ED and AFDW that also included measurements of percent protein and percent lipid content (dataset 2). These 26 organisms included 19 aquatic invertebrates, 2 aquatic plants and 5 aquatic vertebrates and were sampled in the Atlantic and Pacific Oceans between 1962 and 2007.

2.3.2 Linear models

Using dataset one, a significant positive relationship was observed between ED and DW (Figure 2.1a, $R^2 = 0.85$ $p<0.0001$). An even stronger positive relationship was observed between ED and AFDW (Figure 2.1b, $R^2 = 0.97$, $p<0.0001$). Many similar, positive relationships emerged using dataset two. ED was again significantly, positively related to DW (Figure 2.2a, $R^2 = 0.96$, $p<0.0001$). ED was also significantly, positively related to AFDW (Figure 2.2b, $R^2 = 0.99$, $p<0.0001$). ED was significantly, positively related to percent-protein, however the strength of the relationship was much less than was observed for either DW or AFDW (Figure 2.2c, $R^2 = 0.59$, $p<0.0001$). Surprisingly, ED showed no significant relationship to percent-lipid (Figure 2.2d, $R^2 = 0.00$, $p=0.3$).

2.3.3 Model Selection

AICc model selection results for dataset one revealed that all models that included AFDW as a predictor were superior to those including DW, with AIC differing by more than 310 between the best performing DW model relative to the worst performing AFDW model (Table 2.1). Of the 22 candidate models, the best supported model to predict ED was AFDW + aquatic animals (AA) + terrestrial invertebrates (TI; Table 2.1). A second model predicting ED by AFDW + aquatic invertebrates (AI) + aquatic vertebrates (AV) + TI also received substantial support, which splits AA into its two separate parameters (AI and AV). Three additional models received some support in the model selection. AFDW + AA, AFDW + AI + AV and AFDW + AN all exhibited non-zero w_i scores during model selection (Table 2.1). The R^2 value for all five of the top models was 0.98. The predictive equations including correction factors for broad taxonomic groups in these top models are presented in Table 2.2.

AICc model selection results for dataset two produced results similar to the previous dataset, with AFDW + AA ranking as the top model in the set (Table 2.3). Again, the model splitting AA into AI and AV received substantial support and AFDW + AI also received some support. All other models including AFDW as a predictor did not receive empirical support relative to the top model. All models including AFDW were followed in the model selection table by those including DW, then percent protein and lastly, percent lipids (Table 2.3). It should be noted though that all the models including AFDW or DW as predictors in the reduced dataset had high predictive power with $R^2 > 0.96$ (Table 2.3).

2.4 Discussion

We provide a robust and accurate model to estimate the ED of a taxonomically diverse group of organisms using a simple and easily calculated metric: AFDW. The tight correlation between these two variables ($R^2 = 0.97$) represents the association between total digestible energy (AFDW) and ED. Organisms of interest need only be weighed for wet and dry weights, then burned in a muffle furnace to obtain ash weight. This method produces a value for AFDW that can then be used to calculate ED using one of the equations listed in Table 2.2. This procedure takes very little time and has little to no cost requirements besides access to a drying oven and muffle furnace; hundreds of samples can be run in as little as a few days. The prerequisite technical requirements needed to operate a bomb calorimeter or to extract proximate components are also avoided. Weight requirements for the sample are only limited by the power and precision of scales used to measure AFDW. This method can be used to calculate ED for very small organisms and will also allow researchers to easily evaluate individual-level variability of ED for organisms as small as a few milligrams. The removal of ash-weight from measurements also eliminates the error associated with indigestible bone, salt or calcium carbonate fraction can vary considerably among taxa.

AFDW models were improved with the addition of dummy variables for broad taxonomic groups. Correction factors for aquatic animals (AA) and terrestrial invertebrates (TI) resulted in the need for an intercept adjustment of 0.09 and 0.04 respectively. The need for these corrections likely arose from differences between taxonomic groups covered by the dataset. Aquatic plants and algae (APA) were used in the base model to estimate ED when using dummy variables. Differences in ED among taxa for the same AFDW or DW likely arise due to differences in proximate constituents. In particular, APA have structural carbohydrates that make up their cell wall matrices, and thus have typically higher carbohydrate contents than animals (Graham, Graham, & Wilcox, 2009). Low-ED carbohydrates present in the cell walls of APA would bias the overall model towards lower ED values requiring the appropriate corrections for other taxonomic groups. TI are typically more energy dense than APA (Cummins & Wuycheck, 1971), but can have variable levels of chitin and carbohydrate that contribute to total digestible energy (Bell, 1990). Thus, an AFDW value for TI would produce a higher estimate than expected compared to APA in a model excluding dummy variables, but a lower estimate than expected for AA. By using a model set that includes correction factors for varied taxonomic groups, we provide a robust method for estimating ED across a much wider range of taxa than was available previously.

Our results suggest that AFDW is a superior predictor of ED across taxa compared to previously used metrics: DW, lipid or protein content (Table 2.3). Several authors have used constituent predictors to estimate ED of specific groups. Anthony, Roby, & Turco (2000) determined that lipid content was the best determinant of ED variability in fishes. Lipid is roughly twice as energy dense as protein and is easily mobilized for use in metabolic activity, whereas protein is typically more stable, allocated to long-term musculature associated with growth (Jobling, 1994). Both of these body components are typically translated into ED estimates using conversion factors, but can overestimate values when energetic equivalents are taken from the literature (Craig, Kenley, & Talling, 1978; Schloesser & Fabrizio, 2015). Alternatively, DW is often used as a proxy for ED instead of proximate components due to its ease of use and general applicability that avoids the need to borrow conversion values from the literature. The relationship between DW and ED exists due to the inverse relationship between lipid and water content (Flath & Diana, 1985). Thus, DW is positively related to lipid and protein content as well as ED. Hartman & Brandt (1995) first developed a general multi-species as well as species-specific models to estimate ED from DW in fish that have been used in numerous growth and bioenergetics studies (e.g. Johnson & Kitchell, 1996; Penczak et al., 1999; Utz & Hartman, 2009). Another general model has been developed specifically for invertebrates using DW (James et al., 2012) that has also been useful in practice (e.g. Deslauriers, Heironimus, & Chipps, 2016; Hartman, 2017). To our knowledge, no general model exists to estimate the ED of both invertebrates and vertebrates using AFDW as a predictor. Our results agree with previous findings that suggest DW is a strong predictor of ED ($R^2 = 0.85$), however, the removal of ash-weight from DW estimates greatly improves model performance ($R^2 = 0.97$). Initially, the inferior explanatory power of DW compared to AFDW was attributed to gelatinous zooplankton diverging substantially from the model estimating ED from DW. However, excluding these organisms from the dataset did not improve model performance in DW models.

Ash-weight may not be realistic to acquire if samples need to be retained for other purposes. In these cases, DW models could still provide useful insight (see Appendix A for full equation list of DW models). The AFDW model remains preferable due to its greater accuracy as well as its ability to directly compare aquatic invertebrates, vertebrates, aquatic plants and algae as well as terrestrial invertebrates using a single predictive model.

Presently, there is a dearth of data on the ED, DW and AFDW of terrestrial vertebrates, and is limited to passerine birds (Myrcha & Pinowski, 1970; Holmes, 1976). The best supported model presented in this paper consistently underestimates the ED values observed in passerine birds by an average of 8.2% (Figure 2.3). This difference in ED is likely due to fundamental differences in metabolic demands, between terrestrial vertebrates and other organisms examined in our model (Brown et al., 2002). Until further data are available to evaluate the performance of our model on terrestrial vertebrates, we recommend multiplying back-transformed ED results by a value of 1.08 to account for underestimation in the current model. Still, the relatively close agreement between these data and our model suggests that including terrestrial vertebrates is possible and that further development of this model could provide a general method to estimate the ED of any organism regardless of habitat or taxon.

The application of these models will be of immediate utility in bioenergetics and growth studies that require ED estimates for both consumers and their prey. Regularly, these values are taken from the literature instead of being directly measured or estimated (e.g. Moss et al., 2009; Spitz et al., 2010). Although this practice is commonplace, literature values are often unrepresentative, averaging varied taxa together or borrowing ED values from similar species (Hansen et al., 1993). This practice can often introduce substantial error in model estimates. In one example, investigators found that prey consumption was overestimated by as much as 22% when using a model that borrowed

ED values from the literature (Johnson, Pater, & Hansen, 2017). When these values were instead predicted from DW, the authors found a significant reduction in error between observed and predicted values. Analyses like this confirm the accuracy and ease with which these general, multi-species models can be employed. The benefit of our method over previous estimation models is the generality that it provides across species and systems. For instance, aquatic vertebrates typically feed across multiple trophic levels and can assimilate energy from pelagic, benthic and terrestrial systems (Pauly et al., 1998; Vander Zanden & Vadeboncoeur, 2002). The equations provided in Table 2.2 would be of particular use in these situations where researchers aim to answer questions related to growth, diet and foraging behaviour of complex and interconnected systems.

2.5 References

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Tables

Table 2.1. Log likelihood (Log*L*) and Akaike's information criterion corrected for small sample sizes (AICc) for generalized linear models relating energy density to percent dry weight (DW) and percent ash-free dry weight (AFDW), including dummy variables (value of 0 or 1) for large taxonomic groups (AI = aquatic invertebrates; AV = aquatic vertebrates; TI = terrestrial invertebrates; AA = aquatic animals; AN = animal; aquatic plants and algae were used in the base model and were not given a dummy value). The number of model parameters (*k*), cumulative Akaike weights (w_i), adjusted percent R^2 values and the difference between the given and best-fitting model (Δ_i) are presented for each candidate model.

Model	k	Log*L*	AICc	Δ_i	w_i	R^2
AFDW + AA + TI	5	273.03	-535.76	0.00	0.55	0.98
AFDW + AI + AV + TI	6	273.40	-534.37	1.39	0.27	0.98
AFDW + AA	4	270.28	-532.36	3.39	0.10	0.98
AFDW + AI + AV	5	270.42	-530.54	5.22	0.04	0.98
AFDW + AN	4	269.28	-530.36	5.39	0.04	0.98
AFDW + AI	4	255.32	-502.44	33.31	0.00	0.97
AFDW + AI + TI	5	255.33	-500.35	35.41	0.00	0.97
AFDW + AV	4	250.15	-492.09	43.67	0.00	0.97
AFDW + AV + TI	5	250.16	-490.02	45.74	0.00	0.97
AFDW	3	245.37	-484.62	51.14	0.00	0.97
AFDW + TI	4	245.92	-483.63	52.13	0.00	0.97
DW + AN	4	90.41	-172.61	363.15	0.00	0.87
DW + AI + AV + TI	6	91.79	-171.14	364.62	0.00	0.87
DW + AA + TI	5	90.59	-170.87	364.88	0.00	0.87
DW + AA	4	83.73	-159.26	376.50	0.00	0.86
DW + AI + AV	5	84.33	-158.35	377.41	0.00	0.86
DW + AV + TI	5	83.15	-155.99	379.76	0.00	0.86
DW + AV	4	80.20	-152.19	383.57	0.00	0.85
DW + AI + TI	5	80.98	-151.66	384.10	0.00	0.85
DW + AI	4	78.71	-149.22	386.53	0.00	0.85
DW + TI	4	78.64	-149.08	386.67	0.00	0.85
DW	3	77.26	-148.40	387.36	0.00	0.85

Table 2.2. Equations and correction factors (CF) for top performing ($\Delta_i < 10$) generalized linear models relating energy density to percent ash-free dry weight including dummy variables (value of 0 or 1) for large taxonomic groups (AFDW; AI = aquatic invertebrates; AV = aquatic vertebrates; TI = terrestrial invertebrates; AA = aquatic animals; AN = animals). The difference between the given and best-fitting model (Δ_i) and adjusted percent R^2 values are presented for each candidate model.

Model	Δ_i	Equation	CF	R^2
AFDW + AA + TI	0	$\log_{10}(ED) = 1.07*\log_{10}(AFDW) - 0.80$	AA = 0.09, TI = 0.04	0.98
AFDW + AI + AV + TI	1.39	$\log_{10}(ED) = 1.06*\log_{10}(AFDW) - 0.79$	AI = 0.08 , AV = 0.09 , TI = 0.04	0.98
AFDW + AA	3.39	$\log_{10}(ED) = 1.08*\log_{10}(AFDW) - 0.79$	AA = 0.07	0.98
AFDW + AI + AV	5.22	$\log_{10}(ED) = 1.07*\log_{10}(AFDW) - 0.79$	AI = 0.07 , AV = 0.08	0.98
AFDW + AN	5.39	$\log_{10}(ED) = 1.05*\log_{10}(AFDW) - 0.78$	AN = 0.08	0.98

Table 2.3. Regression statistics, log-likelihood (Log*L*) and Akaike's information criterion corrected for small sample sizes (AICc) for generalized linear models of a trimmed dataset comparing energy density values to percent ash-free dry weight (AFDW), percent dry weight (DW), percent protein content and percent lipid content including dummy variables (value of 0 or 1) for large taxonomic groups (AI = aquatic invertebrates; AV = aquatic vertebrates; AA = aquatic animals; aquatic plants and algae were used in the base model and therefore were not given a dummy value). The number of model parameters (*k*), cumulative Akaike weights (w_i), adjusted percent R^2 values and the difference between the given and best-fitting model (Δ_i) are presented for each candidate model.

Model	k	Log*L*	AICc	Δ_i	w_i	R^2
AFDW + AA	4	45.66	-81.42	0.00	0.65	0.99
AFDW + AI + AV	5	46.49	-79.97	1.45	0.32	0.99
AFDW + AI	4	42.40	-74.89	6.54	0.02	0.99
AFDW	3	39.07	-71.05	10.37	0.00	0.99
AFDW + AV	4	39.15	-68.40	13.03	0.00	0.99
DW	3	24.44	-41.79	39.63	0.00	0.96
DW + AI	4	24.85	-39.80	41.62	0.00	0.96
DW + AA	4	24.64	-39.37	42.05	0.00	0.96
DW + AV	4	24.60	-39.30	42.12	0.00	0.96
DW + AI + AV	5	24.87	-36.74	44.68	0.00	0.96
Protein + AA	4	-1.02	11.94	93.36	0.00	0.71
Protein + AI + AV	5	-0.88	14.76	96.18	0.00	0.70
Protein	3	-5.74	18.56	99.98	0.00	0.59
Protein + AI	4	-4.73	19.36	100.78	0.00	0.61
Protein + AV	4	-5.71	21.33	102.75	0.00	0.58
Lipid + AI	4	-12.48	34.87	116.29	0.00	0.29
Lipid + AI + AV	5	-12.47	37.95	119.37	0.00	0.26
Lipid + AV	4	-14.32	38.55	119.98	0.00	0.18
Lipid	3	-17.46	42.00	123.43	0.00	0.00
Lipid + AA	4	-17.28	44.47	125.89	0.00	-0.03*

*negative adjusted R^2 was obtained by fitting a model with low multiple R^2, using multiple predictors

Figures

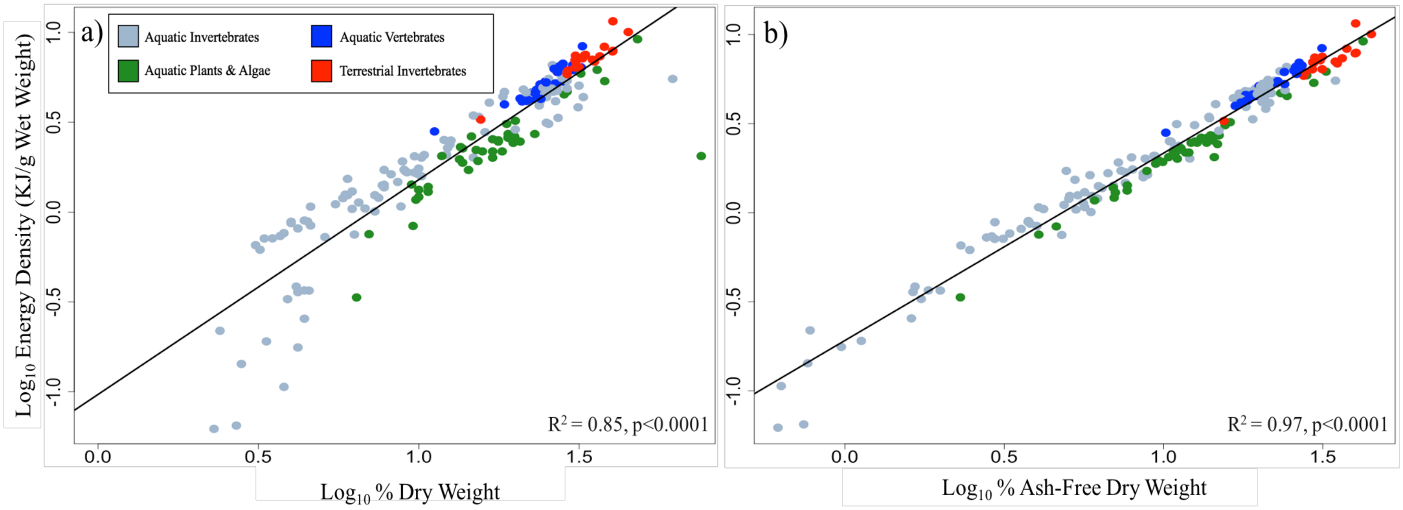

Figure 2.1. Model comparison for full dataset of literature values reporting % dry weight (a) and percent ash-free dry weight (b); both axes on a logarithmic scale.

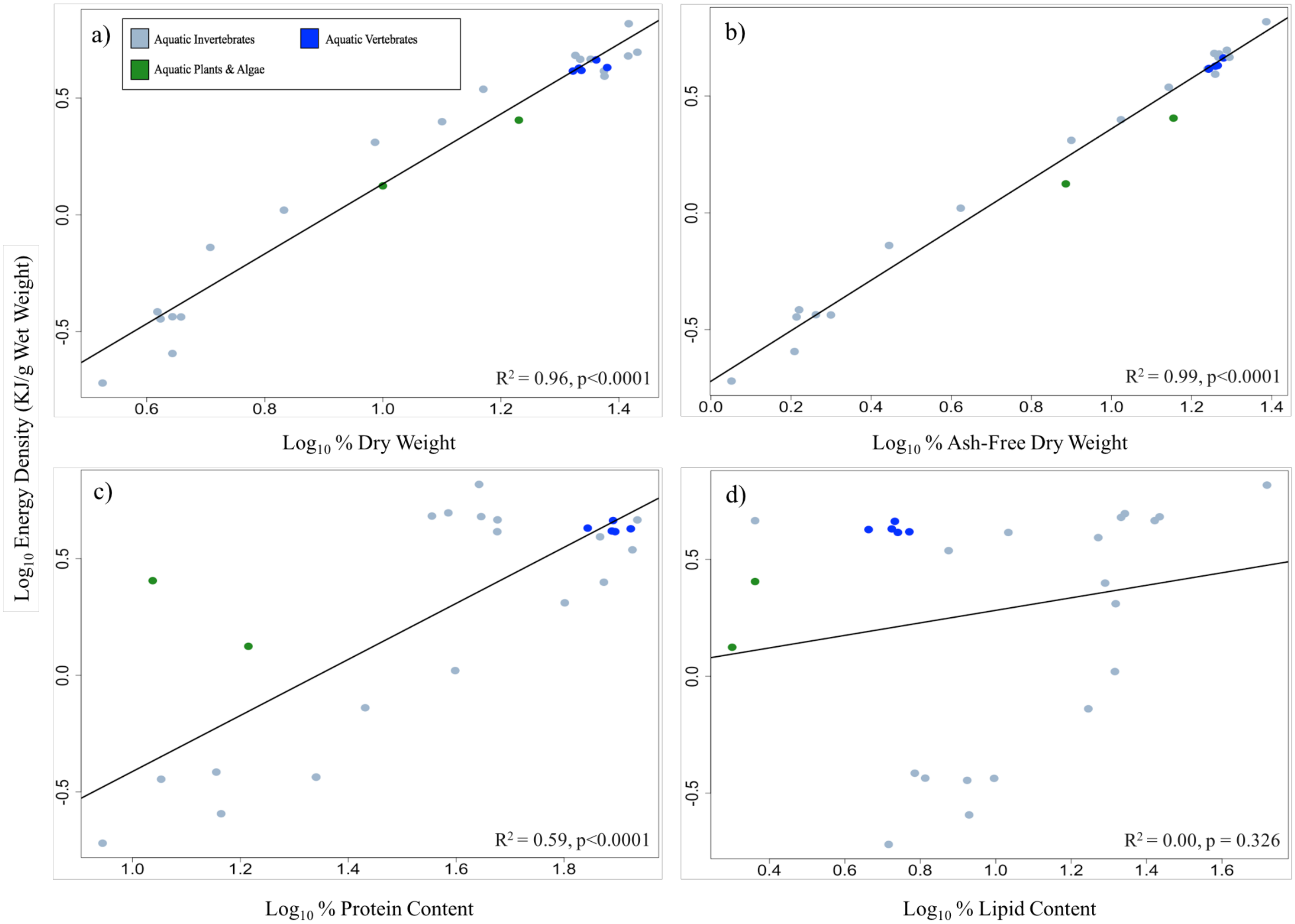

Figure 2.2. Model comparison for trimmed dataset including all hypothesized predictors of energy density: a) $\log_{10}$ percent ash-free dry weight, b) $\log_{10}$ percent dry weight, c) $\log_{10}$ percent protein content, d) $\log_{10}$ percent lipid content.

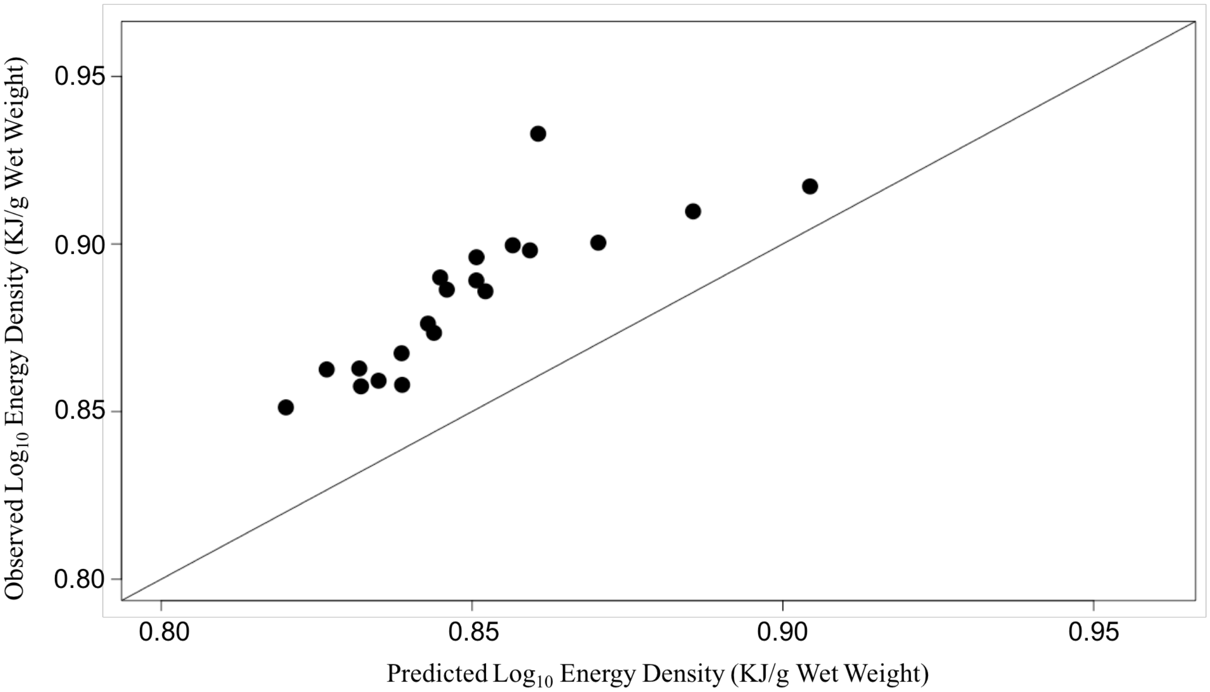

Figure 2.3. Relationship between observed and predicted values for the energy density of passerine birds investigated in Holmes (1976) and Myrcha and Pinowski (1970). Predicted values estimated using the percent ash-free dry weight to energy density model including a correction factor for animals as: $\log_{10}(ED) = 1.05*\log_{10}(AFDW) - 0.78 + 0.08$. 1:1 line plotted in figure.

Chapter 3 – Fine-scale taxonomic and spatiotemporal variability in the energy density of prey for juvenile Chinook Salmon (*Oncorhynchus tshawytscha*)

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Author Contributions: JW and FJ conceived the study and collection technique with the aid of Will Duguid (Dept. of Biology, University of Victoria), JW led data collection and analysis and wrote the manuscript; FJ contributed editorial advice.

3.1 Introduction

The growth and survival of Pacific Salmon species (*Onchorynchus spp.*) is partially dependent on conditions experienced during the early marine period (Pearcy 1992, Mortensen et al. 2000, Beamish et al. 2004, Farley et al. 2007, Duffy & Beauchamp 2011). During this time, individuals that are unable to reach a threshold size are hypothesized to perish due to an increased vulnerability to predators and an inability to meet basic metabolic demands during the winter months (Beamish & Mahnken 2001). Although this hypothesis has been met with recent challenges (Beacham et al. 2017, 2018), marine survival in salmon is still largely understood to be highly dependent on conditions experienced during this early period. Abiotic forces such as upwelling (Wells et al. 2007) and temperature (Mantua et al. 1997, Farley & Trudel 2009) have been tied to juvenile salmon growth and survival. These climatic forces drive ecosystem productivity, impacting bloom timing (Chittenden et al. 2010) and the abundance (Brodeur et al. 2003, Wells et al. 2012) and composition (Zamon & Welch 2005, Bi et al. 2011) of prey resources, which drives regional and temporal variation in growth (see Brodeur et al. 2007). While recent efforts have extensively investigated the effect of prey abundance, a significant knowledge gap continues to exist regarding the effect of prey quality on growth and survival.

Pacific Salmon abundance varies temporally and among species and regions. In the Salish Sea (Strait of Georgia and Strait of Juan de Fuca, British Columbia, Canada; and Puget Sound, Washington, USA), Chinook (*O. tshawytscha*) and Coho Salmon (*O. kisutch*) as well as Steelhead (*O. mykiss*) have experienced record low returns in the past several decades (Beamish et al. 1995, Beamish et al. 2010, Kendall et al. 2017), while other species, such as Pink (*O. gorbuscha*) and Chum Salmon (*O. keta*), have increased in abundance (Beamish et al. 2007). The Salish Sea Marine Survival Project (http://marinesurvivalproject.com/) is a binational research effort aimed to determine the causal forces driving reduced survival in Chinook, Coho and Steelhead. The present study contributes to this effort by examining fine-scale variability in the quality of invertebrate prey available to these salmon, focusing specifically on prey species of juvenile Chinook Salmon.

The diet of juvenile Chinook Salmon is highly variable through ontogeny, with a tendency towards increased fish consumption at larger sizes (Brodeur 1991). In general, juvenile Chinook Salmon feed at a higher trophic level relative to other salmon species (Brodeur & Pearcy 1990), but this trend shows significant regional variability (Brodeur et al. 2007, Hertz et al. 2015). Invertebrate species such as decapod larvae, euphausiids and amphipods can represent a significant component of the diet depending on population and year (Duffy et al. 2010, Riddell et al. 2018). For example, in-shore individuals have been observed to feed less frequently on fish than their off-shore counterparts (Duffy et al. 2010). During their first marine summer, juvenile Chinook Salmon transition from a mainly zooplanktivorous diet to a mainly piscivorous diet and the timing of this shift has been linked to growth and survival (Daly et al. 2009, Duffy et al. 2010, Litz et al. 2017). Because juvenile Chinook Salmon survival appears to be linked to the onset of piscivory, it would follow that the availability of abundant, high-quality prey to promote rapid growth prior to this shift would also be beneficial.

Prey quality, which is regularly used to explain variability in salmon growth (Trudel et al. 2007, Tiffan et al. 2014), can be expressed as the amount of energy contained per unit mass of an organism (energy density; ED). However, direct measurement of ED is rarely performed. Instead, researchers regularly borrow values from the literature and either average species together or take a single species as representative of a larger taxonomic group (e.g. Duffy et al. 2010). This practice, however, may be problematic as ED can vary considerably among similar taxa (Cummins & Wuycheck 1971), and there is substantial variability in the ED of vertebrate and invertebrate taxa preyed upon by salmon (Davis et al. 1998, Dessier et al. 2018). Furthermore, even within a species, ED can vary on both spatial (Schultz & Conover 1997, Ruck et al. 2014) and temporal scales (Wissing & Hasler 1971, Pedersen & Hislop 2001) that are not captured in single-point literature estimates. The degree to which this variability may affect energy budgets for salmon remains unknown and could represent a significant source of error in how we explain differences in growth based on prey quality.

Consequences of unaccounted variability in prey ED may be visualized using bioenergetics models. These models typically take the form:

$$\mathrm{G} = \frac{d\mathrm{W}}{\mathrm{W}\cdot dt} = p\cdot\left[C_{max} - (\mathrm{R}+\mathrm{F}+\mathrm{U})\right]\cdot\frac{\mathrm{ED}_{\mathrm{prey}}}{\mathrm{ED}_{\mathrm{predator}}}$$

where G is growth rate, C_{max} is maximum consumption rate, p is the proportion of maximum consumption rate, R is respiration or metabolism, F is egestion, U is excretion, ED_{prey} is the energy density of prey and $ED_{predator}$ is the energy density of the predator (Kitchell et al. 1977, Hansen et al. 1993). These parameters can then be manipulated to determine the effects of changing climate (Beauchamp et al. 2007, Beauchamp 2009), prey availability (Litz et al. 2018), behaviour (Jørgensen et al. 2016), or toxin accumulation (Trudel & Rasmussen 2006). However, the utility of these models relies on the input of accurate data to inform model parameters. Uncertainty in ED_{prey} can significantly alter growth projections (Bartell et al. 1986). Thus, any improvements to current estimates for diet ED will increase the accuracy of associated bioenergetics models, which could alter current interpretations on the relative importance of prey quality versus quantity (Litz et al. 2018).

ED is most accurately measured via bomb calorimetry (Cummins & Wuycheck 1971). However, this method is limited by cost, time and sample requirements and is not always feasible for assessing small organisms. Due to these limitations, several models have been developed to estimate the energy density of invertebrates and fish (Hartman & Brandt 1995, Ciancio et al. 2007, James et al. 2012). These studies derive both general and species-specific linear models to estimate ED of organisms from the ratio of dry-to-wet mass. Recently, Weil et al. (Chapter 2) developed a general model using percent ash-free dry weight as a predictor of ED. This method allows for a more accurate estimation of ED across most taxonomic groups with a single equation while maintaining the simplicity of previous dry-weight models. In the present study, we use this method to measure the ED of several prey of juvenile Chinook Salmon at the level of the individual zooplankter to determine if variability exists between closely related species and across space and time.

In this study, we aim to test the following hypotheses using the diet of juvenile Chinook Salmon as context: 1) Taxonomic variability in ED exists on a fine-scale within invertebrate prey groups; 2) Seasonal variability in ED of invertebrate prey exists over the course of early marine residence for salmon; and 3) Spatial variability in ED exists on a fine-scale for species within the same marine basin. Using recent diet data from juvenile

Chinook Salmon, we targeted invertebrate and vertebrate prey to closely match those species found during early marine residence. The implications of these previous simplifying assumptions regarding prey ED for juvenile Chinook Salmon were assessed using bioenergetics models, where we tested how growth predictions would differ under fine- and coarse-scale groupings based on prey taxonomy. In addition to testing the above hypotheses, we further refine estimates for ED in specific invertebrate prey groups and provide next steps in determining variability in ED for future researchers investigating the diet of juvenile salmon.

3.2 Methods

3.2.1 Sample Collection

We collected zooplankton samples monthly from April to September 2017 off the coast of Vancouver Island, British Columbia, Canada (Figure 3.1). Species of interest were chosen based on previous investigation into the diet of juvenile Chinook Salmon as part of a trans-national research project, the Salish Sea Marine Survival Project. Three sample sites – Saanich Inlet, Cowichan Bay and Maple Bay (Figure 3.1) – were chosen to assess variability in ED on a fine spatial scale and to ensure the collection of as many target species as possible. We deployed a 0.5m diameter zooplankton net with a 350 µm mesh size at 50m in Cowichan Bay and 100m in Saanich Inlet and Maple Bay, towing obliquely at depth through the scattering layer. Zooplankton tows were retrieved within 5 minutes of full deployment and were emptied into buckets on board the vessel. Samples were returned to the lab for processing within the same day. During the course of zooplankton sampling, one species known to be consumed by juvenile Chinook Salmon, *Hyperia medusarum,* was observed as a parasite on the large scyphozoan jellyfish *Phacellophora camtschatica*. To sample this species, jellyfish were brought on board, where *H. medusarum* were removed and returned to the lab for processing. Because we had previously observed a strong female bias for *H. medusarum* in the diet of juvenile Chinook Salmon (Weil et al. *In Press*), these individuals were separated by sex to determine if differences in ED existed between males and females of this species.

Fish samples were obtained separately from zooplankton sampling events (Oak Bay; Figure 3.1) on July 5 and 12, 2017, by dip-netting visible bait balls. Sampling in a nearby location was necessary due to the absence of visible schools of fish during zooplankton sampling. Pacific Sandlance (*Ammodytes hexapterus*) and Pacific Herring (*Clupea pallasii*) were present in these samples and were regularly captured together. Bay Pipefish (*Syngnathus leptorhynchus*) and Northern Anchovy (*Engraulis mordax*) were observed at the Institute of Ocean Science dock in Patricia Bay (Figure 3.1) during zooplankton sampling and were caught opportunistically. All fish samples were stored frozen on dry ice and returned to the lab for sorting.

3.2.2 Lab Analysis

In the lab, zooplankton samples were poured back through the cod end of the net to reduce the volume of the sample. Live samples were separated to the species level wherever possible. Decapods were sorted to the family level, as species-level differences were not discernable in live individuals for most groups. Individuals were flash frozen in liquid nitrogen to standardize wet-weight and to arrest decomposition. Fish samples were analyzed and stored whole. Samples were stored at -80°C until they could be processed further.

To determine the ED of prey organisms, we employed the estimation model provided by Weil et al. (Chapter 2). This method accurately estimates the ED of individuals using percent ash-free dry weight (AFDW) and can be used for both aquatic invertebrates and vertebrates. Following a three-hour thaw, individuals were blotted until no visible moisture was observed on a KimWipe™ and then wet-weighed on a microbalance to the nearest 0.00001g. Measurements were obtained by weighing each organism in a pre-ashed, aluminum weigh boat and subtracting the mass of the weigh boat from the total. Samples were then placed in a drying oven at 60°C for four days, or until a constant mass was reached, and then weighed again to determine dry weight. We chose 60°C to allow for rapid drying of organisms while ensuring minimal loss of organic content (Jacobs & Grant 1978). Ash-weights were determined by placing dried samples in a muffle furnace at 550°C for three hours (Cummins & Wuycheck 1971) and then re-weighing the samples. The weight of ash was subtracted from the dry-weight to obtain AFDW. Both dry- and ash-weight measurements increased with time following removal from the oven, likely gaining mass from ambient moisture in the air. To standardize measurements, the first value observed on the microbalance was used for all organisms. We attempted to minimize this error by collecting measurements on days with similar air moisture and analyzed samples as quickly as possible following removal from the drying oven or muffle furnace. ED was calculated from AFDW using the equation $\log_{10}(\mathrm{ED}) = 1.07*\log_{10}(\mathrm{AFDW}) - 0.71$.

3.2.3 Data Analysis

ED values calculated from percent ash-free dry weight were visualized between groups using means and 95% confidence intervals. Statistically, all taxonomic, temporal and spatial patterns were compared using pairwise post-hoc Wilcoxon rank sum tests between taxa, including a Benjamini-Hochberg p-value adjustment for multiple comparisons (Benjamini & Hochberg 1995). Taxa were compared within broad groups that are typically averaged in diet studies (e.g. decapods, Duffy et al. 2010). Temporal differences in ED were assessed in species/groups that were collected in more than four months. Spatial differences in ED were assessed by comparing ED values by site in species that were sampled at all three locations. All statistical analyses were computed using R version 3.4.1 (R Core Team 2017).

3.2.4 Bioenergetics Modelling

To assess the degree that variability in ED may affect growth, fine-scale ED values were compared to coarse estimates for a 2015 dataset of juvenile Chinook Salmon diets collected in the same sampling area as the present study (Duguid et al. *Unpubl. Data*). Chinook Salmon stomach contents were sampled non-lethally using gastric lavage (Duguid & Juanes 2017) and were preserved in 5% formalin in seawater. Stomach contents were identified to the same taxonomic level as the present study, except for brachyuran zoeae, which were not classified to the family level. Stomach contents were blotted on a KimWipe™ and weighed for wet-weight. Using these measurements, we determined the proportional contribution of each item to the diet and multiplied its value by either a fine-or coarse-scale ED for that species/group. The average of these values was taken as the composite ED for the diet of each juvenile Chinook Salmon sampled. Coarse-scale ED values for prey were taken from the literature (Table 3.1 in Duffy et al. 2010). For prey groups where a fine-scale ED was not obtained during our sampling, ED was left at its coarse value. Any fish that did not contain prey sampled during the 2017 season were excluded from comparisons between fine and coarse scale ED. The difference between composite fine and coarse scale prey EDs were calculated and used as parameters in a bioenergetics model.

Using the “Wisconsin” bioenergetics model provided by Deslauriers et al. (2017), we projected the growth trajectories of juvenile Chinook Salmon during the first marine summer under variable prey ED conditions. We used physiological parameters provided for Chinook Salmon (Stewart & Ibarra 1991, Plumb & Moffitt 2015) and a seasonal temperature curve from April to October 2015 provided by Ocean Networks Canada (http://www.oceannetworks.ca/data-tools). Predator ED was set constant at 4200 J/g throughout the simulation based on values calculated for juvenile Chinook Salmon in the Salish Sea (Beauchamp, *Unpubl. Data*). Initial weight was set to 4-grams (average of unclipped juvenile Chinook sampled in 2010-2013; Chittenden et al. 2018) to simulate the growth of a typical juvenile Chinook Salmon entering the marine environment. Simulations were run for 180 days to simulate growth between ocean entry in April and the end of the first marine summer in September. Growth was compared for fish differing in composite diet ED, calculated on either a coarse or fine scale. A second comparison was made using the maximum observed difference between coarse and fine-scale estimates. The proportion of maximum consumption rate (C_{max}) was set at 0.25, 0.5 or 1.0 to assess the effect of maximum consumption on growth with varying values of ED.

3.3 Results

3.3.1 Taxonomic Variability in ED

Zooplankton sampling resulted in the collection of 1496 individuals from 18 tows over six discrete sampling days. 71 fish samples were collected over two separate sampling days. Despite these efforts, we did not obtain sufficient sample sizes to fully explore the variability in prey ED for all items detected in juvenile Chinook Salmon diet. However, we were able to obtain sufficient sample sizes to make meaningful comparisons for a few key species, and thus, we have focussed our fine-scale variability on: decapod larvae (zoeae and megalopae) and amphipods. The ED values for samples obtained during the 2017 sampling season are presented in Table 3.1. ED values ranged from a mean of 2175 ± 870 J/g (mean ± 1 SD) for *Octopus spp.* to a mean of 5256 ± 537 J/g for Pacific Sandlance (Figure 3.2). *Euphausia pacifica, Themisto pacifica* and copepods were the most prevalent invertebrate species observed in zooplankton samples.

Decapod larvae are typically grouped together into one taxonomic category for the purposes of bioenergetic modelling for salmon. However, we observed a diversity of decapod larvae in zooplankton collections. Seven families of decapod zoeae were observed: F: Cancridae, F: Grapsidae, F: Majidae, F: Pinnotheridae, F: Xanthidae, F: Paguridae and F: Porcellanidae. For megalopal stages, F: Pinnotheridae were not observed, however all other families observed as zoeae were also observed as megalopae. Mean ED values ranged from 2238 ± 977 J/g (F: Xanthidae) to 3164 ± 589 J/g (F: Majidae) for zoeae and were generally higher for megalopae, with values ranging from 2727 ± 768 J/g (F: Porcellanidae) to 4221 ± 285 J/g (F: Paguridae) (Table 3.1). The overall mean ED for decapod megalopae was consistently greater than for zoeae when families were grouped together (Figure 3.3, p<0.0001). When separated, F: Majidae (p=0.081) and F: Porcellanidae (p=0.538) showed no significant difference between zoeal and megalopal stage ED, but all other comparisons were significantly different. When comparing within the decapod zoeae, F: Grapsidae had a significantly greater ED than F: Cancridae and F: Paguridae and F: Porcellanidae had significantly greater ED than F: Cancridae and F: Paguridae (see Appendix B). Within the megalopae, F: Grapsidae ED was significantly greater than F: Cancridae and F: Xanthidae, F: Paguridae ED was significantly greater than F: Cancridae , F: Porcellanidae and F: Xanthidae and F: Majidae ED was significantly greater than F: Porcellanidae (see Appendix B).

Three amphipod species were observed in zooplankton samples in 2017: *Hyperia medusarum* (2516 ± 382 J/g), *Themisto pacifica* (3397 ± 696 J/g) and *Cyphocaris challengerii* (4289 ± 977 J/g). ED values for all three species were significantly different from one another (Figure 3.4; see Appendix B). Additional variability in ED was observed when *H. medusarum* was separated by sex (Figure 3.5). Females had significantly higher EDs compared to males (p=0.004), with a mean female ED of 2593 ± 385 J/g and a mean male ED of 2387 ± 344 J/g.

3.3.2 Temporal and Spatial Variability in ED

Six species groups were observed in greater than four months and were assessed for temporal changes in ED throughout the season (Table 3.1). Two additional groups, Caridean zoeae and F: Grapsidae megalopae, were observed in greater than four months, but were not included in temporal analyses because of poor sample sizes (< 3 individuals) in most months. Temporal patterns were variable between species and no consistent, statistically significant patterns emerged between months for all species (see Appendix B, Table B.3). Cancrid zoeae had a significantly lower ED in May than in other months (Figure 3.6A). From June through September, cancrid zoeae ED did not vary significantly. Cancrid megalopae showed a general increasing trend in ED throughout the summer (June – September) but this trend was not significant (Figure 3.6B). *T. pacifica* had a significantly lower ED in April compared to June through August, where ED did not change significantly (Figure 3.6C). *T. pacifica* showed a significant decrease in ED between August and September, returning to levels observed in April of that year. *C. challengerii* ED was significantly greater in June compared to April, July and August, however this difference was not significant in May or September. ED values for *C. challengerii* were also significantly greater in September compared to all months except June (Figure 3.6D). Copepods (not separated to the species level) showed minor variability in ED between May and September, decreasing significantly between July and August before increasing back to values experienced earlier in the year in September (Figure 3.6E). *E. pacifica* showed a significant increase in ED in June relative to all other months (Figure 3.6F). ED was also significantly greater in April than was observed in May and July through September, however this difference was much less than was observed in June (mean of 3428 J/g in April compared to 3896 J/g in September).

Four species groups were observed in all three sampling sites and were assessed for fine-scale spatial variability in ED: Copepods, *C. challengerii*, F: Cancridae megalopae and *T. pacifica.* None of these groups exhibited any significant differences in ED between sampling regions (see Appendix B, Table B.4).

3.3.3 Bioenergetic & Growth Differences

The diets of 338 juvenile Chinook Salmon were sampled by Duguid et al. (*Unpubl. Data*) during their 2015 sampling season. One hundred and fifty-nine of these diets contained species that were observed during 2017 sampling, therefore, differing fine and coarse scale ED estimates could be applied. Mean coarse-scale ED for these diets was 3274 ± 633 J/g and mean fine-scale ED was 3411 ± 587 J/g. Differences between fine and coarse scale estimates of composite diet ED ranged from -254 J/g to 783 J/g (Figure 3.7). The mean of this difference was relatively small (137 J/g ± 130 J/g). Five fish were observed with a greater than 450 J/g difference between fine and coarse values and the maximum value for this difference was 783 J/g. The majority of prey volume for fish with >450 J/g differences in ED was represented by *Themisto pacifica* and F: Cancridae megalopae. These two groups both differed greatly from coarse literature values for ED and drove the majority of observed differences.

The growth projection for a 4-gram juvenile Chinook Salmon using average coarse scale composite ED was consistently lower than the projection using fine-scale ED, however, this difference was relatively small for all rates of C_{max} (Figure 3.8). For a C_{max} of 0.25, growth was 10.1% (0.6g) greater for fine-scale compared to coarse-scale ED estimates at the end of the simulation. For C_{max} values of 0.50, juvenile Chinook Salmon were 12.3% (4.3g) heavier when using fine-scale estimates, and 13.2% (29.7g) larger when C_{max} was equal to 1.00. After the first 30 days of simulation, the differential between mean fine- and coarse-scale estimations was less than five percent for all levels of C_{max}. When using the maximum difference observed in a single fish between fine- and coarse-scale ED estimates, the simulated difference in growth was much more pronounced. After 180 days, the growth differential was 82% (2.8g) greater for a C_{max} of 0.25, 109.9% greater for a C_{max} of 0.5 (18.9g) and 125.2% (130.3g) greater for a C_{max} of 1.00.

3.4 Discussion

Several invertebrate prey found in the diet of juvenile Chinook Salmon exhibited variability in ED at the species or family level. In the past, this variability was not accounted for in estimates of diet ED, where prey proportions were multiplied by individual ED for broad taxonomic groups. Decapod megalopae had a greater average ED than zoeae and significant variability existed between families. Amphipods showed variability between species, spanning a differential of several thousand joules per gram. Within one amphipod species, *Hyperia medusarum,* significant differences between female and male ED were observed. Temporal variability in ED was observed for some, but not all groups and no consistent monthly differences were observed. No significant spatial variability was observed between sites for any species investigated. By quantifying ED differences between coarse- and fine-scale estimates of ED in a few key inverebrate groups, we identified the potential magnitude of error associated with misrepresenting prey ED in bioenergetics models. The magnitude of this error was not large on average, but in some cases represented more than a twofold underestimation of growth over a 180-day period.

3.4.1 Taxonomic Variability in ED

Assessing diet composition and its effect on growth for juvenile salmon typically involves grouping species together into broader taxonomic groups. This procedure is done to facilitate analysis and the interpretation of results between prey groups (Sweeting & Beamish 2009) or due to the necessity of acquiring large sample sizes when at sea (Trudel et al. 2018). Indeed, many studies typically use ED values for broad groups to make inferences about the effect of prey quality on growth (e.g. Duffy et al. 2010, Litz et al. 2017). These studies typically borrow ED estimates from a few key sources (e.g. Davis 1993, Davis et al. 1998) and evaluate composite diet ED based on these values. In this study, we show that significant differences exist between species that are typically grouped together. Considering the species composition of these broad groups may alter current interpretations of several studies and provide useful insights for future work.

Typically, fish are considered to be a higher quality food source compared to decapod zoeae and megalopae (Davis 1993, Boldt & Haldorson 2002). Here, we show that several families of decapod megalopae (F: Grapsidae, F: Majidae and F: Paguridae) have relatively high mean ED values (range of 3776 to 4221 J/g) that fall well within the range of fish EDs (Davis et al. 1998). In regions or years where grapsid, majid and pagurid megalopae make up a large component of the zooplankton relative to other species and larval stages, juvenile Salmon may receive an energetic advantage rivalling that of increased fish abundance. In coastal Oregon, USA, Daly et al. (2009) suggested that Chinook Salmon, being more selective, ate a higher quality diet consisting mainly of fish relative to Coho Salmon (*O. kisutch*) to compensate for a lower consumption rate. However, Chinook Salmon in this region also consumed considerably more decapods by weight than Coho Salmon. Thus, it is possible that the consumption of high-quality decapods could also be driving this difference. In a similar study in Southeast Alaska, Weitkamp & Sturdevant (2008) found that Coho Salmon consumed far more decapod larvae than Chinook Salmon, that consumed principally fish. In this study, survival in Coho was far greater than for Chinook Salmon. The authors reasoned that a higher consumption rate in Coho Salmon was responsible and suggested that consumption rate (diet quantity) was more important than prey quality. Our results suggest the possibility of an alternative hypothesis: that these Coho Salmon were feeding on a greater proportion of high-quality decapod groups. This would lend support to the role of diet quality in the growth of salmon in this region. Unfortunately, without a fine-scale description of the decapods consumed, it is impossible to test these hypotheses. Future investigations into the diet of juvenile Salmon should increase the taxonomic scale with which prey groups are assessed to test these hypotheses.

Amphipods have been of particular interest in salmon feeding biology over the past several decades. Several studies have found amphipods, in particular hyperiids, to be important diet items to juvenile Salmon throughout their range (Neville & Beamish 1999, Schabetsberger et al. 2003, Bollens et al. 2010). Beamish et al. (2016) found strong selectivity for two hyperiid species, *T. pacifica* and *Primno abyssalis*, in juvenile Sockeye Salmon migrating from the Harrison River in British Columbia, Canada. The authors hypothesized that enhanced productivity in this stock was tied to feeding on these two species following ocean entry. We found *T. pacifica* to be a relatively high-quality food item (mean of 3397 J/g), lending support to this hypothesis. Other amphipods observed in 2017 were found to vary significantly in ED. *C. challengerii* is a pelagic gammarid amphipod that we found to be highly nutritious (mean of 4289 J/g) and abundant in 2017 but is typically rare in the diet of juvenile Chinook Salmon (Argue et al. 1986, Brodeur & Pearcy 1990, Schabetsberger et al. 2003, Duguid et al. *Unpubl. data*). Conversely, *H. medusarum* was found to be of low-quality (mean 2516 J/g), yet was more regularly found in the diet of juvenile Chinook Salmon in 2015. The regular occurrence of both *T. pacifica* and *H. medusarum* in the diet of juvenile Salmon may be due to their association with gelatinous zooplankton (Harbison et al. 1977), facilitating their capture. Juvenile Chinook Salmon may seek out aggregations of gelatinous zooplankton to feed upon associated hyperiid prey (Schabetsberger et al. 2003). In this case, juvenile Chinook Salmon may be choosing a lower-quality food item to reduce the effort associated with capture for pelagic amphipods.

Juvenile Chinook Salmon are visually oriented, selective predators that make feeding choices based on the size and pigmentation of prey (Schabetsberger et al. 2003). Juvenile Chinook Salmon may select individual hyperiid amphipods, *H. medusarum*, based on size and sex, feeding specifically on large, female individuals (Weil et al. *In Press*). In this study, we show that the ED of *H. medusarum* is significantly greater in females (mean of 2593 J/g) than in males (mean of 2387 J/g). Thus, it is possible that females are being targeted for their greater energetic content. Similar behaviour has been observed for Baltic Herring, *Clupea harengus* (Sandström 1980, Flinkman et al. 1992) and other North Sea pelagic fish (Van Ginderdeuren et al. 2014) that preferentially target large, female copepods over males. This feeding pattern may represent a more widespread phenomenon in visually oriented predators than is currently appreciated.

Analytical sources of error produced through our drying and ashing techniques could have introduced error into ED estimates. In the literature, there are several accepted procedures for drying time and oven temperature when collecting dry- and ash-weights (Cummins & Wuycheck 1971). These values vary substantially depending on the chemical composition of the organism of interest. Further, samples that were removed from the drying oven and muffle furnace gained weight with time, presumably from their contact with moisture in the air. The percent change in weight varied depending on the total weight of the sample, with estimates for smaller organisms containing greater error than was observed for larger organisms. Future studies could minimize this effect by storing samples in a desiccator when taking measurements for multiple samples, and by weighing samples in an arid lab environment.

Due to difficulties in collecting all species of interest, the initial goal for this study of quantifying taxonomic variability for the entire diet of juvenile Chinook Salmon could not be met. Thus, our scope was narrowed to focus on increasing the precision of ED estimates and documenting variability in key groups. The degree to which variability was observed in decapod and amphipod groups serves as an indicator that substantial variability likely exists within other species that are typically grouped together. Future investigation into species- and stage-specific ED values and the temporal monitoring of these groups will provide further insight into the role of prey quality in the diet of juvenile Chinook Salmon and other marine predators.

3.4.2 Temporal and Spatial Variability in ED

Temporal variability was observed between months for most species investigated. No consistent monthly maxima were observed across the six species investigated. Tyler

(1973) found similar variability in invertebrate ED in the North Atlantic, with some species showing an increased ED during summer months and others showing no specific trend. Tyler (1973) also observed maxima and minima in ED during different months depending on species and attributed these differences to variability in feeding, reproductive or molting cycles. It is likely that a similar explanation applies to samples collected in 2017. Unfortunately, limited life history and molt timing data exists for larval invertebrates and only general descriptions of feeding patterns are available. *Themisto pacifica* and *C. challengerii* are described as mainly carnivorous species that feed on copepods and small amphipods (Haro-Garay 2003). Despite their similar feeding habits, both of these species exhibited temporal ED patterns differing in direction and month. *E. pacifica* has a selectively omnivorous diet, suspension feeding on phytoplankton when abundant and switching to heterotrophic feeding when phytoplankton decrease below a threshold density (Mauchline 1967, Nakagawa et al. 2001). A switch to heterotrophic prey in the summer months could explain the observed increase in ED in June, however we would also expect that trend to continue through July and August, which we did not observe. As feeding habit does little to explain the observed temporal differences in ED, reproductive variables may provide better insight. However, to date, no studies have examined the reproductive cycle of *T. pacifica* or *C. challengerii* in the Salish Sea. The key to understanding species-specific temporal variability in ED may come from future investigation into the life history and trophic ecology of these species.

Three groups (cancrid zoeae, megalopae and copepods) that we investigated for temporal variability were not classified to the species level. In these groups, temporal ED differences may be due to fine-species and stage-level variability. Copepods have been investigated thoroughly and exhibit substantial variability by species and stage (Higgs et al. 1995). Few studies have investigated stage and species level ED variability within crab zoeae and megalopae, however, as these groups exhibit a complexity in larval growth similar to copepods, one might expect similar variability to exist.

We did not observe any spatial variability in ED between sites separated by approximately 18 km. Other studies have shown regional and latitudinal variability in the ED of zooplankton (Schultz & Conover 1997, Ruck et al. 2014). The spatial scale we examined in the present study may not have been sufficient to detect regional patterns. As the species we examined (Copepods, *C. challengerii*, F: Cancridae megalopae and *T. pacifica*) are fully planktonic, it is likely that they were transported among sites by oceanographic processes and represent the same prey community. This result may provide reassurance to researchers sampling multiple sites close in space by demonstrating that they can consider a single species' ED as uniform between sites.

3.4.3 Bioenergetics and Growth Effects

We provide evidence that imprecise estimates of ED can introduce error into final growth projections calculated through bioenergetics models. On average, we found the difference between coarse- and fine-scale estimates of composite ED to be small (mean of 137 J/g), however in some cases the error introduced was considerable (up to 783 J/g). This error between coarse- and fine-scale estimates may have significant consequences for how we interpret the output of bioenergetics models. Composite diet ED has been linked to optimal growth temperature and thermal tolerances in Pacific Salmon (Beauchamp 2009). By increasing ED, growth rates were shown to increase especially at higher temperatures. If similar errors to what we observed in the present study exist in analyses in the past, optimal growth temperature and thermal tolerances may have been underestimated. Trudel et al. (2002) simulated growth in Coho Salmon (*O. kisutch*) between diets differing by similar values (837 J/g) to what was observed in the extreme case in the present study (783 J/g). Based on the two-fold difference in growth that they observed over a 180-day period, the authors concluded that the composition of the prey community, as opposed to consumption and metabolism, mediated growth in these fish. We observed similar growth differentials in the present study. Thus, the error that we describe for coarse-scale estimates of ED may rival in magnitude differences in prey composition observed by Trudel et al. (2002).

Bioenergetics models require the validation of input parameters through laboratory analysis and field measurement to confirm the accuracy of their predictions (Hansen et al. 1993). Borrowing parameter estimates from similar species is commonplace in bioenergetics modelling, but can produce a lack of agreement between model predictions and collected data (Ney 1993, Chipps & Wahl 2008). Here, we show that the average difference between fine- and coarse-scale estimates of prey ED can range from 10.1 to 13.2% of final growth estimates, depending on consumption rate. This value falls within the range of other similar errors in parameter estimates. One of the more common errors introduced comes from borrowing predator ED values from larger, mature fish for juveniles (Trudel et al. 2004, 2005). In our simulations, we used field observations of ED for juvenile Chinook Salmon collected from nearby Puget Sound (Beauchamp, *Unpubl. Data*) to avoid this error. The extent of error in growth projections that results from misrepresenting prey ED should be further quantified in future studies by expanding this work to a greater diversity of known prey of juvenile Chinook Salmon.

The mean differential between fine- and coarse-scale estimates of ED was not substantial during the first 30 days, representing less than a five-percent variance between estimates. At the end of the 180-day simulation, we observed a substantial deviation in growth between estimates of mean coarse- and fine-scale ED. However, the assumption that prey ED did not vary over the course of the 180-day simulation period was likely unrealistic. Juvenile Chinook Salmon diet can vary regionally (Brodeur et al. 2007, Hertz et al. 2015), temporally (Thayer et al. 2014), and throughout ontogeny (Duffy et al. 2010). Characteristic changes in diet composition include a switch in feeding mode to piscivory during the late summer for juvenile Chinook Salmon (Daly et al. 2009, Duffy et al. 2010, Litz et al. 2017). Diet composition may also revert back to a mainly zooplanktivorous diet in September in some individuals (Dale et al. 2017, Litz et al. 2017). Future characterization of model error introduced through imprecise prey characterization should involve accounting for these temporal changes in diet composition. A temporally staged model of changes in diet, coupled with variability between fine- and coarse scale ED estimates, would give a more precise estimation of the effect of fine-scale resolution on growth estimates.

3. 5 References

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Tables

Table 3.1. Sample size (n), mean energy density (ED), standard deviation (SD) and coefficients of variation (CV) for all groups captured during the 2017 sampling season including an indicator (*) for months where a group was observed.

Species/Group	n	mean	SD	CV	April	May	June	July	August	September
Copepods	88	2729	725	26.6		*	*	*	*	*
Octopus	5	2175	870	40.0	*			*		
Cumaceans	1	2823	NA	NA		*				
Mysids	2	2858	174	6.1						*
Decapod Zoea										
F: Cancridae	75	2640	710	26.9		*	*	*	*	*
F: Grapsidae	18	3127	421	13.5				*	*	*
F: Majidae	6	3164	589	18.6				*	*	
F: Paguridae	23	2349	755	32.1		*	*	*		
F: Porcellanidae	18	3127	421	13.5				*	*	*
F: Xanthidae	3	2238	977	43.7				*	*	
F: Pinnotheridae	10	3160	920	29.1			*		*	
Decapod Megalope										
F: Cancridae	106	3303	1005	30.4			*	*	*	*
F: Grapsidae	89	3776	988	26.2			*	*	*	*
F: Majidae	8	3902	607	15.6		*	*			
F: Paguridae	17	4221	285	6.7			*			
F: Porcellanidae	4	2727	768	28.2			*			*
F: Xanthidae	39	3189	910	28.5			*	*	*	
Caridean Zoea	54	3584	910	25.4		*	*	*	*	*
Caridean Adult	3	2873	313	10.9						*
Euphausiids										
Euphausia pacifica	251	3411	421	12.3	*	*	*	*	*	*
Thysanoessa spinifera	1	3525	NA	NA			*			
Euphausiid furcillia	4	4069	1254	30.8			*			*
Amphipods										
F: Gammaridae (Unidentified)	8	3946	795	20.1	*	*	*			
Hyperia medusarum	141	2516	382	15.2			*			*
Hyperia medusarum (adult female)	73	2593	385	14.8			*			*
Hyperia medusarum (adult male)	44	2387	344	14.4			*			*
Hyperia medusarum (juv. female)	12	2596	465	17.9			*			*
Hyperia medusarum (juv. male)	12	2690	346	12.9			*			*
Cyphocaris challengerii	171	4289	977	22.8	*	*	*	*	*	*
Themisto pacifica	210	3397	696	20.5	*	*	*	*	*	*
Fish										
Clupea pallasii	36	3925.1	237.9	6.1				*		
Engraulis mordax	4	4332.3	66.0	1.5						*
Ammodytes personatus	30	5255.9	537.1	10.2				*		
F. Sygnathidae	1	4900.7	NA	NA						*

Figures

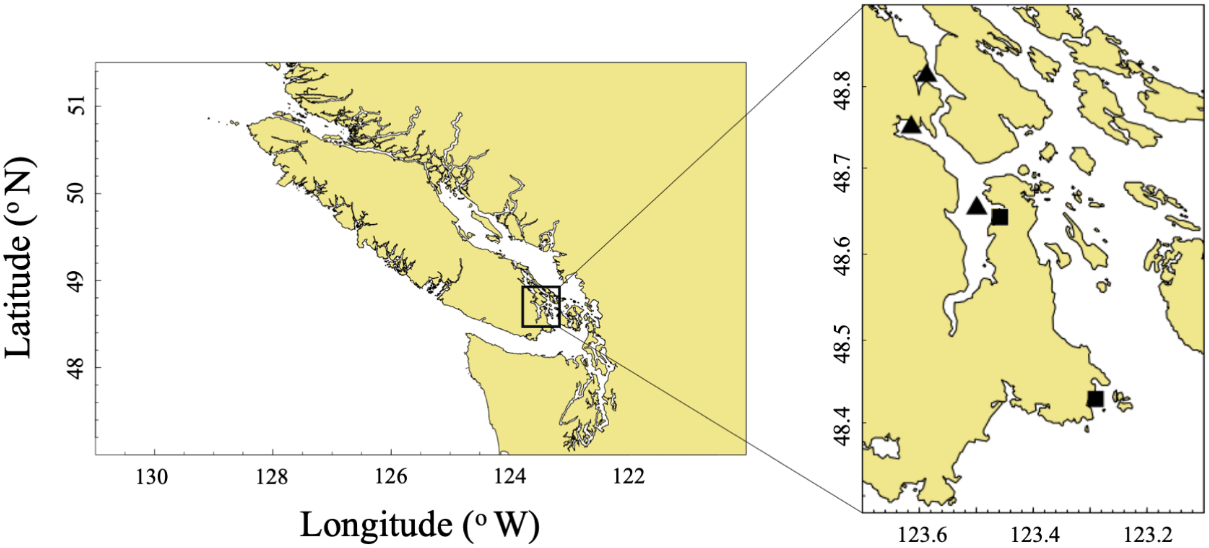

Figure 3.1. Sampling sites off the coast of Vancouver Island, British Columbia, Canada. ▲= zooplankton sampling sites – (from top to bottom) Maple Bay, Cowichan Bay, Saanich Inlet; ■ = juvenile fish sampling sites – (from top to bottom) Patricia Bay, Oak Bay.

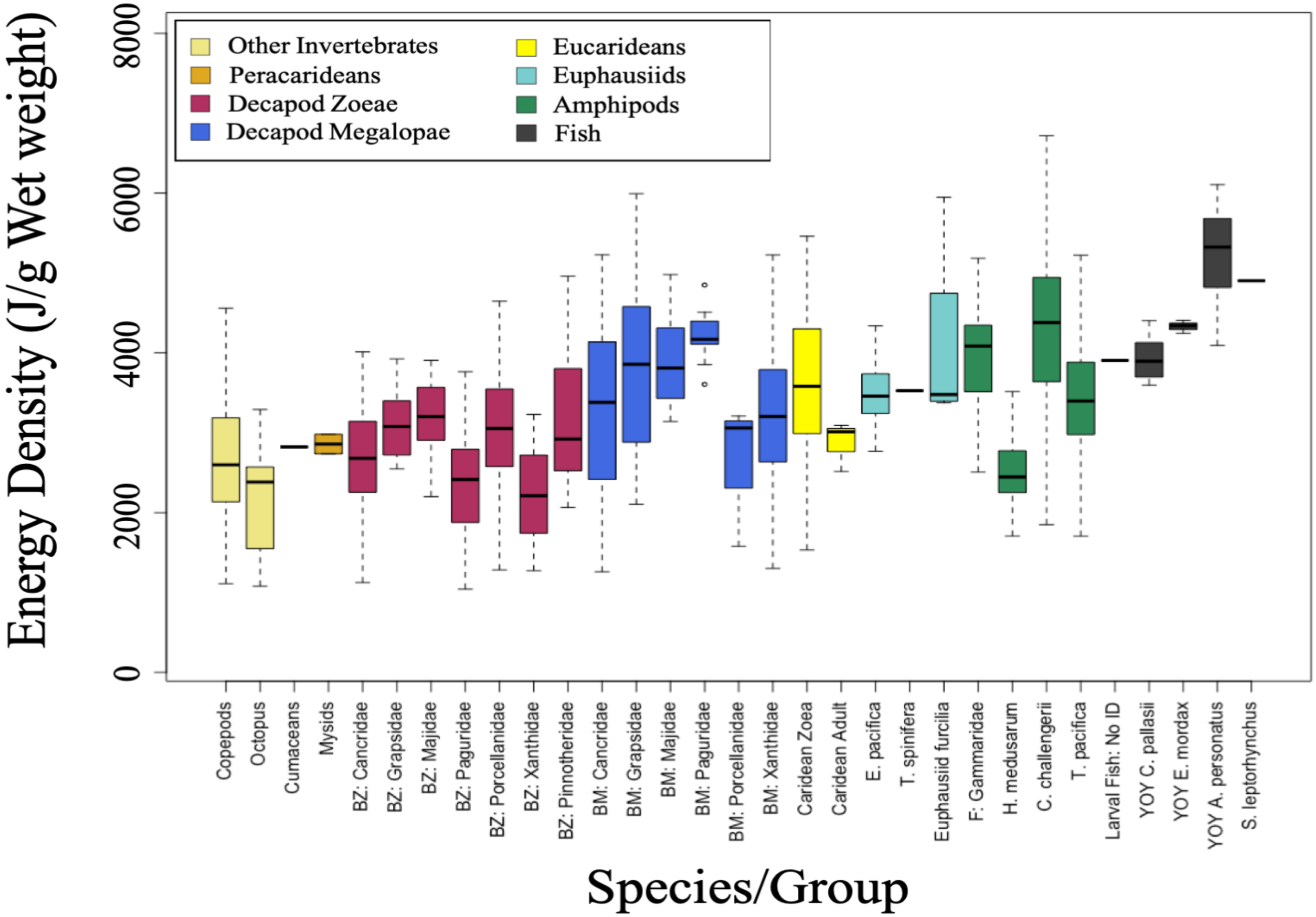

Figure 3.2. Boxplots displaying the range of energy density values for all species or groups obtained during 2017 sampling season. BZ = Brachyuran Zoeae; BM = Brachyuran Megalopae; YOY = Young of the Year.

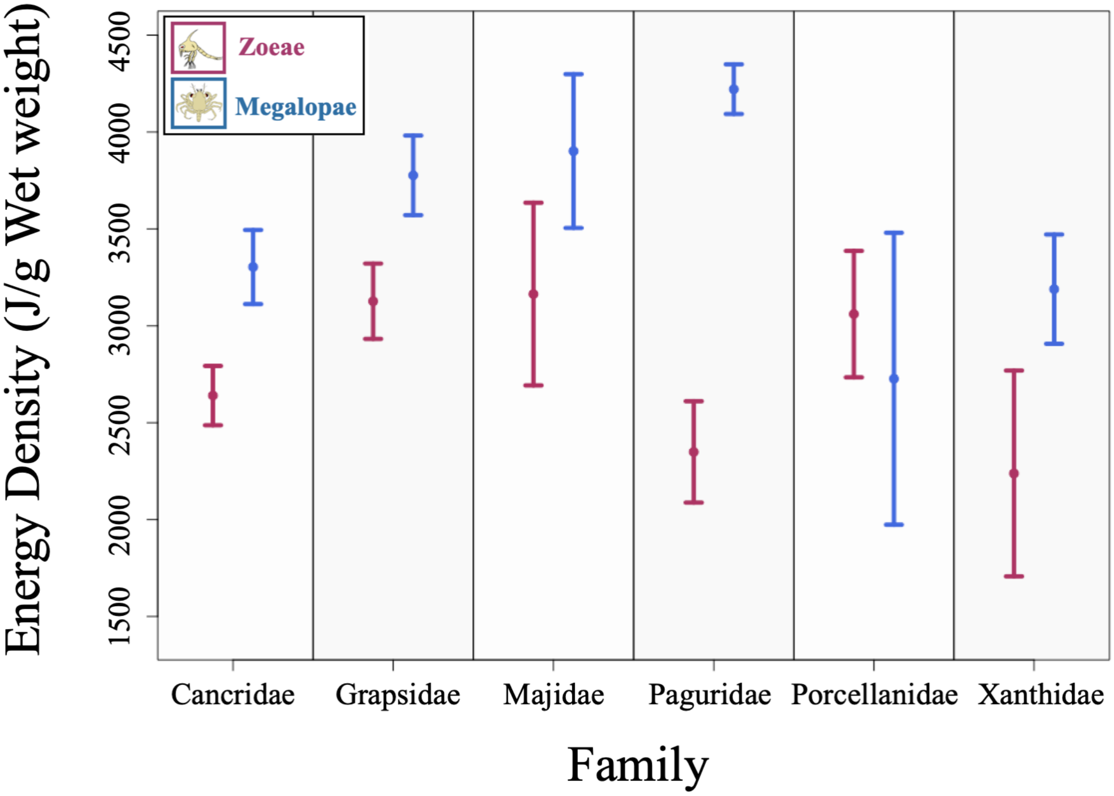

Figure 3.3. Mean energy density (ED) and 95% confidence limits for crab zoeae (pink) and megalopae (blue) separated by family.

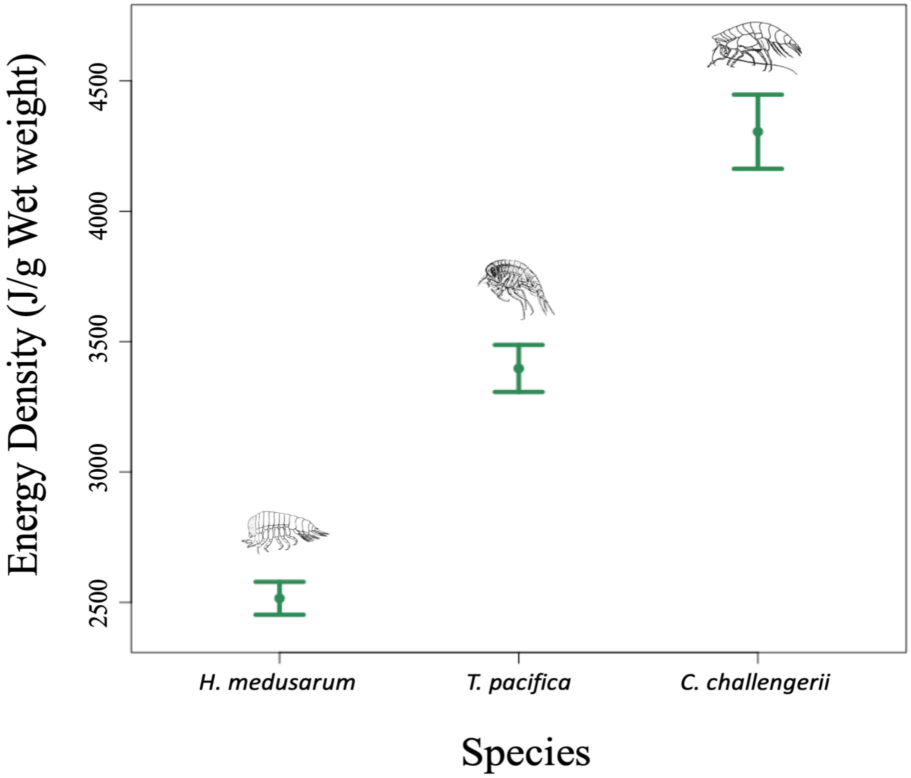

Figure 3.4. Mean energy density (ED) and 95% confidence limits for amphipod species found in the diet of juvenile Chinook Salmon: *Hyperia medusarum, Themisto pacifica* and *Cyphocaris challengerii*.

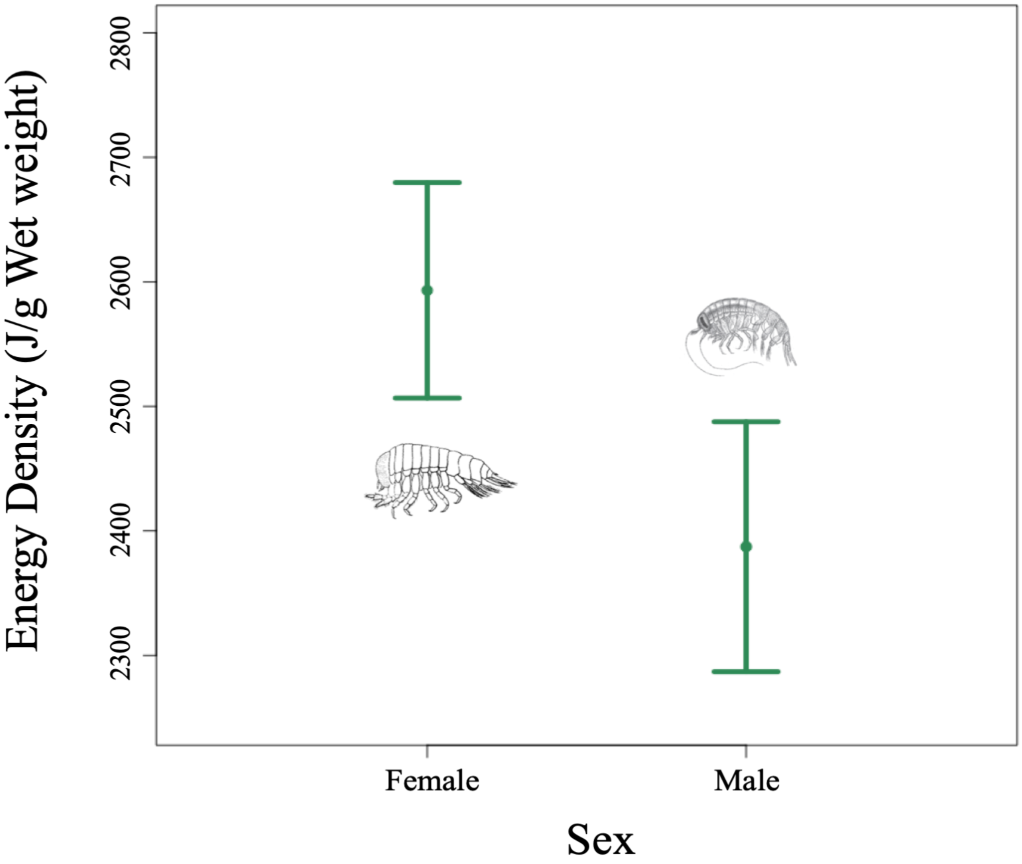

Figure 3.5. Mean energy density (ED) and 95% confidence limits for female and male *Hyperia medusarum*.

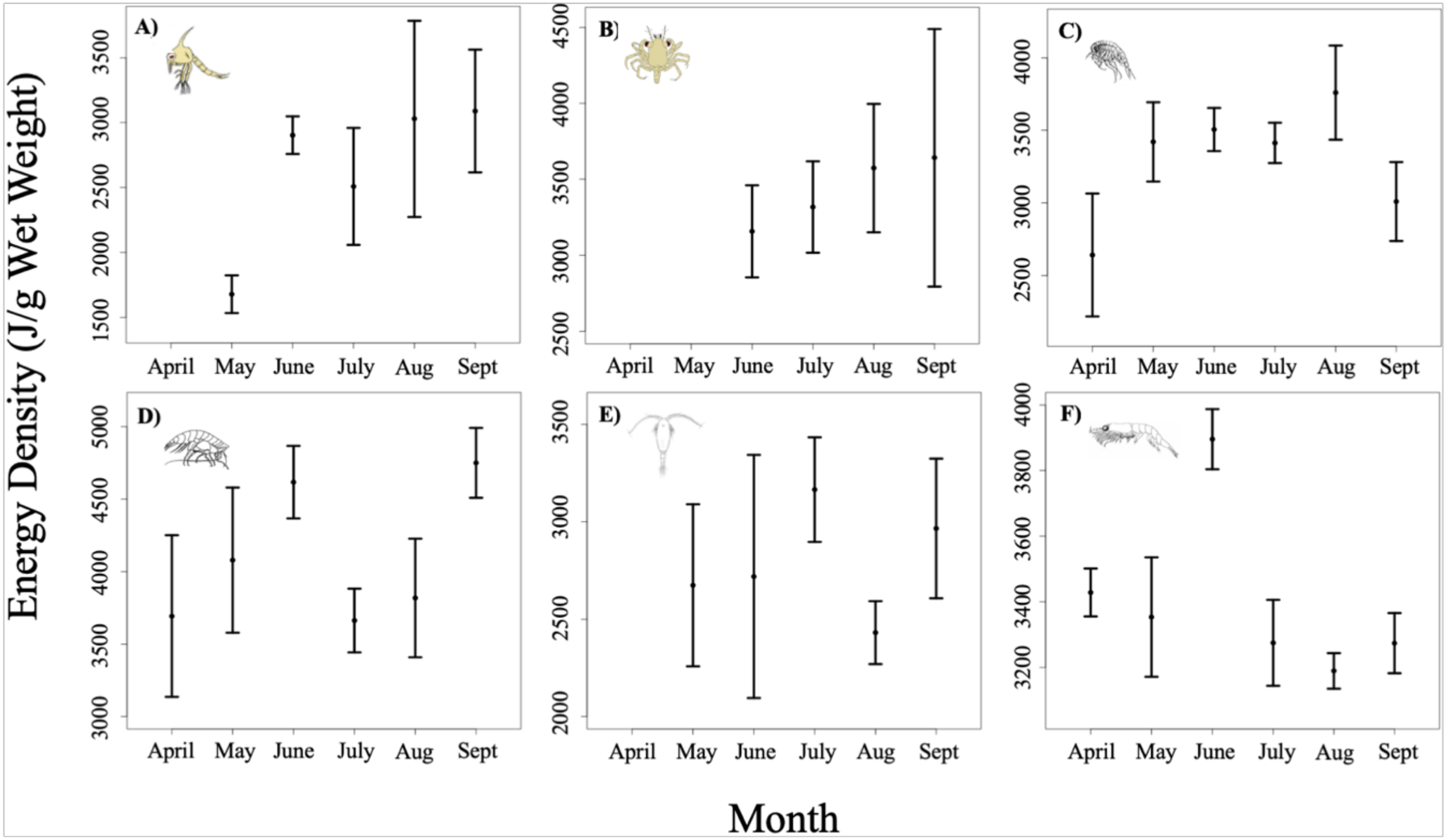

Figure 3.6. Mean energy density (ED) and 95% confidence limits for (A) F: Cancridae zoeae, (B) F: Cancridae megalopae, (C) *Themisto pacifica,* (D) *Cyphocaris challengerii*, (E) copepods and (F) *Euphasia pacifica* sampled between April and September 2017.

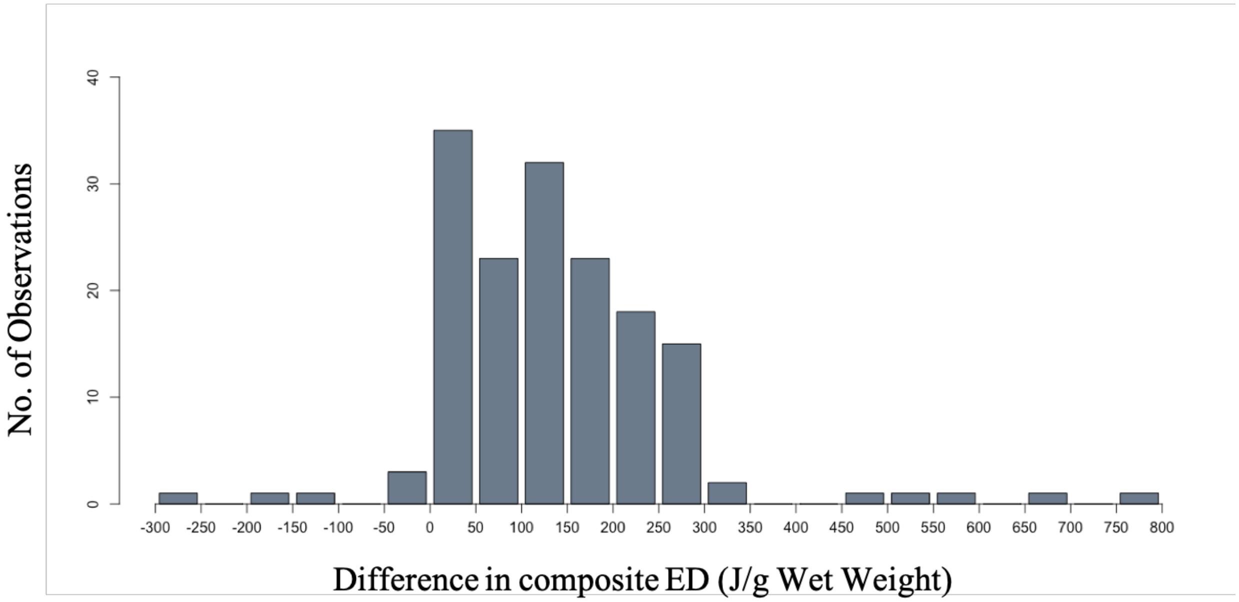

Figure 3.7. Differences between fine and coarse-scale estimates in the composite energy density of diet of juvenile Chinook Salmon sampled in 2015. Fine-scale estimates based upon family level specificity for decapod megalopae/zoeae and species level specificity for amphipods.

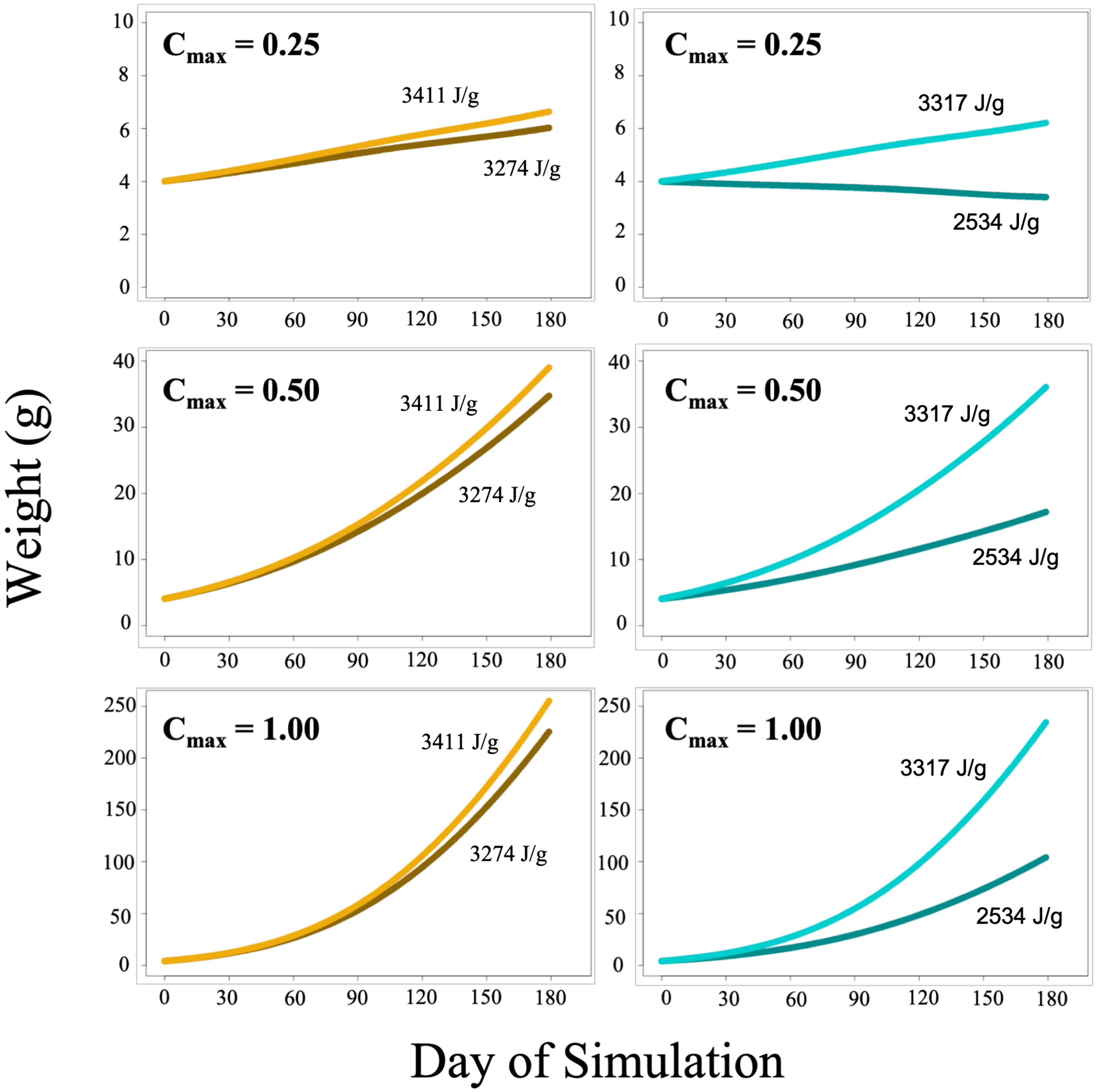

Figure 3.8. Growth projections for a 4-gram juvenile Chinook Salmon feeding at four varying levels of ED: mean observed coarse- (3274 J/g, dark orange) and fine-scale (3411 J/g, light orange) ED and the maximum difference between observed coarse- (2534 J/g, blue) and fine-scale (3317 J/g, cyan) ED in a single fish. Growth is projected at three different rates of maximum consumption (C_{max}): p = 0.25, p = 0.5, p = 1.0.

Chapter 4 – Conclusion

Investigating the energetic role that organisms have within a food-web can reveal important ecological patterns. The overall goal of this thesis was to investigate the ways in which we quantify the energetic content of organisms and to determine the consequences of ignoring taxonomic, temporal and spatial variability in energy density (ED) on growth. As we continue to use bioenergetics models to investigate such varied topics as lifetime growth and foraging (Hayes et al. 2000), toxin accumulation (Trudel & Rasmussen 2006), and climate change effects (Breeggemann et al. 2016), the accurate characterization of organismal ED will be of continued importance. These data are of great importance to fisheries managers that use these input parameters to model the size, growth and health of populations (Hansen et al. 1993, Deslauriers et al. 2017). Thus, this thesis aimed to improve the manner in which prey ED is estimated for taxa and to test the importance of correct parameterization of this value in a specific predator example.

In Chapter 2, I developed a model to aid in the accurate estimation of ED across a wide range of taxa. Using percent ash-free dry weight as a model (AFDW), I retained the simplicity of earlier metrics, while creating a method that had greater utility across taxa. By providing correction factors for broad taxonomic groups, I corrected for biases produced by the variable composition of proximate components in different taxa. Future efforts should expand the taxonomic scope of these models to include terrestrial vertebrates. Presently, only two studies have examined variability in energy content among terrestrial organisms and these studies were limited in taxonomic scope (Myrcha & Pinowski 1970, Holmes 1976). Using these data, I provided a correction for these organisms, however it is currently unclear whether or not this would extend to all terrestrial vertebrates. Measurement of both the ED and AFDW of a greater diversity of organisms would further improve this model's utility.

In Chapter 3, I examined fine-scale taxonomic, temporal and spatial variability in the ED of prey groups important in the diet of juvenile Chinook Salmon. I observed significant variability among decapod zoeae and megalopae as well amphipod species. We did not observe consistent temporal differences in ED among species, and spatial patterns on the scale that we investigated were not significant. These results should lend caution to researchers investigating the role of diet ED in the growth of juvenile Salmon. Using broad taxonomic groups to model growth may produce significant error in model estimates. Conclusions about the effect of prey quality on growth, made on the basis of broad taxonomic groupings (e.g. Duffy et al. 2010, Litz et al. 2017) may need to be re-evaluated in light of investigation into the fine-scale variability in ED between prey species. Future study design should aim to incorporate a fine-scale taxonomic characterization of prey if hoping to accurately test hypotheses related to diet.

Importantly, the results presented in Chapter 3 do not reveal the whole picture in fine-scale variability in ED. As I was unable to collect all species of importance in the diet of juvenile Chinook Salmon, it is likely that my approximation for error in growth projections was an underestimate. Instead, my results provide a case-study for the magnitude of error that is introduced by ignoring fine-scale variability in ED. Future studies should expand on our methods by including greater taxonomic coverage of the species preyed upon by juvenile Chinook Salmon. An in-depth, same season comparison of the diet and prey field at a fine taxonomic scale, would be necessary to fully quantify the range of errors that one would expect from combining species together into broad taxonomic groups. Additionally, the population dynamics of invertebrate prey groups remain understudied. A potential hypothesis to explain our temporal variability results is that seasonal molting and feeding dynamics are driving ED differences. Unfortunately, few such studies have been undertaken for salmon prey species, especially for amphipods (but see Haro-Garay 2003). These species are dominant prey items in certain years (Schabetsberger et al. 2003, Beamish et al. 2016), yet little is known about their population dynamics and reproduction. Certainly, this represents a substantial data gap and prospective avenue for future research.

Ecological patterns are often only considered at the scale in which they are observed and trends that are visible at one level may be blurred at another (Hewitt et al. 2017). This thesis underscores the importance of determining how processes at the fine-scale, such as energetic content, affect broader-scale patterns such as growth. The enhanced resolution of energetic data will help to improve interpretations of how fine-scale changes in diet alter broad scale patterns of growth.

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Appendix A

Table A.1. Dataset 1; data for energy density (ED), percent dry-weight (DW), percent ash-free dry weight (AFDW), percent protein and percent lipid (where available). Species are listed to the lowest taxonomic classification available in the original source.

Broad Taxonomc Group	Class	Species	ED	DW	AFDW	% Protein	% Lipid	Source
Terrestrial Invertebrates	Insecta	F. Carabidae	10.05	45.00	44.93	NA	NA	Chen et al. (2004)
Terrestrial Invertebrates	Insecta	F. Scarabaeidae	7.05	34.80	34.63	NA	NA	Chen et al. (2004)
Terrestrial Invertebrates	Insecta	F. Cerambycidae	7.90	40.30	40.24	NA	NA	Chen et al. (2004)
Terrestrial Invertebrates	Insecta	F. Curculionidae	6.88	35.30	35.12	NA	NA	Chen et al. (2004)
Terrestrial Invertebrates	Insecta	F. Tenebrionidae	7.36	36.70	36.40	NA	NA	Chen et al. (2004)
Terrestrial Invertebrates	Insecta	F. Buprestidae	8.33	37.90	37.62	NA	NA	Chen et al. (2004)
Terrestrial Invertebrates	Insecta	F. Elateridae	6.39	31.60	31.48	NA	NA	Chen et al. (2004)
Terrestrial Invertebrates	Insecta	F. Geotrupidae	7.83	40.20	39.98	NA	NA	Chen et al. (2004)
Aquatic Invertebrates	Malacostraca	Pandalus montagui	5.56	28.00	21.28	NA	NA	Cummins and Wuycheck (1971)
Aquatic Invertebrates	Malacostraca	Pandalus montagui	5.39	29.00	21.46	NA	NA	Cummins and Wuycheck (1971)
Aquatic Invertebrates	Malacostraca	Gammarus duebeni	4.80	26.00	19.24	NA	NA	Cummins and Wuycheck (1971)
Aquatic Invertebrates	Malacostraca	Sphaeroma rugicauda	3.14	25.00	11.00	NA	NA	Cummins and Wuycheck (1971)
Aquatic Invertebrates	Malacostraca	Palaemon serratus (fem)	4.87	26.00	21.32	NA	NA	Cummins and Wuycheck (1971)
Aquatic Invertebrates	Malacostraca	Palaemon serratus (male)	4.36	25.00	20.50	NA	NA	Cummins and Wuycheck (1971)
Aquatic Invertebrates	Malacostraca	Palaemon serratus (immature)	4.73	27.00	20.52	NA	NA	Cummins and Wuycheck (1971)
Aquatic Invertebrates	Malacostraca	Palaemon elegans	4.88	29.00	24.07	NA	NA	Cummins and Wuycheck (1971)
Aquatic Invertebrates	Malacostraca	Palaemonetes varians (adult fem)	5.29	25.00	20.50	NA	NA	Cummins and Wuycheck (1971)
Aquatic Invertebrates	Malacostraca	Palaemonetes varians (adult male)	4.68	25.00	20.50	NA	NA	Cummins and Wuycheck (1971)
Aquatic Invertebrates	Malacostraca	Palaemonetes varians (immature)	4.69	26.00	21.06	NA	NA	Cummins and Wuycheck (1971)
Aquatic Invertebrates	Malacostraca	Hippolyte varians	4.18	24.00	20.40	NA	NA	Cummins and Wuycheck (1971)
Aquatic Invertebrates	Malacostraca	Pacifastacus leniusculus	2.88	20.00	14.92	NA	NA	Cummins and Wuycheck (1971)
Aquatic Invertebrates	Branchiopoda	Leptodora kindtii	0.87	4.00	3.82	NA	NA	Cummins and Wuycheck (1971)
Aquatic Invertebrates	Malacostraca	Hyalella azteca	1.75	10.00	8.00	NA	NA	Cummins and Wuycheck (1971)
Terrestrial Invertebrates	Clitellata	Lumbricus sp.	3.27	15.60	15.48	NA	NA	Cummins and Wuycheck (1971)
Terrestrial Invertebrates	Insecta	Tenebrio molitor	11.54	40.30	40.10	NA	NA	Cummins and Wuycheck (1971)
Aquatic Vertebrates	Actinopterygii	Stellifer rastrifer	4.27	24.00	18.41	69.80	5.30	Di Beneditto et al. (2009)
Aquatic Vertebrates	Actinopterygii	Anchoa filifera	4.60	23.00	19.04	77.80	5.40	Di Beneditto et al. (2009)
Aquatic Vertebrates	Actinopterygii	Pellona harroweri	4.15	21.70	17.51	77.40	5.90	Di Beneditto et al. (2009)
Aquatic Vertebrates	Actinopterygii	Isopisthus parvipinnis	4.13	21.00	17.49	78.50	5.50	Di Beneditto et al. (2009)
Aquatic Vertebrates	Actinopterygii	Trichiurus lepturus	4.24	21.50	18.17	83.90	4.60	Di Beneditto et al. (2009)
Aquatic Invertebrates	Cephalopoda	Loligo sanpaulensis	3.45	14.80	13.90	84.50	7.50	Di Beneditto et al. (2009)
Aquatic Invertebrates	Cephalopoda	Loligo plei	4.63	21.60	19.70	86.30	2.30	Di Beneditto et al. (2009)
Aquatic Invertebrates	Scyphozoa	Cyanea capillata	0.18	4.20	0.97	NA	NA	Doyle et al. (2007)
Aquatic Invertebrates	Scyphozoa	Rhizostoma octopus	0.11	3.80	0.63	NA	NA	Doyle et al. (2007)
Aquatic Vertebrates	Actinopterygii	Engraulis encrasicolus (small, autumn)	5.27	24.96	24.00	NA	NA	Dubreuil and Petitgas (2009)
Aquatic Vertebrates	Actinopterygii	Engraulis encrasicolus (medium, winter)	6.01	27.09	26.17	NA	NA	Dubreuil and Petitgas (2009)
Aquatic Vertebrates	Actinopterygii	Engraulis encrasicolus (medium, spring)	6.27	26.43	25.67	NA	NA	Dubreuil and Petitgas (2009)
Aquatic Vertebrates	Actinopterygii	Engraulis encrasicolus (medium, autumn)	6.70	28.15	27.21	NA	NA	Dubreuil and Petitgas (2009)
Aquatic Vertebrates	Actinopterygii	Engraulis encrasicolus (large, winter)	6.28	27.25	26.44	NA	NA	Dubreuil and Petitgas (2009)
Aquatic Vertebrates	Actinopterygii	Engraulis encrasicolus (large, spring)	6.50	27.54	26.76	NA	NA	Dubreuil and Petitgas (2009)
Aquatic Vertebrates	Actinopterygii	Engraulis encrasicolus (large, autumn)	8.38	32.38	31.44	NA	NA	Dubreuil and Petitgas (2009)
Aquatic Plants & Algae	Ulvophyceae	Monostroma fuscum	9.16	48.10	42.33	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Ulvophyceae	Ulva rigida	4.69	29.00	23.35	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Ulvophyceae	Spongomorpha sp.	1.38	10.70	6.96	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Ulvophyceae	Codium fragile	0.75	7.00	4.06	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Phaeophyceae	Desmarestia herbacea	1.21	10.00	7.00	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Phaeophyceae	Colpomenia sinuosa	0.33	6.40	2.30	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Phaeophyceae	Laminaria saccharina	2.72	23.00	14.95	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Phaeophyceae	Costaria costata	1.30	10.70	7.06	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Phaeophyceae	Agarum cribrosum	2.47	20.70	13.66	NA	NA	Paine and Vadas (1969)

Table A.1. – Continued

Broad Taxonomc Group	Class	Species	ED	DW	AFDW	% Protein	% Lipid	Source
Aquatic Plants & Algae	Phaeophyceae	Agarum fimbriatum	1.92	15.30	9.95	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Phaeophyceae	Hedophyllum sessile	2.01	17.00	11.05	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Phaeophyceae	Nereocystis luetkeana	0.84	9.60	4.61	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Phaeophyceae	Postelsia palmaeformis	1.42	9.50	7.70	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Phaeophyceae	Macrocystis integrifolia	2.18	18.20	12.01	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Phaeophyceae	Pterygophora californica	2.26	13.70	11.37	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Phaeophyceae	Alaria nana	2.59	19.00	14.25	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Phaeophyceae	Egregia menziesii	2.18	17.00	11.73	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Phaeophyceae	Fucus distichus	2.72	19.00	14.06	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Phaeophyceae	Pelvetiopsis limitata	2.64	19.90	13.73	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Bangiophyceae	Porphyra nereocystis	2.30	13.50	11.34	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Bangiophyceae	Porphyra perforata	2.64	14.60	13.14	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Gelidium cartilagineum	5.90	32.00	28.16	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Dilsea californica	2.22	15.10	11.02	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Calliarthron sp.	2.05	76.00	14.44	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Endocladia murlcata	6.19	36.00	32.40	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Prionitis lyallli	3.22	20.00	16.20	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Catlophyllis flabeltulata	1.72	14.30	8.87	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Opuntiella californica	2.47	17.70	12.74	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Gigartina corymbifera	2.55	20.00	14.00	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Gigartina papillata	5.36	38.00	29.64	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Iridaea sp	2.43	19.70	14.78	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Halosaccion glandiforme	2.05	11.80	10.38	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Rhodymenia palmata	2.47	19.70	12.21	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Microcladia coulteri	3.10	18.80	15.60	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Ptilota filicina	2.51	17.70	12.57	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Delesseria deciplens (location 2)	1.97	13.40	9.65	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Polysiphonia sp.	2.18	15.80	10.74	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Pterosiphonia sp.	1.88	13.70	9.45	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Laurencia spectabilis	1.17	9.80	6.08	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Florideophyceae	Odonthallia floccosa	2.59	19.00	13.11	NA	NA	Paine and Vadas (1969)
Aquatic Plants & Algae	Liliopsida	Phyllospadix scouleri	4.52	28.40	24.42	NA	NA	Paine and Vadas (1969)
Aquatic Invertebrates	Malacostraca	Eupagurus bernbardus	4.58	22.90	20.72	NA	NA	Pandian and Schumann (1967)
Aquatic Invertebrates	Malacostraca	Hyperoche medusarum	4.81	21.20	18.06	35.90	27.20	Percy and Fife (1981)
Aquatic Invertebrates	Malacostraca	Parathemisto libellula	4.64	22.50	18.50	47.50	26.40	Percy and Fife (1981)
Aquatic Invertebrates	Malacostraca	Gamarus setosus	4.12	23.70	17.37	47.45	10.80	Percy and Fife (1981)
Aquatic Invertebrates	Malacostraca	Thysanoessa inermis	6.58	26.10	24.35	43.90	52.40	Percy and Fife (1981)
Aquatic Invertebrates	Gastropoda	Clione limacina	1.05	6.80	4.20	39.65	20.70	Percy and Fife (1981)
Aquatic Invertebrates	Hydrozoa	Bougainvillia supercilaris	0.40	4.20	1.64	11.30	8.40	Percy and Fife (1981)
Aquatic Invertebrates	Hydrozoa	Halitholus cirratus	0.40	4.15	1.66	14.30	6.10	Percy and Fife (1981)
Aquatic Invertebrates	Hydrozoa	Sarsia princeps	0.30	4.40	1.62	14.60	8.50	Percy and Fife (1981)
Aquatic Invertebrates	Hydrozoa	Hybocodon prolifer	0.70	5.10	2.78	27.00	17.60	Percy and Fife (1981)
Aquatic Invertebrates	Hydrozoa	Aglantha digitale	0.40	4.40	1.83	21.90	6.50	Percy and Fife (1981)
Aquatic Invertebrates	Tentaculata	Mertensia ovum	0.40	4.55	1.99	21.90	9.90	Percy and Fife (1981)
Aquatic Invertebrates	Nuda	Beroe cucumis	0.20	3.35	1.13	8.80	5.20	Percy and Fife (1981)
Aquatic Invertebrates	Polychaeta	Autolytus spp.	2.50	12.60	10.56	74.80	19.50	Percy and Fife (1981)
Aquatic Invertebrates	Gastropoda	Spiratella helicina	3.90	23.75	18.16	73.60	18.70	Percy and Fife (1981)
Aquatic Invertebrates	Malacostraca	Onisimus litoralis	4.80	26.05	18.57	44.30	21.50	Percy and Fife (1981)
Aquatic Invertebrates	Malacostraca	Anonyx nugax	5.00	27.00	19.41	38.50	22.00	Percy and Fife (1981)
Aquatic Invertebrates	Sagittoidea	Sagitta elegans	2.00	9.70	7.94	63.30	20.80	Percy and Fife (1981)

Table A.1. – Continued

Broad Taxonomc Group	Class	Species	ED	DW	AFDW	% Protein	% Lipid	Source
Aquatic Plants & Algae	Liliopsida	Potamogeton lucens	2.54	17.00	14.28	10.90	2.30	Smirnov (1962)
Aquatic Plants & Algae	Liliopsida	Elodea canadensis	1.33	10.00	7.69	16.40	2.00	Smirnov (1962)
Aquatic Invertebrates	Bivalvia	Mercenaria mercenaria	0.65	3.10	2.31	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Crasssostrea virginica	0.62	3.20	2.47	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Chiome cancellata	0.71	3.30	2.95	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Anadara transversa	0.71	3.50	3.14	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Crasssostrea virginica	0.74	3.70	2.89	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Mercenaria mercenaria	0.76	3.80	3.29	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Pyramidella fusca	0.88	4.00	2.96	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Anadara transversa	0.81	4.20	3.57	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Chiome cancellata	0.90	4.40	3.77	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Chiome cancellata	0.89	4.50	3.76	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Urosalpinx cinerra	0.84	4.60	4.00	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Nassarius vibex	1.07	4.60	4.06	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Nassarius vibex	1.11	5.50	4.87	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Anomia simplex	1.19	5.80	5.05	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Retusa canaliculata	1.25	5.90	5.38	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Crepidula fornicata	1.24	6.00	5.08	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Pecten irradians	1.53	6.00	5.27	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Nassarius vibex	1.04	6.20	5.31	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Retusa canaliculata	1.30	6.20	5.65	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Anachis avara	1.13	6.50	5.60	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Anachis avara	1.01	7.30	5.92	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Crepidula fornicata	1.24	7.30	5.96	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Anachis avara	1.20	7.50	6.21	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Chiome cancellata	1.41	7.70	6.25	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Anachis avara	1.37	7.80	6.42	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Retusa canaliculata	1.42	7.80	6.97	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Pyramidella fusca	1.47	8.60	7.59	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Pinna serrata	1.91	8.90	7.22	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Macoma balthica	1.72	9.00	7.36	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Bittium varium	1.68	9.10	7.61	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Nassarius obsoletus	1.66	9.70	8.64	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Macoma balthica	1.63	9.90	8.91	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Bittium varium	1.58	10.20	8.64	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Maxillopoda	Balanus balanoides	2.01	10.20	8.76	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Maxillopoda	Balanus balanoides	2.08	10.40	9.40	NA	NA	Thayer et al. (1973)
Aquatic Vertebrates	Actinopterygii	Lagodon rhomboides	2.81	11.20	10.17	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Modiolus demissus	2.52	12.00	10.44	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Bittium varium	2.09	12.20	9.33	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Tagelus divisus	2.28	12.30	10.80	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Mitrella lunata	2.38	12.50	11.18	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Mitrella lunata	2.01	14.80	12.09	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Polychaeta	Nereis pelagica	3.39	15.40	13.94	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Mitrella lunata	2.79	16.10	14.86	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Polychaeta	Nereis pelagica	4.07	16.60	14.57	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Cephalopoda	Loligo brevis	4.39	18.30	16.58	NA	NA	Thayer et al. (1973)
Aquatic Vertebrates	Actinopterygii	Brevoortia tyrannus	3.98	18.50	16.80	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Malacostraca	Pinnotheres ostreum	4.66	18.50	17.30	NA	NA	Thayer et al. (1973)
Aquatic Vertebrates	Actinopterygii	Paralichthys dentatus	4.28	20.70	18.36	NA	NA	Thayer et al. (1973)

Table A.1. – Continued

Broad Taxonomc Group	Class	Species	ED	DW	AFDW	% Protein	% Lipid	Source
Aquatic Vertebrates	Actinopterygii	Leistomus xanthurus	4.57	22.10	18.12	NA	NA	Thayer et al. (1973)
Aquatic Vertebrates	Actinopterygii	Symphurus plagiusa	4.61	22.50	19.24	NA	NA	Thayer et al. (1973)
Aquatic Vertebrates	Actinopterygii	Symphurus plagiusa	4.25	22.60	17.97	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Teredo navalis	4.61	22.70	19.34	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Decapoda	Peneus setiferus	4.61	23.30	19.18	NA	NA	Thayer et al. (1973)
Aquatic Vertebrates	Actinopterygii	Paralichthys dentatus	4.80	23.30	19.50	NA	NA	Thayer et al. (1973)
Aquatic Vertebrates	Actinopterygii	Micropogon undulatus	4.60	23.70	19.13	NA	NA	Thayer et al. (1973)
Aquatic Vertebrates	Actinopterygii	Leistomus xanthurus	5.14	23.90	19.96	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Teredo navalis	4.93	24.40	20.89	NA	NA	Thayer et al. (1973)
Aquatic Vertebrates	Actinopterygii	Lagodon rhomboides	4.51	24.50	19.45	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Malacostraca	Carinogammarus mucronatus	4.54	24.70	20.87	NA	NA	Thayer et al. (1973)
Aquatic Vertebrates	Actinopterygii	Mugil cephalus	5.33	24.80	21.40	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Polychaeta	Diopatra cuprea	5.51	25.40	22.38	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Malacostraca	Callianassa stimpsoni	4.68	26.30	21.80	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Malacostraca	Carinogammarus mucronatus	4.14	26.70	21.52	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Malacostraca	Upogebia affinis	5.13	26.70	20.19	NA	NA	Thayer et al. (1973)
Aquatic Vertebrates	Actinopterygii	Lagodon rhomboides	5.21	26.70	21.81	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Malacostraca	Paleomonetes pugio	6.22	27.40	23.21	NA	NA	Thayer et al. (1973)
Aquatic Vertebrates	Actinopterygii	Mugil cephalus	5.32	28.30	22.58	NA	NA	Thayer et al. (1973)
Aquatic Vertebrates	Actinopterygii	Fundulus heteroclitus	5.47	28.50	22.86	NA	NA	Thayer et al. (1973)
Aquatic Vertebrates	Actinopterygii	Fundulus majalis	6.16	30.20	23.95	NA	NA	Thayer et al. (1973)
Aquatic Vertebrates	Actinopterygii	Brevoortia tyrannus	6.58	30.20	26.00	NA	NA	Thayer et al. (1973)
Aquatic Vertebrates	Actinopterygii	Brevoortia tyrannus	6.95	30.90	26.67	NA	NA	Thayer et al. (1973)
Aquatic Vertebrates	Actinopterygii	Gobiosoma bosci	6.39	32.10	25.87	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Tentaculata	Mixed ctenophores	0.06	2.30	0.62	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Tentaculata	Mixed ctenophores	0.22	2.40	0.78	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Tentaculata	Mixed ctenophores	0.06	2.70	0.74	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Tentaculata	Mixed ctenophores	0.14	2.80	0.76	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Tentaculata	Mixed ctenophores	0.33	3.90	1.74	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Nassarius vibex	0.75	6.30	4.79	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Crepidula fornicata	1.72	7.80	4.95	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Macoma tenta	1.62	8.20	5.88	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Gastropoda	Crepidula convexa	1.07	8.80	5.66	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Bivalvia	Macoma tenta	1.67	9.20	6.70	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Polychaeta	Amphitrite ornata	3.10	25.40	12.52	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Malacostraca	Callinectes sapidus	3.35	27.20	19.07	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Malacostraca	Amphithoe longimana	3.83	31.40	20.94	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Malacostraca	Amphithoe longimana	5.06	31.60	21.39	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Malacostraca	Callinectes sapidus	4.37	32.60	17.47	NA	NA	Thayer et al. (1973)
Aquatic Invertebrates	Malacostraca	Libinia dubia	5.51	61.90	34.66	NA	NA	Thayer et al. (1973)
Terrestrial Invertebrates	Insecta	Blattella germanica (instar 1)	6.04	27.00	26.19	NA	NA	Woodland, Hall and Calder (1968)
Terrestrial Invertebrates	Insecta	Blattella germanica (instar 2)	6.37	30.70	29.35	NA	NA	Woodland, Hall and Calder (1968)
Terrestrial Invertebrates	Insecta	Blattella germanica (instar 3)	7.17	32.40	31.04	NA	NA	Woodland, Hall and Calder (1968)
Terrestrial Invertebrates	Insecta	Blattella germanica (instar 4)	7.50	33.10	31.51	NA	NA	Woodland, Hall and Calder (1968)
Terrestrial Invertebrates	Insecta	Blattella germanica (instar 5)	7.46	32.90	31.39	NA	NA	Woodland, Hall and Calder (1968)
Terrestrial Invertebrates	Insecta	Blattella germanica (instar 6)	7.00	30.70	29.44	NA	NA	Woodland, Hall and Calder (1968)
Terrestrial Invertebrates	Insecta	Blattella germanica (adult male)	5.87	29.00	27.55	NA	NA	Woodland, Hall and Calder (1968)
Terrestrial Invertebrates	Insecta	Blattella germanica (instar 5 fem)	7.43	30.80	29.85	NA	NA	Woodland, Hall and Calder (1968)
Terrestrial Invertebrates	Insecta	Blattella germanica (instar 6 fem)	6.92	30.90	29.57	NA	NA	Woodland, Hall and Calder (1968)
Terrestrial Invertebrates	Insecta	Blattella germanica (adult fem)	6.14	29.10	27.91	NA	NA	Woodland, Hall and Calder (1968)

T**able A.2.** Equations and correction factors (CF) for all generalized linear models relating energy density to both percent dry weight (DW) and percent ash-free dry weight (AFDW) including dummy variables (value of 0 or 1) for large taxonomic groups; AI = aquatic invertebrates; AV = aquatic vertebrates; TI = terrestrial invertebrates; AA = aquatic animals; AN = animals). The difference between the given and best-fitting model (Δ_i) and adjusted percent R^2 values are presented for each candidate model.

Model	Δ_i	Equation	CF	R^2
AFDW + AA + TI	0	$\log_{10}(ED) = 1.07*\log_{10}(AFDW) - 0.80$	AA = 0.09, TI = 0.04	0.98
AFDW + AI + AV + TI	1.39	$\log_{10}(ED) = 1.06*\log_{10}(AFDW) - 0.79$	AI = 0.08 , AV = 0.09 , TI = 0.04	0.98
AFDW + AA	3.39	$\log_{10}(ED) = 1.08*\log_{10}(AFDW) - 0.79$	AA = 0.07	0.98
AFDW + AI + AV	5.22	$\log_{10}(ED) = 1.07*\log_{10}(AFDW) - 0.79$	AI = 0.07 , AV = 0.08	0.98
AFDW + AN	5.39	$\log_{10}(ED) = 1.05*\log_{10}(AFDW) - 0.78$	AN = 0.08	0.98
AFDW + AI	33.31	$\log_{10}(ED) = 1.08*\log_{10}(AFDW) - 0.77$	AI = 0.05	0.97
AFDW + AI + TI	35.41	$\log_{10}(ED) = 1.08*\log_{10}(AFDW) - 0.77$	AI = 0.05 , TI = 0.00	0.97
AFDW + AV	43.67	$\log_{10}(ED) = 1.04*\log_{10}(AFDW) - 0.71$	AV = 0.04	0.97
AFDW + AV + TI	45.74	$\log_{10}(ED) = 1.04*\log_{10}(AFDW) - 0.71$	AV = 0.04 , TI = 0.00	0.97
AFDW	51.14	$\log_{10}(ED) = 1.05*\log_{10}(AFDW) - 0.72$	--	0.97
AFDW + TI	52.13	$\log_{10}(ED) = 1.06*\log_{10}(AFDW) - 0.72$	TI = -0.02	0.97
DW + AN	363.15	$\log_{10}(ED) = 1.21*\log_{10}(DW) - 1.15$	AN = 0.14	0.87
DW + AI + AV + TI	364.62	$\log_{10}(ED) = 1.18*\log_{10}(DW) - 1.10$	AI = 0.12 , AV = 0.18 , TI = 0.17	0.87
DW + AA + TI	364.88	$\log_{10}(ED) = 1.20*\log_{10}(DW) - 1.14$	AA = 0.14 , TI = 0.16	0.87
DW + AA	376.5	$\log_{10}(ED) = 1.24*\log_{10}(DW) - 1.13$	AA = 0.09	0.86
DW + AI + AV	377.41	$\log_{10}(ED) = 1.22*\log_{10}(DW) - 1.10$	AI = 0.08 , AV = 0.12	0.86
DW + AV + TI	379.76	$\log_{10}(ED) = 1.13*\log_{10}(DW) - 0.96$	AV = 0.10 , TI = 0.10	0.86
DW + AV	383.57	$\log_{10}(ED) = 1.17*\log_{10}(DW) - 1.00$	AV = 0.08	0.85
DW + AI + TI	384.1	$\log_{10}(ED) = 1.21*\log_{10}(DW) - 1.07$	AI = 0.06 , TI = 0.09	0.85
DW + AI	386.53	$\log_{10}(ED) = 1.23*\log_{10}(DW) - 1.08$	AI = 0.04	0.85
DW + TI	386.67	$\log_{10}(ED) = 1.17*\log_{10}(DW) - 1.00$	TI = 0.07	0.85
DW	387.36	$\log_{10}(ED) = 1.19*\log_{10}(DW) - 1.02$	--	0.85

Appendix B

Table B.1. P-values from a post-hoc pairwise Wilcoxon rank sum test corrected for multiple comparisons between families of decapod zoeae (A) and megalopae (B). Bold values represent significant relationships.

A)

Family	Cancridae	Grapsidae	Majidae	Paguridae	Porcellanidae
Grapsidae	**0.023**	-	-	-	-
Majidae	0.189	0.770	-	-	-
Paguridae	0.189	**0.002**	0.107	-	-
Porcellanidae	**0.013**	0.770	0.770	**0.002**	-
Xanthidae	0.495	0.189	0.393	0.770	0.215

B)

Family	Cancridae	Grapsidae	Majidae	Paguridae	Porcellanidae
Grapsidae	**0.008**	-	-	-	-
Majidae	0.173	0.824	-	-	-
Paguridae	**0.002**	0.173	0.191	-	-
Porcellanidae	0.277	0.102	**0.020**	**0.002**	-
Xanthidae	0.505	**0.008**	0.071	**<0.0001**	0.469

Table B.2. P-values from a post-hoc pairwise Wilcoxon rank sum test corrected for multiple comparisons between amphipod species: A) *Hyperia medusarum*, B) *Themisto pacifica* and C) *Cyphocaris challengerii*. All comparisons were statistically significant

Species	*C. challengerii*	*H. medusarum*
H. medusarum	**<0.0001**	-
T. pacifica	**<0.0001**	**<0.0001**

Table B.3. P-values from a post-hoc pairwise Wilcoxon rank sum test corrected for multiple comparisons between monthly sampling of A) F: Cancridae zoeae, B) F: Cancridae megalopae, C) *Themisto pacifica*, D) *Cyphocaris challengerii,* E) Copepods and F) *Euphausia pacifica*. Bold values represent significant relationships.

A) F: Cancridae Zoeae

Month	April	May	June	July	August
May	-	-	-	-	-
June	-	**0.000**	-	-	-
July	-	**0.017**	0.292	-	-
August	-	**0.012**	0.814	0.659	-
Sept	-	**0.003**	0.659	0.446	0.905

B) F: Cancridae Megalopae

	April	May	June	July	August
May	-	-	-	-	-
June	-	-	-	-	-
July	-	-	0.870	-	-
August	-	-	0.680	0.870	-
Sept	-	-	0.870	0.870	0.870

C) *Themisto pacifica*

	Apr	May	June	July	August
May	**0.026**	-	-	-	-
June	**0.010**	0.854	-	-	-
July	**0.010**	0.661	0.561	-	-
August	**0.010**	0.257	0.237	0.161	-
Sept	0.179	0.098	**0.016**	**0.023**	**0.01**

D) *Cyphocaris challengerii*

	April	May	June	July	August
May	0.686	-	-	-	-
June	**0.019**	0.081	-	-	-
July	0.761	0.193	**<0.0001**	-	-
August	0.834	0.699	**0.013**	0.402	-
Sept	**0.013**	**0.015**	0.402	**<0.0001**	**0.003**

E) Copepods

	April	May	June	July	August
May	-	-	-	-	-
June	-	0.981	-	-	-
July	-	0.074	0.327	-	-
August	-	0.563	0.845	**0.001**	-
Sept	-	0.354	0.563	0.586	0.061

F) *Euphausia pacifica*

	Apr	May	June	July	August
May	1.000	-	-	-	-
June	**<0.0001**	**<0.0001**	-	-	-
July	**0.046**	0.479	**<0.0001**	-	-
August	**<0.0001**	0.093	**<0.0001**	0.666	-
Sept	**0.005**	0.346	**<0.0001**	0.666	0.292

Table B.4. P-values from a post-hoc pairwise Wilcox rank sum test corrected for multiple comparisons between sampling sites of A) Copepods, B) *Cyphocaris challengerii,* C) F: Cancridae megalopae and D) *Themisto pacifica*.

A) Copepods

Location	Cowichan	Maple Bay
Maple Bay	0.910	-
Saanich	0.910	1.000

B) *Cyphocaris challengerii*

	Cowichan	Maple Bay
Maple Bay	0.33	-
Saanich	0.33	0.33

C) F: Cancridae Megalopae

	Cowichan	Maple Bay
Maple Bay	0.11	-
Saanich	0.11	0.610

D) *Themisto pacifica*

	Cowichan	Maple Bay
Maple Bay	0.471	-
Saanich	0.215	0.058