Fine-scale taxonomic and temporal variability in the energy density of invertebrate prey of juvenile Chinook salmon *Oncorhynchus tshawytscha*

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ABSTRACT: Variation in the energy content of prey can drive the diet choice, growth and ultimate survival of consumers. In Pacific salmon species, obtaining sufficient energy for rapid growth during early marine residence is hypothesized to reduce the risk of size-selective mortality. In order to determine the energetic benefit of feeding choices for individuals, accurate estimates of energy density (ED) across prey groups are required. Frequently, a single species is assumed to be representative of a larger taxonomic group or related species. Further, single-point estimates are often assumed to be representative of a group across seasons, despite temporal variability. To test the validity of these practices, we sampled zooplankton prey of juvenile Chinook salmon to investigate fine-scale taxonomic and temporal differences in ED. Using a recently developed model to estimate the ED of organisms using percent ash-free dry weight, we compared energy content of several groups that are typically grouped together in growth studies. Decapod megalopae were more energy rich than zoeae and showed family-level variability in ED. Amphipods showed significant species-level variability in ED. Temporal differences were observed, but patterns were not consistent among groups. Bioenergetic model simulations showed that growth rate of juvenile Chinook salmon was almost identical when prey ED values were calculated on a fine scale or on a taxon-averaged coarse scale. However, single-species representative calculations of prey ED yielded highly variable output in growth depending on the representative species used. These results suggest that the latter approach may yield significantly biased results.

KEY WORDS: Energy density · Ash-free dry weight · Diet choice · Bioenergetics · Invertebrate · Decapod · Amphipod

1. INTRODUCTION

The growth and survival of Pacific salmon (*Oncorhynchus* spp.) are 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 or an inability to meet basic metabolic demands during the winter months (Beamish & Mahnken 2001). Although the hypothesis of size-selective survival has been met with recent challenges (Beacham et al. 2017, 2018), marine survival of juvenile salmon is still largely understood to be highly dependent on conditions experienced during the early marine period. Abiotic forces such as upwelling (Wells et al. 2007), temperature (Mantua et al. 1997, Farley & Trudel 2009) and nutrient availability (Thomson et al. 2012) have all been tied to juvenile salmon growth and increased survival. These abiotic 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 influence 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 (but see Daly et al. 2010, Hertz et al. 2016, Litz et al. 2017).

Pacific salmon size and abundance vary 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 dramatic declines in marine survival over the past several decades (Beamish et al. 1995, 2010, Kendall et al. 2017), The Salish Sea Marine Survival Project (http://marinesurvivalproject.com/) is a binational research effort aimed to determine the causal forces driving reduced survival in these species. The present study contributes to this effort by examining fine-scale variability in the quality of invertebrate prey available to these salmon, focussing specifically on prey of juvenile Chinook salmon.

Prey quality, which is regularly used to explain variability in salmon growth (Trudel et al. 2007, Tiffan et al. 2014), can be expressed as energy density (ED), defined as the amount of energy contained per unit mass of an organism. However, direct measurement of ED is rarely performed. Instead, researchers regularly use values from the literature (e.g. Beauchamp et al. 2007, Armstrong et al. 2008, Tiffan et al. 2014). In doing so, a single ED value is often assumed to be representative of a broad taxonomic group. This value is typically inferred through 1 of 2 coarse-scale methods: (1) by taking an average of several species; or (2) taking a single species to be representative of a larger taxonomic group. Both of these coarse-scale methods for determining prey ED are reported in the literature and can even be employed together (e.g. Duffy et al. 2010). It is rare for researchers to estimate ED at a fine taxonomic scale (i.e. species or family). This practice may be problematic, as ED can vary considerably among related taxa (Cummins & Wuycheck 1971), and between vertebrate and invertebrate prey (Davis et al. 1998, Dessier et al. 2018). Furthermore, within groups, ED can vary on temporal scales (Wissing & Hasler 1971, Pedersen & Hislop 2001) that are not captured in single-point literature measurements. 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.

Direct measurement of ED is obtained via bomb calorimetry (Cummins & Wuycheck 1971). However, this method is limited by cost, time and sample requirements and is not always feasible for very small organisms where large numbers of individuals may be needed for a single analytical sample. Due to these limitations, several models have been developed to estimate the ED of invertebrates and fish (Hartman & Brandt 1995, Ciancio et al. 2007, James et al. 2012, Weil et al. 2019a). 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. (2019a) developed a general model using percent ash-free dry weight (AFDW) as a predictor of ED. This method allows for a more accurate estimation of ED across taxonomic groups with a single equation while maintaining the simplicity of previous dry weight models. In the present study, we employ this method to assess variability in ED across prey groups and seasonal scales important to juvenile Chinook salmon at the level of the individual zooplankter.

Consequences of underestimated variability in prey quality may be visualized using bioenergetics models. These models estimate growth from values of consumption rate, metabolism and the ED of both predators and prey. These parameters can then be manipulated to determine the effects of changing climate (Beauchamp et al. 2007, Beauchamp 2009), prey availability (Litz et al. 2019), behaviour (Jørgensen et al. 2016) or toxin accumulation (Trudel & Rasmussen 2006) on growth. However, the utility of these models relies on the input of accurate data to inform model parameters. Uncertainty in the ED of 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.

In this study, we aimed to test the following hypotheses: (1) fine-scale (species or family level) taxonomic variability in ED exists within invertebrate prey groups important to juvenile Chinook salmon; and (2) temporal variability in the ED of invertebrate prey exists during the first 6 mo spent at sea. Using a bioenergetics model, we then compared how differences between fine- and coarse-scale estimates of prey ED affected growth estimates for juvenile Chinook salmon. In doing so, we aimed to assess how current practices of coarse-scale taxonomic grouping could misrepresent the early growth of juvenile Chinook salmon in bioenergetics models.

2. MATERIALS AND METHODS

2.1. Sample collection

We collected zooplankton samples monthly from April to September 2017 in the Southern Gulf Islands of the Salish Sea, British Columbia, Canada (Fig. 1). Species groups were targeted based on their observation in a concurrent study of the diet and growth of juvenile Cowichan River Chinook salmon (W.D.P. Duguid et al. unpubl. data; a paper complementary to the present study). Three sample sites, located within 20 km of each other (Saanich Inlet, Cowichan Bay and Maple Bay; Fig. 1) were chosen to ensure the collection of as many target species as possible. We deployed a 0.5 m diameter, 350 µm mesh zooplankton net at 50 m depth in Cowichan Bay and at 100 m in Saanich Inlet and Maple Bay, towing at depth. Zooplankton tows were retrieved within 5 min of deployment and were emptied into buckets on board the vessel. Live samples were returned to the lab for processing within the same day. One species consumed by juvenile Chinook salmon, *Hyperia medusarum,* occurs as a parasite on the large scyphozoan jellyfish *Phacellophora camtschatica,* but is rarely encountered in plankton samples. To sample this species, *P. camtschatica* medusae were corralled on the surface with a net and bucket, before being brought on board where *H. medusarum* were removed. Because we had previously observed a strong female bias for *H. medusarum* in the diet of juvenile Chinook salmon (Weil et al. 2019b), these individuals were separated by sex to determine if differences in ED existed between males and females of this species.

2.2. Lab analysis

In the lab, live zooplankton samples were poured back through the cod end of the net to reduce the volume of the sample. Zooplankters were separated to the lowest possible taxonomic level. Most taxa were identified to species while decapod larvae 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. All samples were stored at −80°C until ED analysis.

To determine the ED of prey organisms, we employed the estimation model of Weil et al. (2019a). This method accurately estimates the ED of individuals using percent AFDW. Following a 3 h thaw, individuals were blotted until no visible moisture was observed on a KimWipe™ and then wet weighed on a microbalance to the nearest 0.00001 g. Measurements were obtained by weighing each organism in a preashed, aluminium weigh boat. Samples were placed in a drying oven at 60°C for 4 d, 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
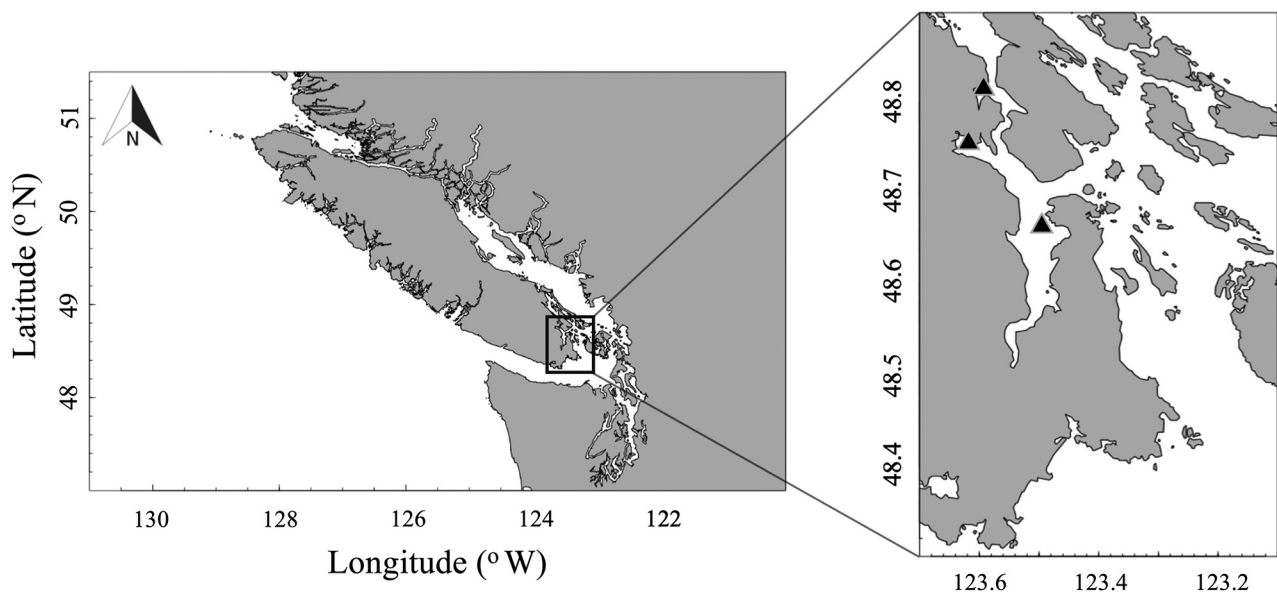

Fig. 1. Sampling locations (▲) off the coast of Vancouver Island, British Columbia, Canada; from north to south: Maple Bay, Cowichan Bay, Saanich Inlet

furnace at 550°C for 3 h (Cummins & Wuycheck 1971) and then re-weighing the samples. The weight of ash was subtracted from the initial dry weight and then divided by wet weight to obtain percent AFDW. We attempted to minimize measurement error by taking weight measurements on days with similar ambient air moisture and analysing samples as quickly as possible following removal from the drying oven or muffle furnace. ED is calculated in kilojoules per gram from percent AFDW using the equation $\log_{10}(ED) = 1.07 \times \log_{10}(AFDW) - 0.71$ (from Weil et al. 2019a). ED values throughout this paper are reported in J/g to remain consistent with the literature.

2.3. Data analysis

We assessed fine-scale taxonomic differences in ED by comparing mean values of ED among related species or families to the coarse-scale groupings used in most diet studies (typically resolved at the taxonomic level of order). We informed our choice of coarse-scale groups by performing a qualitative review of recent studies that examined the diet of juvenile Chinook salmon. We assessed temporal differences in ED in species/groups where multiple individuals were collected in at least 4 of 6 months. ED values calculated from percent AFDW were visualized between groups using means and 95% confidence intervals. Data were tested for normality using a Shapiro-Wilk test within coarse-scale taxonomic groups, and residuals were plotted to ensure no temporal autocorrelation between months. We evaluated differences in ED among related species/families or between months using a non-parametric Kruskal-Wallis test. We made post hoc comparisons between groups using a pairwise Wilcoxon rank sum test, including a Benjamini-Hochberg p-value adjustment for multiple comparisons (Benjamini & Hochberg 1995). We considered differences between median rank sums significant at a level of $\alpha = 0.05$. All statistical analyses were conducted using R statistical software (R Core Team 2018).

2.4. Bioenergetics modelling

We simulated growth rate for juvenile Chinook salmon using the 'Wisconsin' bioenergetics model developed by Kitchell et al. (1977), and implemented in Fish Bioenergetics 4.0 (Deslauriers et al. 2017). Growth was projected during the first 4 mo at sea under different prey ED scenarios. We used physiological parameters provided for adult Chinook salmon

(Stewart & Ibarra 1991, Plumb & Moffitt 2015) and a seasonal temperature curve from April to August 2015 provided by Ocean Networks Canada (www. oceannetworks.ca/data-tools). Predator ED was set at a constant 4200 J g^{-1} throughout the simulation based on observations of juvenile Chinook salmon in the Salish Sea over a similar period (D.A. Beauchamp unpubl. data). Initial weight was set to 4 g (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. As ED comparisons were made solely among invertebrates, simulations were limited to 120 d to simulate growth between ocean entry in April to the end July, a period before fish typically dominate the diet in the Salish Sea (Duffy et al. 2010, Chittenden et al. 2018, W.D.P. Duguid et al. unpubl. data). The proportion of maximum consumption rate (C_{max}) was set at 0.25, 0.5 or 1.0 to assess the effect of feeding rate on growth with varying values of ED. As we were quantifying the effect of varying ED alone, prey ED was held at a constant value throughout the simulation. Growth was compared for juvenile Chinook salmon differing in diet ED, calculated on either a fine-scale, a taxon-averaged coarse scale or using the minima and maxima of the single-species representative coarse-scale method described below.

In the bioenergetics model, juvenile Chinook salmon diets were based on a 2015 study of diets collected in the same sampling area as the present study (W.D.P. Duguid et al. unpubl. data). In the previous study, Chinook salmon stomach contents were sampled from July to October 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 in the present study, with the exception of brachyuran zoeae, which were treated as a single group. Stomach contents were blotted on a KimWipe™ and wet weight was recorded. For the present analysis, all prey sampled in 2015 were pooled to create a single 'mean diet' sample. This sample was then constrained to include only those groups also observed in 2017 where fine-scale differences between related groups were compared (decapods and hyperiid amphipods; see Table 2). Although the simulation period in the bioenergetics model only overlapped with sampling in July (Duguid & Juanes 2017), other studies in the same region have demonstrated the importance of decapods and amphipods to the diet throughout April, May and June (Chittenden et al. 2018). The proportion of each fine-scale group was multiplied by either a fine-scale, or 1 of 2 coarse-scale ED values to obtain a unique to-

tal diet ED value for the sample, differing only in the taxonomic resolution of the diet. Fine-scale values of ED were calculated at the species or family level from 2017 samples, as described above. The 2 coarse-scale estimation methods used were chosen based on methods typically observed in the literature (e.g. Duffy et al. 2010). The first coarse-scale estimate was calculated as the average of all fine-scale estimates within a larger taxonomic group sampled in 2017 (i.e. decapods, hyperiids), and was termed the 'taxon-averaged coarse-scale'. The second coarse-scale estimate was calculated by taking the mean fine-scale value for a single species in a coarse group and using it as representative of all individuals in that group, termed the 'single-species representative coarse-scale'. This process was repeated for each possible combination of representative taxa observed in 2017 with a sample size of 10 or greater to create a range of diet ED values. The minimum and maximum values produced using this method, as well as taxon-averaged coarse-scale and fine-scale values were each used in a unique simulation to quantify variability in growth among these methods.

3. RESULTS

3.1. Taxonomic variability in ED

We collected 1395 individual zooplankters from 18 tows over 6 discrete sampling days. We did not obtain sufficient sample sizes to fully explore fine-scale taxonomic ED variability within all coarse-scale groups observed in juvenile Chinook salmon diets. However, we were able to obtain sufficient sample sizes to make meaningful comparisons among multiple species for several key groups, and therefore focussed our analysis of fine-scale taxonomic variability in ED solely on decapod larvae (zoeae and megalopae) and amphipods.

Decapod larvae are typically grouped together into 1 taxonomic category for the purposes of bioenergetic modelling for salmon. However, we observed a diversity of decapod larvae with variable ED values in zooplankton collections. Seven families of decapod larvae were observed: Cancridae, Grapsidae, Majidae, Pinnotheridae, Xan-

thidae, Paguridae and Porcellanidae (Fig. 2). We observed both megalopae and zoeae for all families except Pinnotheridae, for which we only collected zoeae. Mean ± SE of ED for each family and larval stage are described in Table 1. Median rank sum ED values for decapod megalopae were consistently greater than for zoeae when families were grouped together ($p < 0.0001$, Fig. 3). When separated, significant family-level ED variability was observed (Kruskal-Wallis test, $p < 0.0001$). ED of cancrid, grapsid, pagurid and xanthid megalopae were all significantly greater than their zoeal counterparts (Fig. 3). When comparing decapod zoeae among families, Grapsidae and Porcellanidae had significantly greater ED values than Cancridae and Paguridae. Megalopae also showed significant ED variability among families (Kruskal-Wallis test, $p < 0.0001$), with Grapsidae being significantly greater than Cancridae and Xanthidae; Paguridae significantly greater than Cancridae, Porcellanidae and Xanthidae; and Majidae significantly greater than Porcellanidae.

Three amphipod species were collected in 2017: *Hyperia medusarum*, *Themisto pacifica* and *Cyphocaris challengerii.* ED values were significantly different among species (Kruskal-Wallis test, $p < 0.0001$) and varied widely (Table 1). Additional variability in ED was observed when *H. medusarum* was separated by sex, with females exhibiting a significantly higher ED compared to males ($p = 0.004$, Table 1).
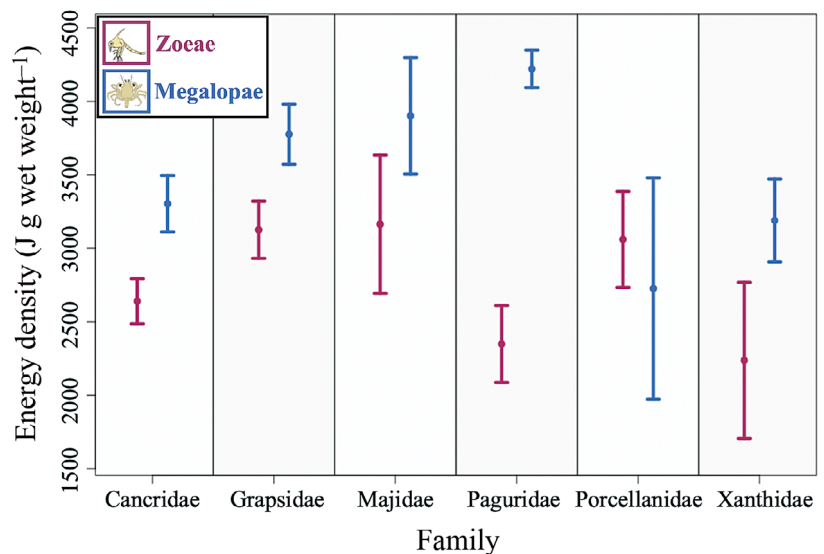

Fig. 2. Mean energy density (ED) and 95% confidence limits for decapod zoeae (pink) and megalopae (blue) separated by family. For all families, megalopae had a significantly greater ED compared to zoeae, except for Porcellanidae

3.2. Temporal variability in ED

Six species groups were observed in at least 4 of 6 sampled months and were assessed for temporal changes in ED (Table 1). Significant monthly dif- ferences in ED were observed (Kruskal-Wallis test, $p < 0.01$ for all groups except cancrid megalopae); however, temporal trends were not consistent among taxa (Fig. 4). Cancrid zoeae had a signifi- cantly lower ED in May compared to later months,

Table 1. Overview of the variability in fine-scale species/group energy density (ED) values observed during 2017 sampling. Sample size (N), mean ED and standard error (SE) for all species/groups are reported. Monthly ED values are reported as mean ± SE (N). Dashes (–) represent months where no individuals were observed

Group/taxon	N	Grand mean ± SE (J g^{-1})	Apr	May	Jun	Jul	Aug	Sept
Copepods	88	2729 ± 77	—	2674 ± 212 (18)	2719 ± 318 (10)	3165 ± 137 (20)	2431 ± 82 (32)	2966 ±183 (8)
Octopus	5	2175 ± 389	1316 ± 234 (2)	—	—	2748 ± 276 (3)	—	—
Cumaceans	1	2823	—	2823 (1)	—	—	—	—
Mysids	2	2858 ± 123	—	—	—	—	—	2858 ± 123 (2)
Decapod zoeae								
Cancridae	75	2640 ± 82	—	1679 ± 123 (15)	2902 ±74 (44)	2508 ± 230 (7)	3029 ± 386 (4)	3090 ± 242 (5)
Grapsidae	18	3127 ± 99	—	—	—	2968 ± 151 (7)	3288 ± 123 (10)	2622 (1)
Majidae	6	3164 ± 240	—	—	—	3189 ± 370 (4)	3112 ± 207 (2)	—
Paguridae	23	2349 ± 157	—	1781 ± 206 (10)	2809 ± 160 (11)	2660 ± 267 (2)	—	—
Porcellanidae	58	3060 ± 93	—	—	3134 ± 134 (30)	2912 ± 193 (14)	3052 ± 174 (14)	—
Xanthidae	3	2238 ± 564	—	—	—	1274 (1)	2720 ± 508 (2)	—
Pinnotheridae	10	3160 ± 291	—	—	4957 (1)	—	2960 ± 237 (9)	—
Decapod megalopae								
Cancridae	106	3303 ± 98	—	—	3157 ± 154 (45)	3316 ± 153 (39)	3573 ± 216 (20)	3641 ± 1368 (2)
Grapsidae	89	3776 ± 105	—	—	3281 ± 391 (4)	3649 ± 171 (20)	3824 ± 131 (64)	5236 (1)
Majidae	8	3902 ± 215	—	3343 ± 202 (2)	4088 ± 236 (6)	—	—	—
Paguridae	17	4221 ± 69	—	—	4221 ± 69 (17)	—	—	—
Porcellanidae	4	2727 ± 384	—	—	2625 ± 524 (3)	—	—	3032 (1)
Xanthidae	39	3189 ± 146	—	—	3957 (1)	3017 ± 229 (15)	3268 ± 195 (23)	
Caridean zoeae	54	3584 ± 124	—	2925 ± 346 (4)	3424 ± 981 (3)	3405 ± 151 (18)	3724 ± 195 (25)	4294 ± 398 (4)
Caridean adults	3	2873 ± 181		—	—	—	—	2873 ± 181 (3)
Euphausiids								
Euphausia pacifica	251	3411 ± 27	3428 ± 37 (36)	3353 ± 93 (37)	3896 ± 47 (50)	3275 67 (30)	3190 ± 28 (61)	3274 ± 47 (37)
Thysanoessa spinifera	1	3525	—	—	3525 (1)	—	—	
Euphausiid furcilliae	4	4069 ± 627	—	—	5947 (1)	—	—	3443 ± 50 (3)

Table 1 (continued)

| Group/taxon	N	Grand mean ± SE (J g^{-1})	Apr	May	Jun	Jul	Aug	Sept
Amphipods								
Gammaridae (unidentified)	8	3946 ± 281	3519 ± 1011 (2)	—	4089 ± 251 (6)	—	—	—
Cyphocaris challengerii	171	4305 ± 73	3693 ± 285 (8)	4079 ± 255 (17)	4617 ± 128 (41)	3663 ± 112 (33)	3819 ± 209 (16)	4750 ± 123 (56)
Hyperia medusarum	141	2537 ± 33	—	—	2631 ± 60 (51)	—	—	2484 ± 37 (90)
Hyperia medusarum (adult females)	73	2593 ± 45	—	—	2757 ± 147 (11)	—	—	2569 ± 46 (62)
Hyperia medusarum (adult males)	44	2387 ± 52	—	—	2547 ± 110 (16)	—	—	2296 ± 45 (28)
Hyperia medusarum (juvenile females)	12	2596 ± 134	—	—	2596 ± 134 (12)	—	—	—
Hyperia medusarum (juvenile males)	12	2690 ± 100	—	—	2690 ± 100 (12)	—	—	—
Themisto pacifica	210	3397 ± 48	2642 ± 216 (12)	3421 ± 139 (34)	3506 ± 76 (73)	3413 ± 71 (53)	3760 ± 166 (19)	3010 ± 138 (19)
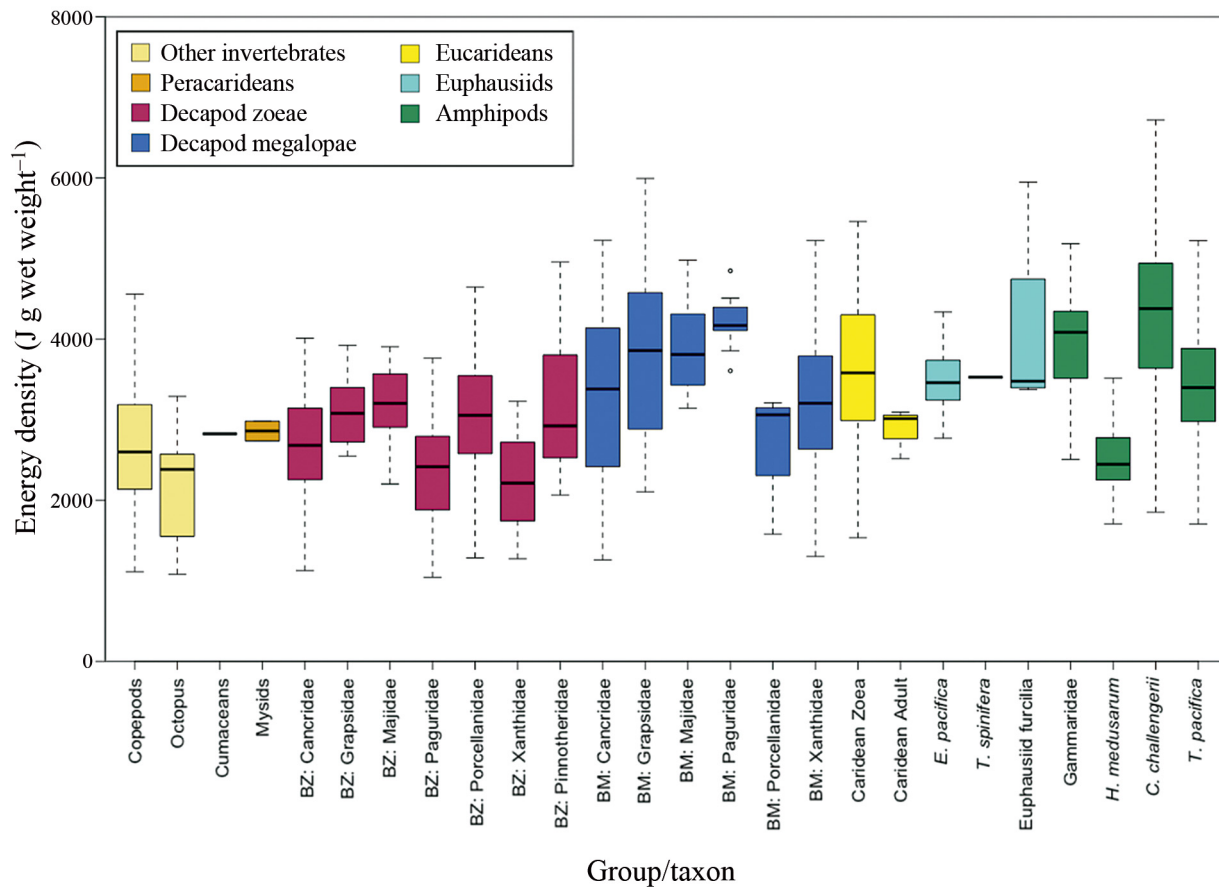
Fig. 3. Energy density (ED) values showing variation among taxa traditionally grouped together in ED analyses. Box plots display the range of energy density values for all invertebrate species or groups sampled during the 2017 season. BZ: brachyuran zoeae; BM: brachyuran megalopae. Boxes display the middle 50% of data points, bold lines represent the median value and whiskers denote the smallest and largest values within 1.5 times the interquartile range. Outlying values greater than this range are presented as single points outside of whiskers
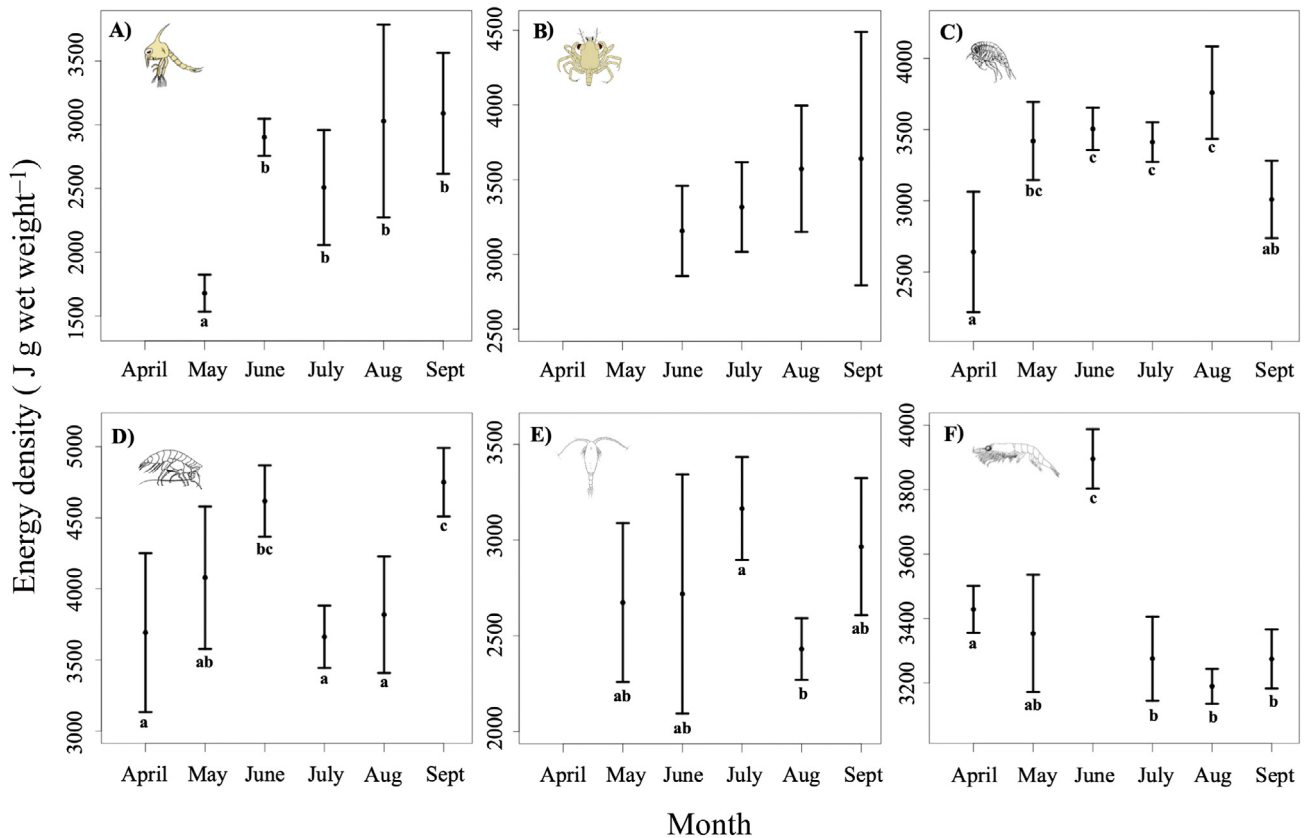
Fig. 4. Mean energy density (ED) and 95% confidence limits for (A) cancrid zoeae, (B) cancrid megalopae, (C) *Themisto pacifica*, (D) *Cyphocaris challengerii*, (E) copepods and (F) *Euphasia pacifica* sampled between April and September 2017. Different lowercase letters below confidence limits indicate significant differences (p < 0.05), as determined by multiple pairwise Wilcoxon rank sum tests. Monthly differences in ED were observed for all groups except cancrid megalopae, but variability was not consistent between groups

when ED did not vary significantly (Fig. 4A). Cancrid megalopae showed a general increasing trend in ED from June through September, but this trend was not significant (Fig. 4B). *T. pacifica* had a significantly lower ED in April compared to May through August, when ED did not change significantly (Fig. 4C). In September, *T. pacifica* experienced a significant decline in ED from values observed in June through August. *C. challengerii* ED values were greatest in June and September compared to other months (although May and June values were not significantly different; Fig. 4D). Copepods (not separated to the species level) showed little variability in ED between May and September, although this group did show a significant decrease between July and August (Fig. 4E). *Euphausia pacifica* had significantly greater ED values in April and June compared to other months (although April and May values were not significantly different; Fig. 4F).

3.3. Bioenergetic and growth differences

The diets of 322 juvenile Chinook salmon were sampled by W.D.P. Duguid et al. (unpubl. data) from July to October 2015. Of these individuals, 259 contained zooplankton species for which fine-scale ED was measured in 2017, and these species were pooled to create the mean diet sample. The proportional mass of contributing prey groups to our example diet is described in Table 2. These groups represented 43, 35, 14 and 9% of the total proportional prey mass observed in the diet in July, August, September and October 2015, respectively. Prey fish were not included in these analyses despite their importance in the diet, due to insufficient taxonomic coverage in 2017 sampling. Whole-diet ED calculated using fine-scale taxonomic groupings was 3125 J g^{-1}. Taxon-averaged coarse-scale grouping of prey resulted in a diet ED of 3189 J g^{-1}. For our single-species representative coarse-scale approach, 9 decapod groups and 2 hy-

Table 2. Fine- and taxon-averaged coarse-scale energy density (ED) and prey proportions used to calculate whole-diet ED for juvenile Chinook salmon in bioenergetics models. Prey groups listed were observed in both juvenile Chinook salmon with non-empty stomachs during 2015 sampling in the Salish Sea as well as in 2017 prey sampling (n = 259)

Coarse-scale group	Fine-scale group	Fine-scale ED (J g^{-1})	Taxon-averaged coarse-scale ED (J g^{-1})	Proportion of diet (%)
Decapod	Cancrid megalopae	3303	3236	47.67
Decapod	Xanthid megalopae	3189	3236	15.76
Decapod	Brachyuran zoeae	2757	3236	12.18
Decapod	Porcellanid zoeae	3127	3236	6.04
Decapod	Porcellanid megalopae	2727	3236	2.08
Decapod	Grapsid megalopae	3776	3236	0.97
Decapod	Pinnotherid megalopae	3160	3236	0.85
Decapod	Majid megalopae	3902	3236	0.34
Decapod	Pagurid megalopae	4221	3236	0.06
Decapod	Pagurid zoeae	2349	3236	<0.01
Hyperiid	*Hyperia medusarum*	2516	2898	10.20
Hyperiid	*Themisto pacifica*	3397	2898	3.84
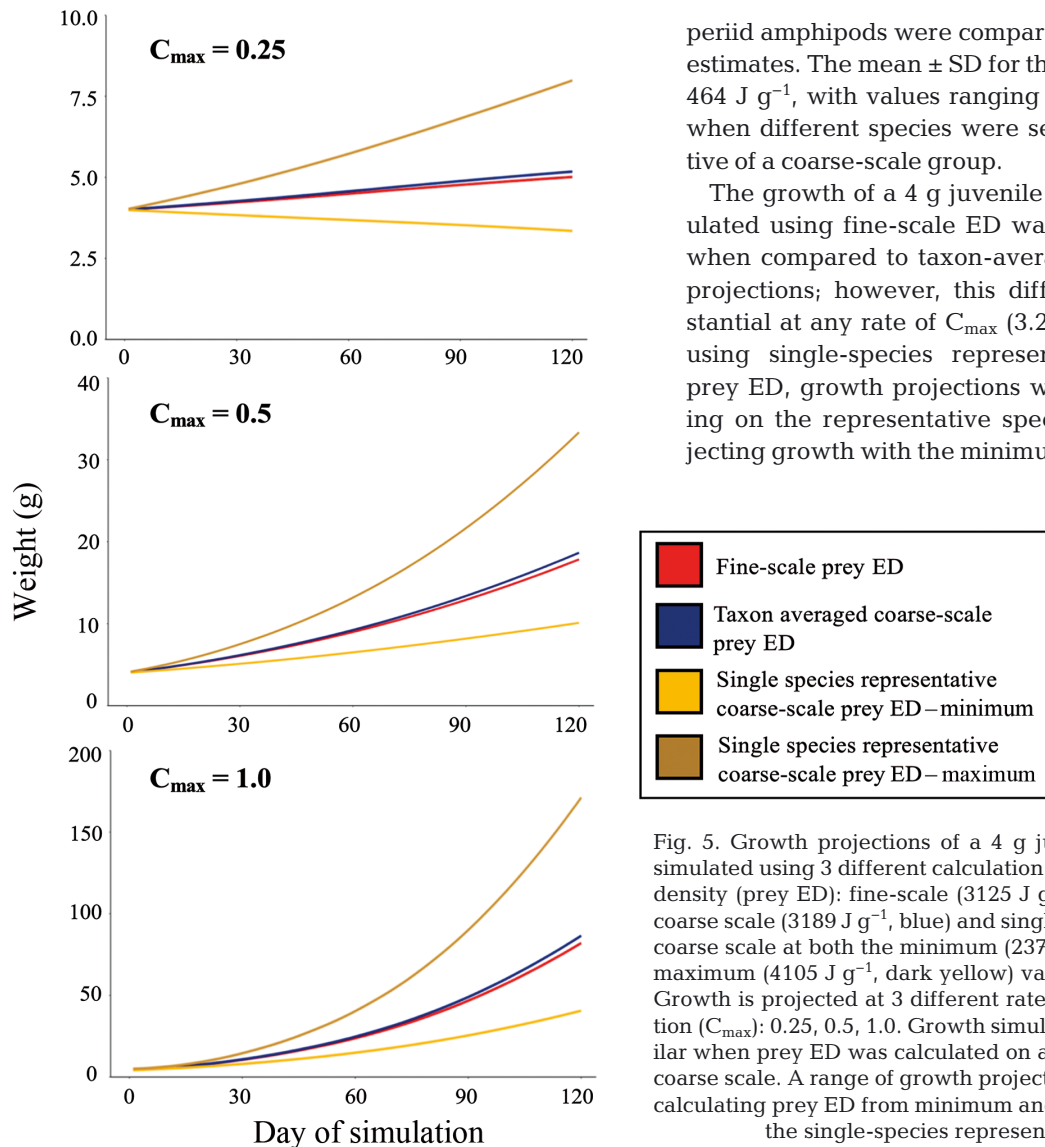
periid amphipods were compared, for a total of 18 ED estimates. The mean ± SD for these values was 3175 ± 464 J g^{-1}, with values ranging from 2372–4105 J g^{-1} when different species were selected as representative of a coarse-scale group.

The growth of a 4 g juvenile Chinook salmon simulated using fine-scale ED was consistently smaller when compared to taxon-averaged coarse-scale ED projections; however, this difference was not substantial at any rate of C$_{max}$ (3.2–5.5%, Fig. 5). When using single-species representative estimates for prey ED, growth projections were variable depending on the representative species used. When projecting growth with the minimum ED value produced

Fig. 5. Growth projections of a 4 g juvenile Chinook salmon simulated using 3 different calculation methods for prey energy density (prey ED): fine-scale (3125 J g^{-1}, red), taxon-averaged coarse scale (3189 J g^{-1}, blue) and single-species representative coarse scale at both the minimum (2372 J g^{-1}, light yellow) and maximum (4105 J g^{-1}, dark yellow) values that were observed. Growth is projected at 3 different rates of maximum consumption (C$_{max}$): 0.25, 0.5, 1.0. Growth simulated after 120 d was similar when prey ED was calculated on a fine- or taxon-averaged coarse scale. A range of growth projections was observed when calculating prey ED from minimum and maximum values using the single-species representative method

with this method, we observed a 33–51% reduction in final weight compared to fine-scale ED estimates, depending on C_{max}. Final weights projected using the maximum ED value estimated with this method were 59–109% heavier across the range of C_{max} values compared to fine-scale ED estimates. Thus, while growth projections made using taxon-averaged coarse-scale ED may closely approximate those made with fine-scale ED estimates, using a single-species representative approach has the potential to substantially alter growth outputs, depending on representative species used.

4. DISCUSSION

Several invertebrate prey groups found in the diet of juvenile Chinook salmon exhibited ED variability across species and families, but also within single species, depending on life stage and sex. Typically, this fine-scale variability is not accounted for in estimates of diet ED, where ED values for individual species are taken from literature values for broad groups (e.g. Duffy et al. 2010). These studies typically borrow ED values from a few key sources (e.g. Davis 1993, Davis et al. 1998) and evaluate diet ED based on average values, or take a single species as representative of a larger group. We determined that while significant taxonomic variability exists between invertebrate taxa, averaging values of these groups together will produce similar whole-diet ED estimates to those determined through fine-scale taxonomic classification. While this method saves time in sorting and analysing prey, it still relies on the direct sampling of zooplankton in diet studies.

The other method we tested for estimating coarse-scale prey ED, using a single species as representative of a larger group, can produce a much wider range of whole-diet ED estimates. Estimates calculated using each combination of species observed in 2017 produced values ranging from 2372–4105 J g⁻¹. Based on these results, we would advise against this method, unless a detailed *a priori* knowledge of the fine-scale taxonomic components of the diet is available. For instance, given our sampling, using xanthid and pagurid zoeae as well as porcellanid megalopae as representative of their respective groups would all produce a low-biased estimate of whole diet ED, whereas using grapsid, majid and pagurid megalopae as representatives would all produce a high-biased estimate. In general, using solely zoeae as being representative of all decapod larvae would also produce a low-biased estimate. Similarly for

hyperiid amphipods, using *Hyperia medusarum* to represent the group would produce a low-biased estimate, whereas using *Themisto pacifica* would produce a high-biased estimate for the ED contribution of this group. If choosing this method, sample bias may be avoided by visually surveying the diet for key groups at sea and employing a single-species estimate when the majority of the diet is composed of a unique species or group.

Several studies have found amphipods, in particular hyperiids, to be important diet items for juvenile salmon throughout their range (Neville & Beamish 1999, Schabetsberger et al. 2003, Bollens et al. 2010). Beamish et al. (2016) found strong selectivity for 2 hyperiid species, *T. pacifica* and *Primno abyssalis*, in juvenile sockeye salmon *Oncorhynchus nerka* migrating from the Harrison River in British Columbia, Canada. The authors hypothesized that enhanced productivity in this stock was tied to feeding on these 2 species following ocean entry. In our study, *T. pacifica* was observed to have greater ED values than other hyperiid amphipods and most decapod larvae, lending support to this hypothesis. The regular occurrence of both *T. pacifica* and *H. medusarum* in the diet of juvenile salmon may be due to the association of amphipods with gelatinous zooplankton (Harbison et al. 1977), facilitating their capture. Juvenile Chinook salmon may even seek out aggregations of gelatinous zooplankton to feed upon associated hyperiid prey (Schabetsberger et al. 2003). Weil et al. (2019b) observed an association between the abundance of medusae in the environment and predation by juvenile Chinook salmon on a specific hyperiid amphipod, *H. medusarum*. They observed selective feeding based on size and sex, where fish preferentially fed upon large, female individuals. In the present study, we show that the ED of *H. medusarum* was significantly greater in females (mean of 2593 J g⁻¹) than in males (mean of 2387 J g⁻¹). Is it possible that females are being targeted by Chinook salmon 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 fishes (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.

Temporal variability was observed for most groups investigated, but ED trends did not covary by month. 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 moulting cycles. Unfortunately, life history and moult timing data are limited for planktonic invertebrates and only general descriptions of feeding patterns are available. It is likely that individuals collected in this study were sampled during different stages of moulting or gonad development, though without species-specific descriptions of these processes, factors affecting temporal trends will likely remain poorly understood. *T. pacifica* and *Cyphocaris 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. *Euphausia 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 with higher ED in the summer months could explain the observed increase in ED in June, although we would also expect that trend to continue through July and August, which we did not observe. Reproductive variables may provide additional insight towards temporal ED variations. However, to date, no species-specific study has examined the reproductive cycle of *T. pacifica* or *C. challengerii* in the Salish Sea. A single study describes the reproductive cycle of *T. pacifica* in Southeastern Alaska on a 6–8 wk cycle (Wing 1976), which unfortunately fails to explain the significantly lower values observed in April and September in the present study. 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, cancrid megalopae and copepods) investigated for temporal variability were not classified to the species level. In these groups, temporal ED differences may be due to further fine-scale species- and stage-level variability than we examined here. Additionally, in each of these groups, we observed at least 1 month with a sample size of <10, which limits the explanatory power of these results, and could contribute to the lack of significant differences observed. Copepods have been investigated thoroughly and exhibit substantial variability in ED 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.

The bioenergetics model we used had several assumptions and limitations that qualify our results. Importantly, as we used a 'mean diet' to assess variability between ED estimates, we assumed that prey ED did not vary over the course of the 120 d simulation. While this allowed us to isolate and specifically test the effect of variable prey ED on growth, it ignored potential ontogenetic shifts in diet that may occur (e.g. Duffy et al. 2010). We attempted to mitigate any effects of a switch in diet by limiting the temporal scale of the simulation to the first 120 d at sea, when a small predator size and an associated gape limitation would prevent a transition away from a primarily invertebrate feeding mode. Differences in oxygen consumption rate between adult and juvenile Chinook (Trudel & Welch 2005) as well as variable predator activity costs (Trudel & Rasmussen 2006) are other well-known pitfalls of the bioenergetics models that we employed. Unfortunately, refining these variables would require additional lab or field experiments outside the scope of the present study. Further, there is currently no technique to explicitly model energy expenditure associated with prey search, capture, handling and digestibility. This limitation is of particular relevance to growing juvenile Chinook salmon that have the option of feeding on both invertebrate and vertebrate prey. While the availability of energy-dense invertebrate prey early in life may facilitate growth and a faster switch to a piscivorous feeding mode, the added costs associated with feeding primarily on invertebrates, even if they have high ED values, compared to fish make it unlikely that predators will continue to feed on invertebrates when they can limit energetic costs and maximize efficiency by switching to fish prey.

We determined fine-scale taxonomic variability in ED for several invertebrate groups important to the diet of juvenile Chinook salmon in the Salish Sea. However, 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). Our results represent only a snapshot of the total variability that likely exists in the diet of juvenile Chinook salmon. Notably, juvenile Chinook salmon typically experience a change in feeding mode to piscivory during the late summer (Daly et al. 2009, Duffy et al. 2010, Litz et al. 2017), typically occurring after the period simulated in our bioenergetics models. Indeed, the largest proportion of mass in the diet of juvenile Chinook salmon is typically made up of vertebrate prey (Brodeur & Pearcy

1990, Brodeur et al. 2007, Daly et al. 2009, Hertz et al. 2015). Thus, the next logical extension of this work would be a detailed investigation into species- and stage-specific ED values for fish prey. Further, although our bioenergetics modelling suggested that averaging similar species together may not introduce significant error into ED estimates for decapod larvae and hyperiid amphipods, this method should also be extended to test groups of fish prey as well. Fully characterizing fine-scale taxonomic and temporal variability in ED for both invertebrates and fish will aid in creating a more complete of view of the role of prey quality in juvenile salmon foraging ecology.

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