From earth and ocean: Investigating the importance of cross-ecosystem resource linkages in estuaries of the Pacific Northwest

by

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Abstract

Similar to how political boundaries do not reflect the cultural ties and ancestral lineages of human history, classical ecological perspectives often do not account for the complex relationships amongst ecosystems at local, regional or global scales. Cross-ecosystem resource linkages provide crucial subsidies to many ecosystems on Earth. Resource subsidies can contribute to the productivity, form, and function of recipient ecological communities. However, a subsidy's importance can vary widely among landscapes as a result of resource availability, ecosystem characteristics and consumer traits. Estuaries are composed of highly connected habitats that reside at the interface between terrestrial, freshwater and marine environments. Consequently, they are ideal systems to explore the importance of resource subsidies and how their role can vary spatially. This thesis examines the assimilation of, and response to resource subsidies in estuaries of the Northeastern Pacific. I focus on two spatial subsidies: terrestrial resources delivered to estuaries via the movement of freshwater, and salmon resources that enter coastal watersheds during fall spawning seasons. First, I show that species-specific distributions of live spawning salmon, their associations with terrestrial predators, and physical characteristics of individual systems drive salmon subsidies to riparian forests and estuaries. I then focus on subsidy responses in two estuarine consumers; soft-shell clam (*Mya arenaria*) and Dungeness crab (*Metacarcinus magister*). Through the use of stable isotopes, I demonstrate that landscape-level traits such as watershed size and salmon density drive the assimilation of subsidies in both species and that location within an estuary can mediate responses in sedentary consumers. However, terrestrial-derived subsidies also influence the size of individuals, suggesting this resource may have farther-reaching effects. Finally, I compare the dietary composition of three consumers and find that subsidy contributions increase with availability while accounting for other estuarine resources. Mobile consumers may benefit most, by being better able to exploit heterogeneous resource pools. This thesis demonstrates that terrestrial- and salmon-derived resource subsidies contribute to the resource base in estuarine ecosystems and that terrestrial subsidies may have the most pronounced effects. Ecosystems are connected, but the strength of these connections varies. It is therefore crucial to place resource dynamics within the context of specific landscapes and species to properly evaluate subsidy importance.

Keywords: Fisheries; Great Bear Rainforest; landscape ecology; *Mytilus edulis*; Pacific salmon; resource connectivity

*To my mother, Mary Janet Stoody, and my father,
David James Harding.*

I am forever grateful for their love, support and the values they instilled in me. They provided me with countless opportunities to discover, appreciate, and respect the natural world. They taught me to always consider others as we walk through this life. I have turned to these teachings many times throughout this degree.

“It is often said that science is ethically neutral and value-free. Such statements, in our opinion, are seriously misleading and in some respects quite false. It is, of course, obvious that a scientific discovery, once published ... can be used in exceedingly diverse ways, with consequences that may be good or bad, or commonly a complicated mixture of both. The activities of scientists and technologists, however, are conditioned and directed at every turn by considerations of human values. This is true over the whole range of activity, from the most basic research to the applications of science in technology.”

-The American Association for the Advancement of Science, 1975.

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List of Acronyms

AICc	Akaike information criterion corrected for small sample sizes
CPUE	Catch Per Unit Effort
DFO	Department of Fisheries and Oceans
POM	Particulate organic matter
SOM	Sediment organic matter

Chapter 1. Introduction

Classical views of isolated and compartmentalized food webs are giving way to broader understandings of landscape-level processes that influence the form and function of ecological communities (Polis et al. 1997). Within this broader context is the consideration of cross-ecosystem resource subsidies as a crucial component of intact landscapes (Polis et al. 2004, Richardson and Sato 2015). The movement of material and energy across ecosystem boundaries can constitute large proportions of the resource base that drives most communities on Earth, particularly in hydrologically connected ecosystems (Correll et al. 1992, Leroux and Loreau 2008). However, the importance of resource subsidies will vary over space and time due to natural variability in landscape traits and specific consumer life histories (Anderson et al. 2008, Yang et al. 2008).

Estuaries are excellent examples of highly connected ecosystems. They link terrestrial, freshwater and marine ecosystems and provide a conduit for the movement of water, organisms, detritus and dissolved nutrients between landscapes (Polis et al. 1997, Carr et al. 2003, Howe 2012). They are productive and open ecosystems (Elliott and Whitfield 2011) that are depositional in nature (Milliman and Syvitski 1992), capable of receiving substantial resource influx from upstream and offshore sources (Chester and Larrance 1981, Correll et al. 1992, Brion et al. 2008, Sakamaki et al. 2010, Vinagre et al. 2010). However, the importance of resource subsidies in estuarine ecology is less clear.

Within the Northeastern Pacific, no other subsidy topic has been studied more than Pacific salmon (*Oncorhynchus spp.*). A wide body of research has documented the importance of Pacific salmon in linking offshore marine productivity to coastal ecosystems (Cederholm et al. 1999, Gende et al. 2002, Naiman et al. 2002, Janetski et al. 2009). Although significant amounts of salmon nutrients are retained in coastal watersheds, large proportions are also moved downstream to estuaries (Gende et al. 2004a, Mitchell and Lamberti 2005, Cak et al. 2008). The significance of salmon subsidies in estuaries was only recently proposed in the mid 1990’s (Reimchen 1994) with occasional mentions in passing (Wipfli et al. 1998, Cederholm et al. 1999, Lessard and Merritt 2006). Otherwise, research on the topic is extremely limited focusing primarily on dissolved nutrient responses (Fujiwara and Highsmith 1997, Jauquet et al. 2003, Cak et al. 2008).

Terrestrial-derived resource subsidies also constitute a substantial proportion of resource inputs into estuaries, particularly in areas that receive high amounts of precipitation such as the Northeastern Pacific (Pojar et al. 1991). Although terrestrial subsidies can elevate organic content in estuaries (Hopkinson et al. 1999, Alliot et al. 2003, Sakamaki et al. 2010), few studies have attempted to detect productivity responses (Hoffman et al. 2007, Bănaru and Harmelin-Vivien 2009, Oczkowski et al. 2011) and even fewer have tested the degree to which responses can vary across landscapes (Harding and Reynolds 2014a, Harding et al. 2015). Although estuaries are one of the most productive habitats globally (Elliott and Whitfield 2011), the importance of resource inputs likely varies even at regional scales as a result of the complex interactions with surrounding landscapes.

This thesis explores the importance of salmon- and terrestrial-derived resource subsidies in estuaries of the Northeastern Pacific. I test hypotheses across natural gradients in salmon density, watershed size, and other landscape characteristics to investigate responses to resource subsidy inputs while accounting for the inherent variability among ecosystems. I begin in Chapter 2 by exploring how patterns in spawning salmon distributions, associations with terrestrial predators, and watershed-level traits determine the distribution of salmon nutrients within and among coastal watersheds and estuaries. In Chapters 3 and 4, I focus on two widespread estuarine consumers of the Northeastern Pacific: the soft-shell clam (*Mya arenaria*) and the Dungeness crab (*Metacarcinus magister*). I evaluate relationships between consumer traits (stable isotope ratios, size and abundance) and landscape characteristics to assess the importance of resource subsidies and how this varies within and across estuaries. Chapter 3 investigates subsidy response patterns in soft-shell clams while considering additional factors such as intertidal height, temperature, location within estuaries and clam age. Chapter 4 examines responses in Dungeness crabs and considers additional factors including estuary area and nutrient inputs from nitrogen-fixing alder trees.

Chapter 5 investigates the dietary composition of estuarine consumers in more detail. I consider a range of inferred dietary sources to examine variability in diets and how strongly this variability correlates with landscape characteristics. I attempt to assess these relationships within the context of providing insight about what types of species may benefit most from resource subsidies and whether watershed-level traits can indicate when a subsidy is most likely to be important. In Chapter 6, I provide a general overview of these results and contextualize how this thesis has contributed to what we know about the role of resource subsidies in estuarine ecosystems.

Chapter 2. Landscape structure and species interactions drive the distribution of salmon-derived nutrients in coastal watersheds[1]

2.1. Abstract

The disproportionate effects of uniquely important species can drive ecosystem processes and shape communities. Here we demonstrate how spawning salmon distributions within streams, and the associated responses of salmon predators, mediate the effect of salmon as a nutrient subsidy to adjacent riparian forests and downstream estuaries. We demonstrate how subsidies can vary spatially, within and among watersheds, through differences in pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon distributions within 16 streams on the central coast of British Columbia over a five year period. Spawning adult pink salmon were concentrated in lower reaches of all streams, whereas chum salmon shifted from lower to upper stream reaches as stream size, or the area of spawning habitat, increased. Salmon carcasses transferred to riparian areas by grey wolves (*Canis lupus*) were concentrated in lower stream reaches and estuaries; particularly shallow reaches of larger streams surrounded by large meadow expanses. Pink salmon carcasses transferred by black and grizzly bears (*Ursus americanus* and *U. arctos*) were also concentrated in lower reaches while chum carcasses were transferred throughout the spawning reaches of streams in much higher numbers. Lower proportions of salmon carcasses were exported downstream into estuaries when streams had longer spawning reaches. Total carcass input to estuaries varied between years and was dominated by pink salmon. These results show how subsidy effects of salmon vary between and within watersheds, as a result of species

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[1] A version of this chapter is in preparation for publication with Jennifer N. Harding, Rachel D. Field, Elizabeth J. Pendray, Noel R. Swain, Marlene A. Wagner, and John D. Reynolds

associations and local landscape traits and provide a nuanced, species- and spatially-explicit understanding of salmon carcass distribution.

2.2. Introduction

Relationships between the diversity and abundance of species and ecological processes (the amount, distribution and flow of matter or energy) are a fundamental tenet in ecology (Elton 1927, Odum 1968). Diverse communities are usually more stable, productive, and efficient at utilizing available resources than homogeneous communities as a result of higher numbers of energy pathways (Chapin et al. 1997). More recent perspectives have demonstrated how larger-scale characteristics, such as landscape structure, can set the stage for flows of energy between ecosystems via biotic and abiotic mechanisms (Turner 1989, Polis et al. 1997, Loreau and Holt 2004). Landscape ecology or ‘meta-ecosystem’ perspectives integrate the role of larger-scale mechanisms into how ecosystems function (Turner 1989, Loreau et al. 2003). Similar to how political boundaries do not reflect the cultural ties and ancestral lineages of human history, classical ecological perspectives, with the individual organism as a the primary point of reference, do not account for the complex relationships amongst ecosystems at local, regional or global scales (Loreau and Holt 2004, Polis et al. 2004). Cross-boundary resource exchanges in material, organisms and energy can form a major component of the resource base within ecosystems (Polis et al. 1997, Anderson et al. 2008, Hocking and Reynolds 2011). Although energy exchange amongst ecosystems is universal, cross-boundary resource subsidies play a larger role within certain landscapes (Loreau and Holt 2004). Nutrient linkages that are not limited by spatial proximity but rather driven by abiotic processes such as El Niño producing high rainfall (Holmgren et al. 2001), or biotic processes such as migration, can link spatially disparate ecosystems (Gravel et al. 2010).

Pacific salmon (*Oncorhynchus* spp.) provide one of the most ecologically important examples of broad-scale, cross-boundary life histories in the animal kingdom (Groot and Margolis 1991, Janetski et al. 2009). Freshwater habitats mark the beginning and end of a life cycle that is mostly spent in productive oceanic feeding grounds. Semelparous salmon rear in, and then return to, natal streams as adults to reproduce, thereby importing mass quantities of marine-derived material into coastal ecosystems throughout the North Pacific Rim. A wide body of research has documented the importance of Pacific salmon in linking offshore marine productivity to coastal ecosystems (Cederholm et al. 1999, Gende et al. 2002, Naiman et al. 2002). After spawning, their nutrient-rich carcasses are dispersed throughout streams, forests and estuaries by predators, scavengers and the movement of water (Cederholm et al. 1989, Quinn et al. 2009). Black and grizzly bears (*Ursus americanus* and *U. arctos*) can transfer large quantities of salmon-derived material from streams to riparian forests (Frame 1974, Hilderbrand et al. 1999, Reimchen 2000) as they exploit this predictable and accessible annual pulse of protein that constitutes a crucial resource during their preparation for winter dormancy (Quinn et al. 2003, Hilderbrand et al. 2011). Grey wolves (*Canis lupus*) are another major predator that can transfer salmon carcasses to riparian areas (Darimont et al. 2003). Isotope evidence suggests that wolves shift their diet from ungulates to more accessible salmon prey during fall spawning events (Darimont and Reimchen 2002, Darimont et al. 2008). Partially-consumed salmon carcasses deposited in riparian forests by these predators can increase soil organic content (Bartz and Naiman 2005, Gende et al. 2007), elevate nutrient content, shift diversity of riparian plant communities (Bilby et al. 2003, Hocking and Reynolds 2011), and provide substantial resources to terrestrial invertebrate communities (Hocking et al. 2009, 2013). Although salmon play crucial roles in stream ecosystems as a source of nutrients and disturbance (Janetski et al. 2009, Harding et al. 2014), considerable proportions of carcasses are also exported to estuaries (Gende et al. 2004a), which can elevate dissolved nutrient concentrations and provide substantial resource inputs into estuarine food webs (Cak et al. 2008, Harding and Reynolds 2014a, Harding et al. 2015). However, differences in salmon nutrient input to estuaries likely vary as a function of spawner distributions and stream length as carcasses are transported generally short distances downstream and are retained within pools and organic debris within streams (Cederholm and Peterson 1985, Minakawa and Gara 2005, Strobel et al. 2009).

To date, Pacific salmon have generally been grouped together in terms of their effect as resource subsidies despite variation in life histories. While all Pacific salmon likely subsidize coastal ecosystems to some extent, potential contrasts in how each species responds to habitat gradients may set the stage for more complex relationships between carcass dispersal mechanisms and thus subsidy potential of each salmon species (Hooper et al. 2005). A crucial consideration when assessing the subsidy potential of salmon is their distribution within streams. Variation in the distribution of live spawning salmon between species, or amongst streams, will affect the distribution of salmon-derived nutrients. The transfer rates of salmon carcasses to riparian forests by predators, or the export of carcasses downstream, may vary across space based on variability in spawning salmon distributions and other landscape traits such as stream size and depth.

In this paper we test how differences in the distribution of salmon species across heterogeneous landscapes can affect subsidy potential. We investigated how patterns in the distribution of live salmon, and the dispersal of dead ones, varied across coastal watersheds of the Northeastern Pacific that span a natural gradient in size, salmon density and other characteristics. First, we looked for differences in how live spawning pink (*O. gorbuscha*) and chum (*O. keta*) salmon distributed within streams. We focussed on these two salmon species because they constituted more than 95% of total salmon within our study area and thus are most important as a resource subsidy. We predicted that spawning pink salmon would concentrate in lower stream reaches, and chum in upper reaches, potentially because larger chum can successfully spawn in higher flows and larger substrate sizes of upper stream reaches (Hunter 1959, Scott and Crossman 1973, Hale et al. 1985, Raleigh and Nelson 1985). We then assessed patterns in salmon carcass transfer to riparian areas from adjacent spawning reaches by black and grizzly bears and grey wolves. From field observations, we predicted that wolf-transferred carcasses would concentrate in lower reaches of larger streams and therefore consist disproportionately of pink salmon given our previous predictions. We also expected that bear-transferred carcasses would occur throughout spawning reaches, particularly in upper portions of streams, across all stream sizes and consist mainly of chum salmon given preference for their larger size (Frame 1974). We also predicted the magnitude of predator-transferred carcasses would correlate positively with salmon density (Quinn et al. 2003) and negatively with stream depth due to reduced predator access to spawning salmon. Given our expectation that pink salmon will dominate lower stream reaches we also predicted that higher proportions of pink salmon carcasses would be exported into estuaries compared to chum salmon and that longer spawning reaches would reduce the proportion of carcasses that reach estuaries (Strobel et al. 2009). We use our findings to illustrate how species-specific responses, functional associations between species, and habitat traits can mediate the subsidy effects of salmon across coastal landscapes.

2.3. Methods

2.3.1. Study Area

We studied 16 salmon-bearing watersheds within 45 km of Bella Bella (52°9’N, 128°8’W) on the central coast of British Columbia, Canada (Figure 2.1). This region lies within the Coastal Western Hemlock-biogeoclimatic zone and receives some of the highest levels of precipitation on the continent (Pojar et al. 1991). Landscapes in this part of North America remain largely intact due to their remoteness, restricted access, governance by First Nations, and support from conservation coalitions (Price et al. 2009).

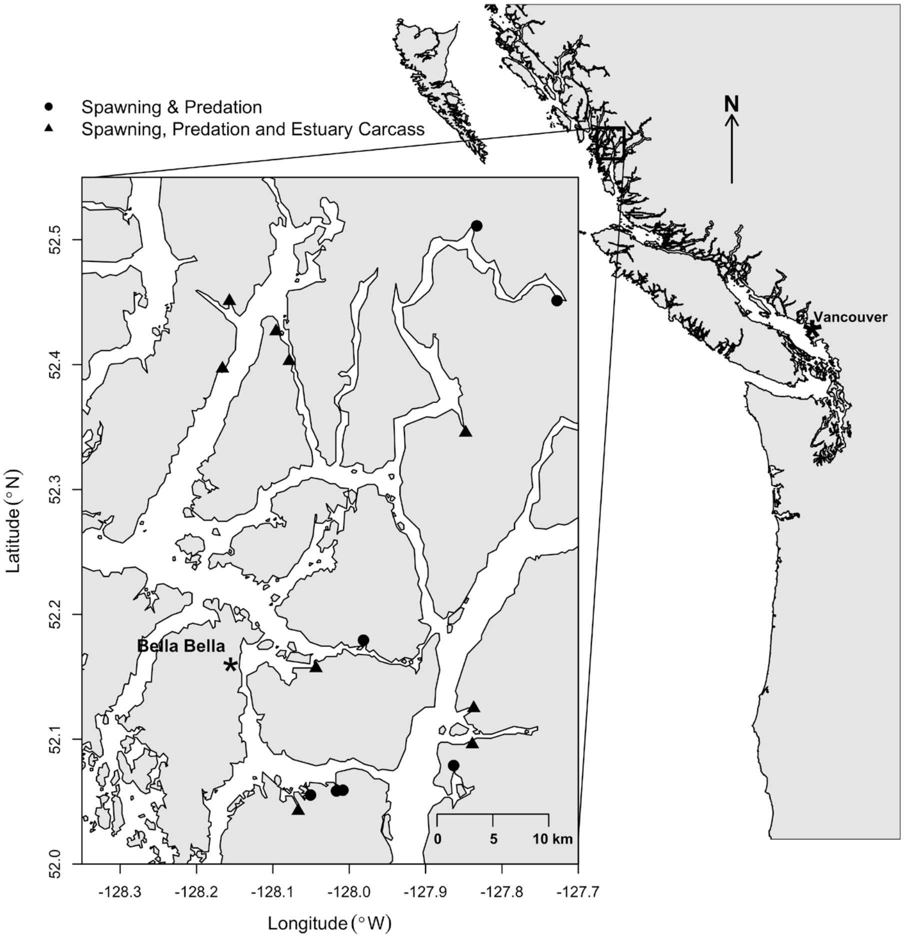

Figure 2.1. **Study area in the vicinity of Bella Bella, on British Columbia's central coast. Circles indicate spawning and predation study sites 2009-2013, triangles indicate where estuary salmon carcasses were also in 2008 and 2009.**

2.3.2. Salmon Surveys

Live and dead pink and chum salmon were enumerated over a period of five years (2009-2013). Not all streams were surveyed every year (Table A.1). We limited our analyses to pink and chum salmon as these species dominate our study region and account for 90-100% of total adult salmon spawners, with much smaller numbers of coho (*O. kisutch*) and a limited presence of sockeye (*O. nerka*) and Chinook salmon (*O. tshawytscha*).

Live salmon were counted in each stream 1 to 3 times per year during peak spawning periods, when the total numbers of actively spawning salmon are the highest. The first section counted in each stream was the spawning habitat in lower stream reaches below the highest extent of tidal coverage, which varied in length (Table A.1). The remaining spawning sections upstream of the estuaries were divided into sections ranging 50-200 m in length depending stream size, resulting in three to ten stream sections per site (excluding the lowest sections). Sections were measured in 50 m lengths or less using laser range finders accurate to the nearest meter. We counted live spawning salmon as we moved upstream and dead fish when returning back downstream. The entire spawning reach of each stream was surveyed. Most of these terminated at impassable barriers such as waterfalls or logjams. Sites that did not have barriers to migration were surveyed upstream until there were no longer salmon present. Enumeration of live and dead salmon was by visual estimation from riverbanks when possible, and from within streams when bankside vantage points were not present (i.e., canyons). Typically a 5-10 m length of stream was estimated at a time and totals were tallied once the end of a section was reached. At high densities, salmon were estimated in groups of tens to hundreds at a time and counted individually at lower densities. If weather conditions or turbidity prevented accurate enumeration, counts were omitted from analyses. Due to large differences in coloration and size, pink and chum salmon can easily be distinguished during counts. All crews were experienced in salmon enumeration and Canadian Department of Fisheries and Oceans (DFO) integrates our count data into regional salmon escapement estimates. We accounted for variation in salmon body mass among different spawning populations by weighing 5 dead adult salmon of each sex for each species from a subset of streams covering our study region. We selected salmon that were pre-spawn mortalities and relatively fresh. These mean salmon masses were applied to the remaining study sites sharing island groups, channels or mainland inlets.

Salmon carcasses were counted individually when possible and estimated in groups when necessary (e.g., bottom of large pools). Carcass categories were: senescent (spawned out), bear transferred, wolf transferred, and unknown. Carcasses were enumerated for each section of stream including a 10 m band of the riparian zone on either side of the stream channel for wolf- and bear-transferred carcasses, the riparian area known to contain the highest numbers of predated carcasses (Cederholm et al. 1989). Senescent carcasses were identified as those that had no sign of predation and were within stream channels or along banks. If the level of decomposition prohibited species identification or confirmation of predation, it was categorized as unknown and omitted from analyses.

Large differences between bear and wolf predation enable a considerable degree of certainty in determining which predator has consumed a salmon carcass. Bears consume multiple parts of a salmon including the brain, eggs and muscle tissue (Reimchen 2000, Gende et al. 2004b), while wolves almost exclusively consume the head (Darimont et al. 2003). While these patterns may not be universal, they are supported by our own observations of active predation and scavenging within our study region (Field and Reynolds 2013). We therefore categorized salmon that had been preyed upon as follows: wolf-transferred carcasses were counted as missing their heads or brains, occasionally with parts of the jaws still attached (Figure 2.2). There was no other part of the carcass consumed. Carcasses could have smaller bite marks but lacked major rips and tears to the rest of the body. Bear-transferred carcasses included evidence of consumed eggs, bites and tears to body cavity and trunk muscle tissue, large bites or claw marks in the dorsal hump, and consumed brains (Figure 2.3). When signs of predation were unclear carcasses were recorded as unknown and omitted from analyses. For each site, only one salmon count per year was used in analyses. Counts occurred as close to peak spawning periods as time permitted. When more than one count was completed in a given year we chose the count that had the highest number of live spawning pink and chum salmon combined.

Figure 2.2. **Wolf-transferred salmon carcasses with missing heads and minimal damage to body and trunk, no other parts of body consumed. Photo credit: Morgan Hocking (main), John Reynolds (inset).**

Figure 2.3. **Bear-transferred carcasses with tears to body and trunk muscles tissue with eggs often consumed. Photo credit: Ben Rabinovitch (main), Morgan Hocking (inset).**

In 2008 and 2009 intensive surveys were conducted for carcasses in the estuaries of a subset of 9 of our study sites (Table A.2). Intensive estuary surveys occurred separately from upstream counts because they were restricted to windows of low tide. All exposed carcasses, and submerged carcasses to -2.4 m (below 0 m tide) were counted by species. Carcasses that could not be identified to species were omitted from analysis. Individual carcasses were counted whenever possible and estimated when there were large accumulations. For the latter; areas of carcass accumulations were measured and multiplied by mean carcass counts from several random 1 m^2 quadrats subsampled from the accumulation. We were unable to consider predation in estuary carcass analyses as predation data collection began in 2009 for upstream sections and it was difficult to discern whether a carcass was actually consumed within an estuary or washed downstream afterwards.

2.3.3. Habitat characteristics

Habitat data were not collected every year as many of these metrics do not change substantially year-to-year. These measurements included the area of spawning habitat, stream depth, and estuary meadow area. Other data that could vary annually, such as stream discharge and salmon spawning density, were collected for each year. Spawning area (stream size) was calculated as the total length of spawning habitat within a stream multiplied by the mean wetted width. Stream depth and wetted width were measured at 12 random transects along a study reach. Each study reach length was determined by multiplying the mean stream bankfull width (mean width of the stream channel at its highest point before flooding banks) by 30 (Bain and Stevenson 1999). Estuary meadow area was measured by sketching meadows on air photos and calculating areas using the Government of British Columbia's mapping website *iMap*BC (Government of British Columbia 2006). Stream discharge was measured during each of the peak salmon-spawning periods of 2008 and 2009 at 3 randomly selected transects in each stream using a Flo-Mate 2000^{TM} portable flow meter. Stream discharge, the cubic meters of water output per second, was calculated by multiplying stream flow by the cross-sectional areas of water at each transect location. Salmon densities were calculated as the total count of each salmon species divided by spawning reach or section area.

We did not determine the number of wolves or bears at any of our sites. Similar to Quinn et al. (2003), we were not examining the responses of wolves or bears to salmon density, but rather the spatial patterns of wolf and bear consumption of salmon and resulting subsidies to riparian areas. Although the number of predators would affect the total number of salmon transferred to riparian areas, we were more interested in the spatial patterns of such transfers, including differences between pink and chum salmon, and links to physical characteristics of streams.

2.3.4. Statistical Analyses

We used generalized linear mixed-models to estimate the number of live spawners, wolf-transferred carcasses, and bear-transferred carcasses per section of stream. This allowed us to account for the hierarchical structure and non-normal distribution of count data (Zuur et al. 2009, Bolker et al. 2009). We tested for the effects of distance upstream, stream size and salmon species, including two-way interactions between all three variables, on number of live, wolf-transferred and bear-transferred chum and pink salmon per stream section. For wolf and bear analyses we also tested the effects of mean stream depth and estuary meadow area. We used the glmmADMB package in R using a negative binomial distribution with two random effects to account for intrinsic differences between sites and years beyond the scope of the dataset. We competed all models using Akaike Information Criterion corrected for small sample sizes (AICc), which selects the most parsimonious model of the candidate set of models given the data. Zero-inflation parameters were included in live spawner and bear, but not wolf, analyses based on visual inspection of the data and the resulting lower AICc values of the global model (the model containing all covariates considered). All covariates were centered in all analyses to avoid inaccuracies in slope estimates for main effects as they can vary considerably depending on the presence of interaction terms (Schielzeth 2010). A binary 'dummy' variable was included in all analyses to investigate the differences between pink and chum salmon species (0 = pink, 1 = chum) following the recommendations of Schielzeth (2010). Multicollinearity amongst all variables was generally low, with all variance inflation factors less than 3 and Pearson correlation coefficients less than 0.6 (Zuur et al. 2009, 2010). The open-source statistical software R was used for all analyses (R Core Team 2012).

We used a multi-model approach for wolf and bear analyses as top model weights were below 0.95 (Burnham and Anderson 2002). For multi-model inference we constructed models with scaled covariates (mean of 0 and standard deviation of 2) to enable direct comparison of effect sizes amongst covariates between wolf and bear analyses (Gelman 2008, Grueber et al. 2011, Barton 2012). Two data points were omitted from wolf and bear analyses due to leverage of the effects of salmon density (Crawley 2007). These were the two highest values of pink salmon section densities (6.4 and 7 salmon/m^2; remainder of data range pink and chum combined 0-2.8 salmon/m^2). Candidate models were limited to the subset of models with a ΔAICc less than 4 (Burnham and Anderson 2002). Parameter estimates for each variable were averaged across the candidate model set using the natural average method. Top model weights for both live spawner and estuary carcasses analyses were 0.99 and did not require model averaging.

Generalized-linear models were used to estimate the ratio of salmon estuary carcasses to the total number of salmon (live and dead) for each stream. In these analyses we used the total number of salmon within a stream, as opposed to section-specific numbers. Estimates of the total number of salmon in each stream were generated by DFO using the area-under-the-curve method (AUC) from salmon counts conducted by the Heiltsuk First Nation, Simon Fraser University and DFO (Irvine et al. 1992). When insufficient counts were completed for AUC estimation, peak abundance estimates were used, which are strongly correlated with AUC estimates in the stream we studied (Hocking and Reynolds 2011). We used a binomial distribution for proportional carcass data and re-fit with a quasibinomial to address overdispersion observed in model residuals. This did not change coefficient estimates but did increase standard errors around the estimates. Models were ranked using AICc and quasi-information criterion for small sample sizes (QICc) for binomial and quasibinomial models respectively (Lee and Nelder 1999, Anderson and Burnham 2002, Bolker 2014). Both AICc and QICc model rankings and weights were identical.

2.4. Results

In our study area, mean weights in different streams for pink and chum ranged between 0.9-1.3 kg and 2.5-3.6 kg, respectively. Over five years (2009-2013), a total of 718 sections of stream were surveyed for live and dead salmon. Section counts ranged between 0 and 7,200 and 0 and 1,990 for live pink and chum salmon spawners, 0 to 333 and 0 to 22 for wolf-transferred pink and chum salmon carcasses, and 0 to 165 and 0 to 194 for bear-transferred pink and chum carcasses, respectively. Estuary carcass counts (2008 and 2009) ranged between 0 and 21,909 and 8 and 7,820 for pink and chum carcasses, respectively. The supplemental information provides more detailed site-level summaries and model specifics.

2.4.1. Live Spawning Salmon

In small streams, both pink and chum spawning salmon were most abundant in lower stream reaches. However, as spawning area increased, pink salmon remained in lower reaches while chum salmon moved into upper stream reaches (Figure 2.4). The best model predicting spawner distributions had an Akaike weight >0.99, a pseudo-R^2 of 0.20, and contained all variables considered including distance upstream, total spawning area, and salmon species (Table A.3).

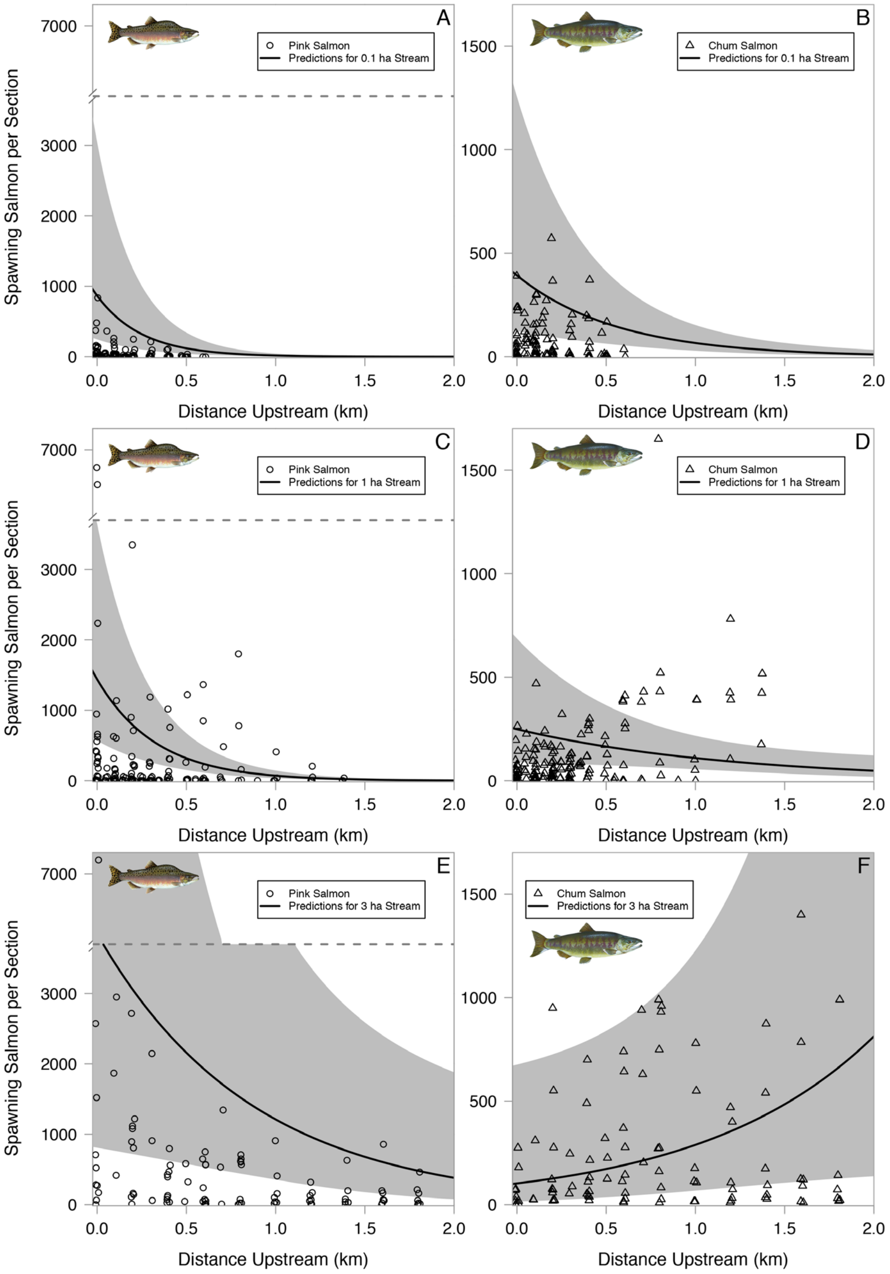

Figure 2.4. Live chum and pink salmon distributions. Pink salmon in left column, chum in right column. The top row shows observed data points for small streams, defined as the lower 25th percentile of stream areas. The prediction lines are for the top model, and based on a stream with 0.1 ha spawning area. The middle row illustrates a medium-sized stream, with observed data points between the 25th and 75th percentile of stream areas, and prediction lines for a 1 ha spawning area stream. The bottom row shows observed data points above the 75th percentile of stream sizes with prediction lines for a stream with a 3 ha spawning area. Shaded polygons indicate 95% confidence bands around model predictions.

2.4.2. Predation

Over five years we counted 1,424 and 3,871 wolf- and bear-transferred carcasses, respectively. Wolves transferred over three times more pink (1,125) than chum (299) carcasses. Bears transferred approximately half the number of pink (1,079) than chum (2,792) carcasses (Figure 2.5A-B). Section-level proportions of salmon transferred by wolves did not vary by salmon species, and bears transferred higher proportions of salmon than wolves, in particular chum salmon (Figure 2.5C-D). Stream-level proportions of wolf-transferred carcasses ranged between 0 and 3.6% and 0 and 8.1% for pink and chum salmon, respectively. Total proportions of bear-transferred carcasses ranged between 0 and 9.6% and 0 and 23.3% for pink and chum salmon, respectively. These estimates are low given the limited 10 m band of riparian area we surveyed and the discounting of unknown carcasses. The number of wolf-transferred carcasses decreased with increasing distance upstream for both pink and chum salmon (Figure 2.6A). Bear-transferred pink carcasses decreased similarly, but to a lesser degree than wolf carcasses, while bear-transferred chum carcasses increased in upstream sections (Figure 2.6B). Salmon density had a much lower effect on wolf-transferred carcasses than for bears, with wolf-transferred pink carcasses increasing only slightly at higher pink salmon densities (Figures 2.6C-D). The number of bear-transferred carcasses for both species increased with salmon density.

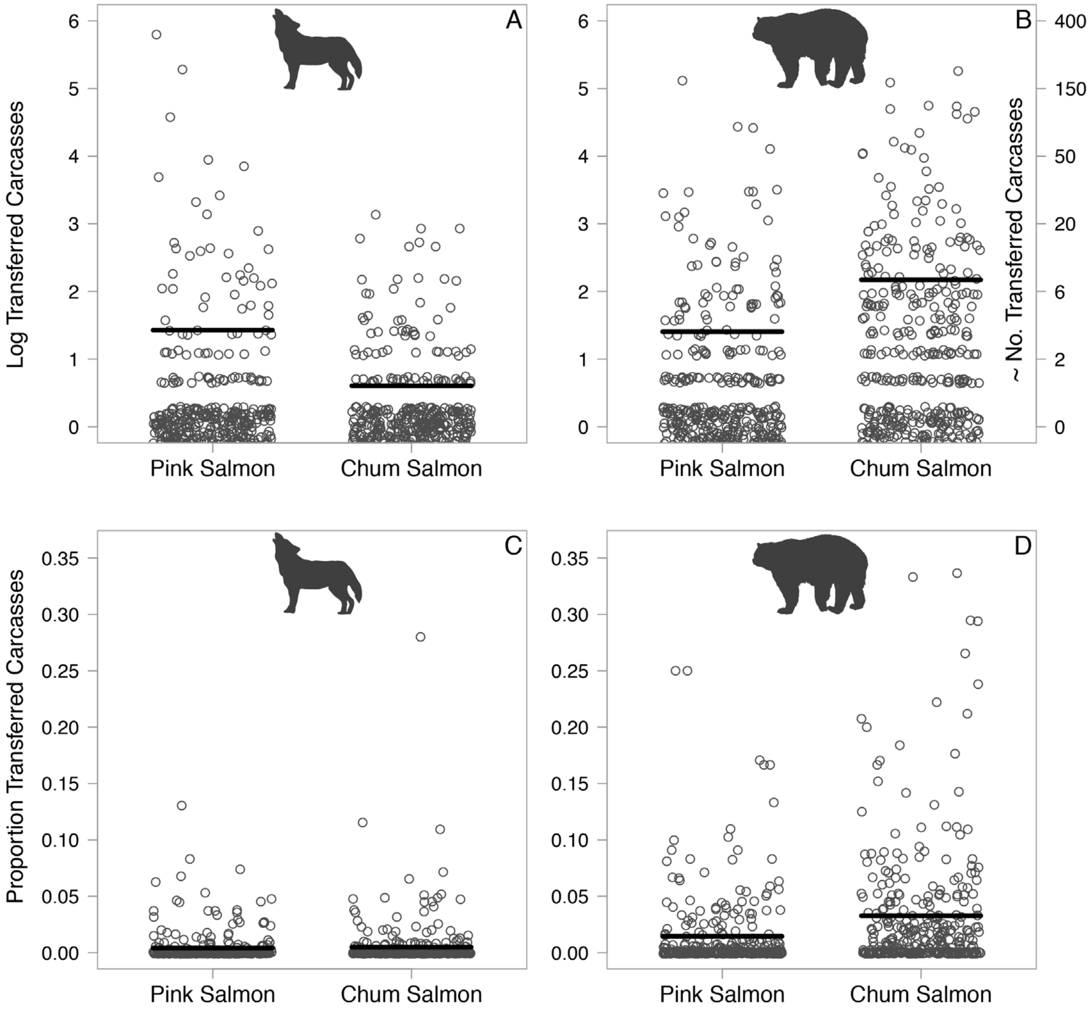

Figure 2.5. **Log-transformed counts of wolf- and bear-transferred carcasses for each salmon species per stream section (panels A and B). Proportion of total salmon consumed by wolves and bears per stream section (panels C and D). Proportions were calculated as the number of wolf- or bear-consumed carcasses relative to total salmon (sum of wolf and bear consumed, senescent and live) per stream section. Horizontal lines indicate mean values.**

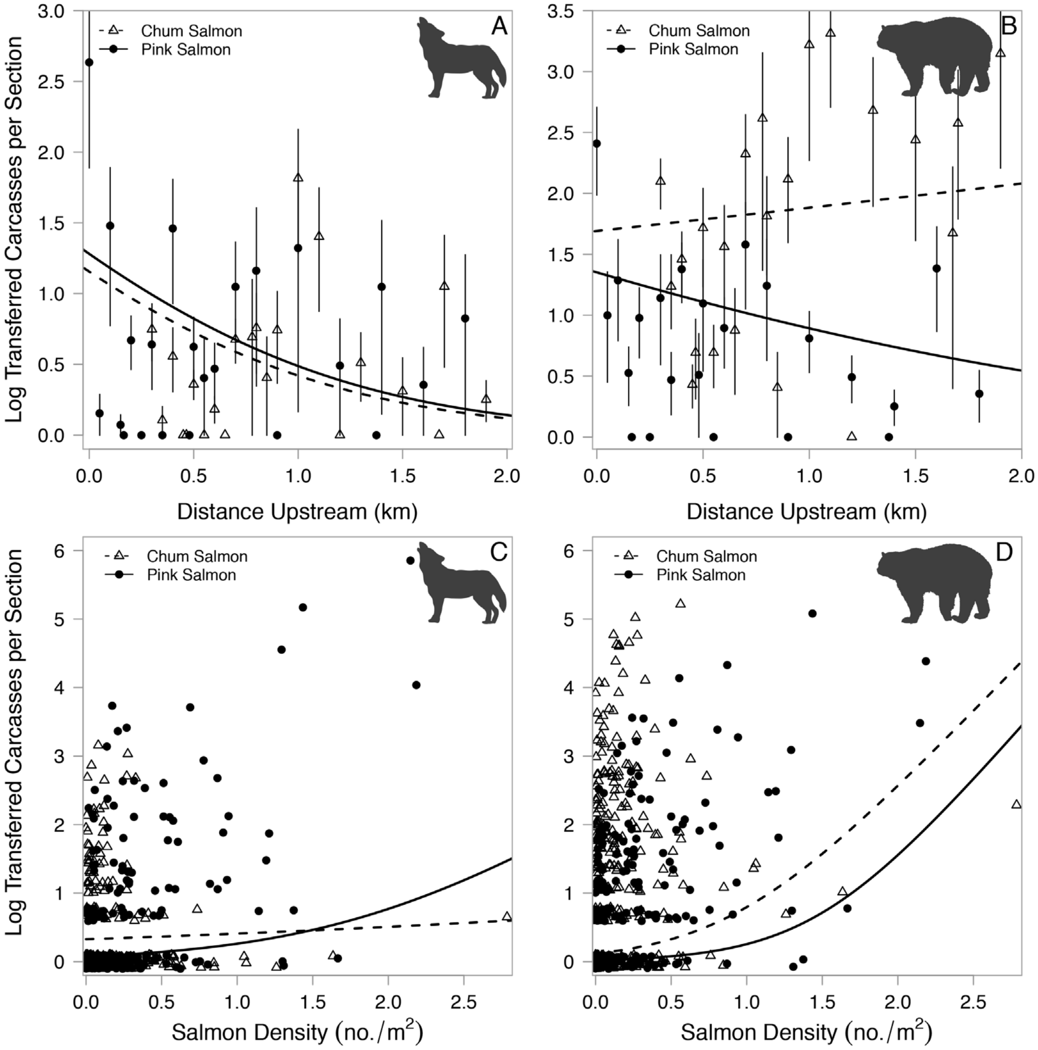

Figure 2.6. **Log-transformed counts of wolf- and bear-transferred carcasses for each salmon species per stream section with increasing distance upstream (panels A and B) and increasing salmon density (panels C and D). Data points are mean values with 95% confidence intervals for panels A and B and raw data points for panels C and D. Lines represent model predictions for each species with all other covariates held at mean values.**

The strongest correlates of wolf-transferred salmon were habitat traits; riparian areas adjacent to larger and shallower spawning areas, and surrounded by larger estuary meadows contained the largest numbers of wolf-transferred carcasses (Figure 2.7A). The negative correlation between distance upstream and wolf-transferred carcasses did not change with stream size but did strengthen at higher salmon densities (Figure 2.7A). For bear-transferred carcasses the negative correlation with distance was only notable when associated with pink salmon carcasses (Figure 2.7B). Bear consumption of salmon increased in streams with larger spawning areas but stream depth and estuary meadow had negligible or uncertain effects (Figure 2.7B). General patterns suggest that habitat traits drive wolf transfer of salmon carcasses while salmon density and species drive patterns in bear carcass transfers to riparian areas. Akaike weights for the top wolf and bear models were 0.59 and 0.10, with candidate sets consisting of 3 and 30 models, respectively (Anderson and Burnham 2002, Burnham and Anderson 2002). Averaged models had pseudo-R^2 = 0.24 for both analyses and are presented in Table A.4.

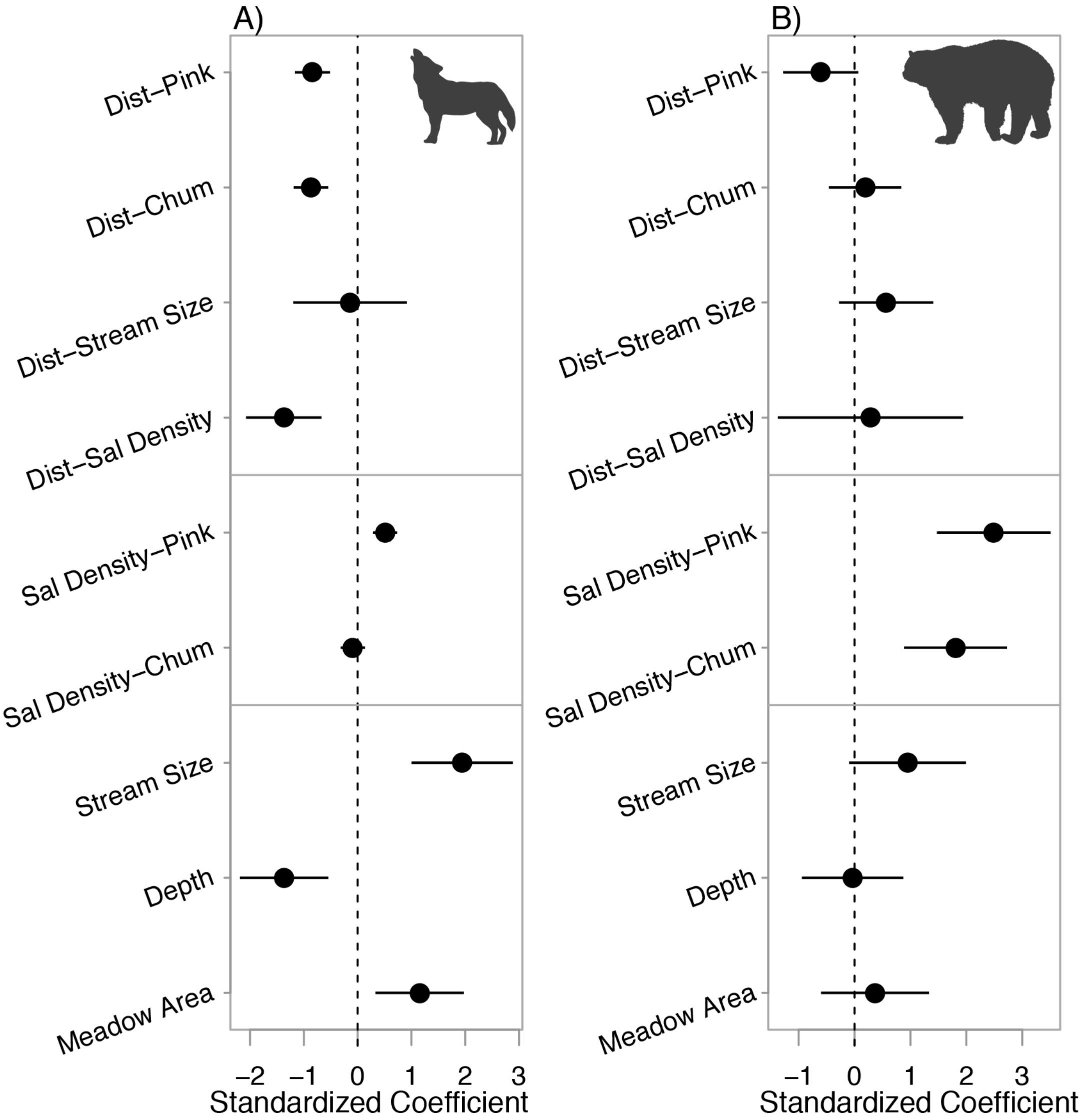

Figure 2.7. **Standardized coefficients (mean = 0, standard deviation = 2) with 95% confidence intervals for all covariates considered in the (A) wolf candidate model set and (B) bear candidate model set. Coefficient values indicate the average change in number of transferred carcasses per stream section as the associated covariate values increase by 2 standard deviations. Dist=distance upstream (km), Sal Density= salmon density (no./m^2), Stream Size = total spawning area. The top two rows show the relative effects of distance upstream on both wolf- and bear-transferred pink and chum carcasses as presented in Figure 6A-B. The two middle rows, isolated by horizontal lines, show the relative effect sizes of salmon density as presented in Figure 6C-D. Two variables separated by a hyphen indicate the effect of the interaction between those two covariates on wolf- or bear-transferred carcasses.**

2.4.3. Estuary Carcasses

The proportion of salmon carcasses that reached estuaries decreased with longer spawning reaches in streams. This negative correlation was stronger for pink salmon than chum salmon, opposite to our predictions (Figure 2.8A-B). The most parsimonious model describing the proportion of salmon carcasses in estuaries had a weight of evidence of 0.99 and included spawning length, an interaction between spawning length and salmon species, and upstream salmon density (Table A.5). Stream discharge and year were absent from this model. Estuaries below streams with spawning reaches less than approximately 1 km had higher proportions of pink carcasses while those below longer streams had higher proportions of chum carcasses (Figure 2.8B). Higher upstream salmon densities increased the proportion of estuary carcasses although shorter spawning reaches also resulted in large carcass proportions reaching estuaries (Figure 2.8C). Total numbers of estuary carcasses were highly variable between the two years. Carcass numbers, biomass, and biomass density were much lower in 2008 than 2009, which was a high pink-return year (Figure 2.9A-C). Chum salmon comprised the majority of 2008 carcass inputs into estuaries but pink salmon comprised the majority of carcasses in 2009, and for both years combined, even when correcting for differences in salmon size (biomass) and estuary size (biomass density).

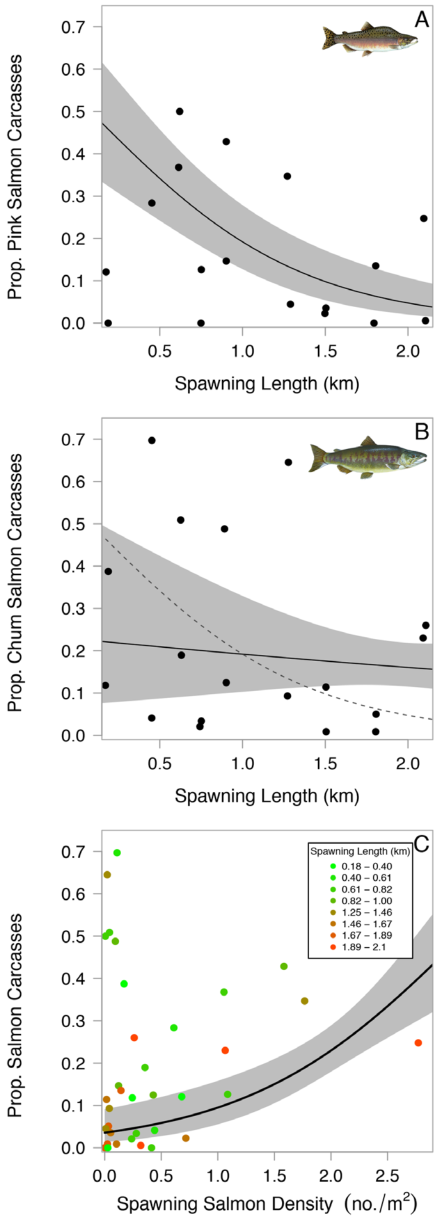

Figure 2.8. **Proportion of salmon carcasses in estuaries relative to total spawning salmon population as a function of length of spawning reach for: A) pink salmon and B) chum salmon. C) Proportion of salmon carcasses in estuaries as a function of total salmon density. Raw data points are colored according to spawning reach length. Solid lines and shaded polygons show model predictions and 95% confidence bands with all other covariates held at mean values. The dotted line in panel B shows pink model trend line for visual comparison between salmon species indicating chum carcasses become more abundant per stream section at approximately 1 km upstream.**

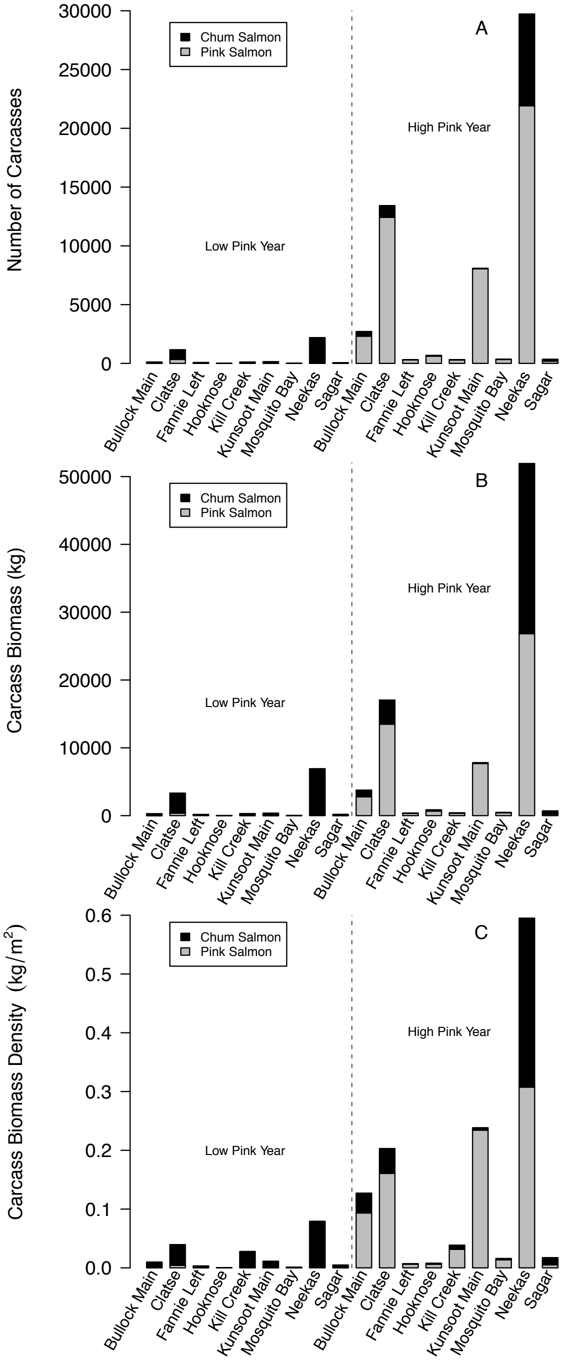

Figure 2.9. **Relative contributions of salmon carcasses to each estuary for a low pink return year (2008) and a high pink return year (2009). Panels show: A) total number of carcasses; B) total biomass of carcass and C) biomass density of carcasses. Salmon biomass was calculated by measuring the weight of 5 dead adult salmon of each sex for each species in a subset of study streams covering our study area in 2009. Biomass densities are calculated for the total area of exposed estuary at 0m tides.**

2.5. Discussion

The distribution of live pink and chum salmon was mediated by stream size, with the two species diverging in spawning distribution as stream size increased. Although these salmon species have similar spawning habitat requirements and overlap when spawning, chum salmon have a wider range of suitable habitat criteria due to their larger size. This includes spawning reaches with more variable discharge (Neave 1966a) and higher water velocities (Hale et al. 1985, Raleigh and Nelson 1985), and larger spawning substrate sizes (Hunter 1959). Chum may occupy upper reaches in larger streams as a density-dependent response to saturated habitat by pink salmon in lower reaches. Alternatively, higher peak discharge, or scour depths in upper reaches of larger catchments could constrain pink salmon to downstream areas. It is also possible that pink salmon may prefer smaller particle sizes and plane-bed channels of lower reaches while chum prefer upstream pool-riffle channel structures (Neave 1966b, Montgomery et al. 1999). Larger salmon, such as chum, are also able to dig nests in coarser particle sizes (DeVries 1997), enabling offspring to survive periods of high substrate scour (Montgomery et al. 1996). These contrasts in distribution set the stage for differences in how each species can subsidize adjacent landscapes, which have not been considered previously.

We were correct in our expectation that there would be more wolf-transferred salmon in estuaries and lower stream reaches, but we were wrong in our prediction that pink salmon would constitute the majority of wolf transfers. Wolf transfer of salmon carcasses was strongly driven by habitat characteristics, such as shallow reaches of larger streams surrounded by large open meadows, and not merely by the density or species of salmon.

Bear-transferred carcasses showed a different pattern. Distance upstream correlated negatively with the number of bear-transferred pink carcasses but had a negligible relationship with chum carcasses. There was a strong bias towards chum, indicating a potential bear preference for chum, possibly due to their larger size as suggested by Frame (1974). This bias could also be an artefact of the observation that bears consume salmon throughout stream reaches, of which chum salmon increasingly dominate in upper reaches of larger streams. Our analyses suggest that, on average, bears are transferring more chum than pink carcasses to riparian zones throughout stream reaches, regardless of stream size. In addition, the disparities between bear-transferred pink and chum salmon carcasses in riparian areas increased with distance upstream. This, supported by previous work showing that bear carcass transfers are density-dependent (Quinn et al. 2003), suggests bears are going where the highest salmon densities, particularly of chum salmon, are spawning and stream habitat traits are less important. Our expected effect of depth was contrary to work by Quinn et al. (2009) that reported larger percentages of carcass transfers at deeper streams. In our study region, depth did not influence amounts of bear carcass transfers; but deeper streams did correlate with reduced numbers of wolf transfers. Our contrasting results could relate to differences in stream depth, fish distribution or other habitat characteristics between Alaska and British Columbia. Reductions in wolf carcass transfers may reflect their limited ability to catch salmon in deeper spawning reaches.

Overall, the total quantity of salmon carcasses transferred to riparian zones by wolves and bears was highest in estuaries and declined upstream. This was due to decreases in total wolf-transferred carcasses and corresponding reductions in the number of pink carcasses transferred by bears. Therefore, the number of salmon carcasses transferred was roughly equal between salmon species in lower reaches but shifted to chum predominance in upper reaches of larger streams that was largely driven by bears. Overall, subsidy potential may be higher with chum salmon given their larger size, but this is contingent on the amount of carcass left by predators.

The use of a 10 m-wide riparian band to assess carcass transfers is appropriate as the majority of carcass transfers are thought to occur within the first 10 m of a stream (Cederholm et al. 1989). However, bears also transport salmon farther into adjacent forests, and this distance can vary with the salmon density, fish freshness, and whether a bear is lower in social hierarchies (Reimchen 2000, Gende and Quinn 2004, Quinn et al. 2009).

As we anticipated, salmon carcass inputs into estuaries were dominated by pink salmon as a result of pink salmon loading in lower stream reaches. We also expected, that as stream size increased, proportions of pink salmon carcasses in estuaries would remain relatively stable while chum carcass proportions would decrease as a result of the longer distances between chum spawner accumulations in upper reaches and estuaries. Our results contradicted these predictions, with pink carcass proportions decreasing more than chum carcasses as stream size increased. Although carcasses have been shown to travel short distances (Cederholm and Peterson 1985, Cederholm et al. 1989, Minakawa and Gara 2005, Strobel et al. 2009) high discharge events can cause longer distance transport (Glock et al. 1980). Thus, high rainfall and variable discharge regimes in our study region, which were not necessarily captured by our spot flow measurements, may export larger proportions of carcasses from upstream reaches. However, lower than expected proportions of pink carcasses below longer streams may be explained if portions of pink carcasses are washed seaward out of intertidal areas due to their smaller size. Alternative salmon metrics, such as biomass per unit stream discharge, may be more appropriate for other salmon inputs such as particulate matter or dissolved nutrients (Johnston et al. 2004, Cak et al. 2008).

Total carcass inputs into estuaries were highly variable between the two years. This could be driven by differences in pink salmon abundances that cycle between even and odd years. In 2008, a low pink-return year, carcass inputs were dominated by chum salmon and total numbers were much lower than the following pink-dominant year. Over both years combined total carcass inputs were dominated by pink salmon. This suggests that pink salmon populations could drive longer-term patterns in estuarine responses to salmon carcass subsidies (Harding et al. 2015). It is also possible that the comparatively prolonged spawning seasons of chum salmon could bias our carcass counts if the majority of chum salmon were still alive during surveys. However, the higher numbers of live pink salmon observed in lower reaches of streams, and the fact that chum salmon generally start spawning earlier than pink salmon within our study region, supports our confidence in these results (Neave 1966a). We did not observe notable separation of spawning periods between salmon species within sites during data collection.

We have shown how the potential effects of salmon nutrient subsidies in coastal ecosystems vary within and across landscapes, by species of salmon, and through associations with major predators. Studies do not currently consider taxonomic variability in salmon subsidy potential or spatial variability beyond average site-level salmon density metrics and comparisons of above and below salmon migration barriers (Hocking and Reimchen 2002, Mathewson et al. 2003, Harding and Reynolds 2014b).

These analyses could provide a framework to guide future studies investigating productivity responses to salmon subsidies in coastal systems that consider how subsidy effects on recipient ecosystems might be influenced by patterns in spawning salmon density and distribution and predator presence and abundance to further improve our understanding of complex, multi-scale ecosystem dynamics and processes. This work also highlights the importance of sound management decisions in the conservation and protection of salmon and large predator populations to maintain ecologically important functional associations that maintain nutrient linkages between offshore marine productivity and coastal forests and estuaries (Chapin et al. 1997, Helfield and Naiman 2006, Artelle et al. 2013).

Chapter 3. Location is everything: Evaluating the effects of terrestrial and marine resource subsidies on an estuarine bivalve[2]

3.1. Abstract

Estuaries are amongst the world's most productive ecosystems, lying at the intersection between terrestrial, freshwater and marine environments. They receive substantial inputs from adjacent landscapes but the importance of resource subsidies is not well understood. Here, we test hypotheses for the effects of both terrestrial- and salmon-derived resource subsidies on the diet (inferred from stable isotopes of muscle tissue), size and percent nitrogen of the soft-shell clam (*Mya arenaria*), a sedentary estuarine consumer. We examine how these relationships shift across natural gradients among 14 estuaries that vary in upstream watershed size and salmon density on the central coast of British Columbia, Canada. We also test how assimilation and response to subsidies vary at smaller spatial scales within estuaries. The depletion and enrichment of stable isotope ratios in soft-shell clam muscle tissue correlated with increasing upstream watershed size and salmon density, respectively. The effects of terrestrial- and salmon-derived subsidies were also strongest at locations near stream outlets. When we controlled for age of individual clams, there were larger individuals with higher percent nitrogen content in estuaries below larger watersheds, though this effect was limited to the depositional zones below river mouths. Pink salmon exhibited a stronger effect on isotope ratios of clams than chum salmon, which could reflect increased habitat overlap as spawning pink salmon concentrate in lower stream reaches, closer to intertidal clam beds. However, there were smaller clams in estuaries that had higher upstream pink salmon densities, possibly due to differences in habitat requirements. Our study

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highlights the importance of upstream resource subsidies to this bivalve species, but that individual responses to subsidies can vary at smaller scales within estuaries.

3.2. Introduction

Cross-ecosystem resource linkages can structure and stabilize recipient communities (Polis et al. 1997, 2004). Resource linkages, or subsidies, can be driven by abiotic mechanisms (Spiller et al. 2010, Lovelock et al. 2011), and biological processes (Sánchez-Piñero and Polis 2000, Stapp and Polis 2003). The effects of subsidies can also vary among ecosystems (Marczak et al. 2007, Nowlin et al. 2008), individuals (Anderson et al. 2008, Yang et al. 2010), and with the timing, quality or quantity of resource inputs (Yang et al. 2010, Marcarelli et al. 2011). Interface and hydrologically-linked landscapes such as estuaries have a particularly high potential to benefit from subsidies as upstream resources conveyed downstream provide nutrient inputs to these low-lying recipient ecosystems (Correll et al. 1992, Leroux and Loreau 2008, Richardson et al. 2009). Estuaries are at the intersection of terrestrial, freshwater and marine ecosystems and provide a conduit for the movement of resources among landscapes (Polis et al. 1997, Carr et al. 2003). They are productive, depositional and open ecosystems (Milliman and Syvitski 1992, Elliott and Whitfield 2011), capable of receiving substantial resource inputs from external sources (Chester and Larrance 1981, Sakamaki et al. 2010, Vinagre et al. 2010). However, the importance of resource subsidies in estuarine ecology remains less clear.

Locally-derived resources within estuaries have been thought to be of primary importance (Deegan and Garritt 1997, Chanton and Lewis 2002). However, more recent work has shown that externally-derived resources can form a major component of available estuarine resources (Darnaude et al. 2004a, Bănaru et al. 2007, Connolly et al. 2009). The magnitude of resource subsidy influx can also scale with the size of upstream ecosystems and stream flow (Sakamaki et al. 2010, Harding and Reynolds 2014a). Many of the previously mentioned studies have centered largely on the use of stable isotopes to investigate subsidy effects. Although they are a powerful tool in ecology, enabling us to trace resource pathways and relative contributions of potential energy sources (Fry et al. 1977, Peterson and Fry 1987), they are limited beyond confirmation of resource assimilation (Marcarelli et al. 2011). Consequently less is known about the biological importance of subsidies in estuaries.

Terrestrial-derived resources are often thought to be of lower quality than estuarine or marine sources (Deegan and Garritt 1997). Although they can elevate organic content in estuaries (Hopkinson et al. 1999, Alliot et al. 2003, Sakamaki et al. 2010), few studies have attempted to detect productivity responses from them (Hoffman et al. 2007, Bănaru and Harmelin-Vivien 2009, Oczkowski et al. 2011) and even fewer have tested the degree to which responses can vary across landscapes (Harding and Reynolds 2014a). Although estuaries are one of the most productive habitats globally (Elliott and Whitfield 2011), this likely varies even at regional scales as a result of the complex interactions with surrounding landscapes.

Around the Northern Pacific Rim, many estuaries also receive pulsed ‘counter-flow’ inputs of enriched marine-derived material from the annual migration of Pacific salmon (*Oncorhynchus* spp.). Because Pacific salmon die after spawning, they can function as one-way nutrient vectors, acquiring the majority of their body mass at sea (Groot and Margolis 1991), then transporting this mass back to natal streams. Their carcasses, which are relatively rich in nitrogen and phosphorus, are scattered throughout streams and riparian habitats by predators, scavengers and water flow. Due to the higher trophic level of salmon, and contrasts in biochemistry between marine and terrestrial systems, salmon nutrient subsidies can be differentiated from terrestrial sources using stable isotope ratios of nitrogen and carbon ($\delta^{15}N$ and $\delta^{13}C$); where salmon-derived material is enriched and terrestrial-derived material is depleted in heavy isotopes (Peterson and Fry 1987, Hocking and Reynolds 2011, Harding and Reynolds 2014a). The net effects of Pacific salmon in coastal ecosystems can vary (Janetski et al. 2009, Harding and Reynolds 2014a), ranging from nutrient subsidies through excretion and deposition of eggs and carcasses (Gende et al. 2002, Naiman et al. 2002, Hocking and Reynolds 2011), to benthic disturbance and nutrient export from juvenile salmon emigration and adults digging and defending nests (Moore et al. 2007, Tiegs et al. 2011, Kohler et al. 2013). In addition to streams and forests, estuaries also receive substantial amounts of salmon-derived nutrients from upstream watersheds (Gende et al. 2004a, Mitchell and Lamberti 2005, Cak et al. 2008). Although dissolved nutrient concentrations increase in estuaries during salmon spawning (Jauquet et al. 2003, Cak et al. 2008) and many estuarine organisms are known to consume carcasses (Reimchen 1994), few studies have investigated the importance of salmon subsidies in these communities (Fujiwara and Highsmith 1997, Cak et al. 2008, Harding and Reynolds 2014a).

Sedentary consumers such as bivalves not only provide an opportunity to investigate the importance of terrestrial- and salmon-derived resource subsidies in estuarine food webs, but also how these relationships might change spatially within, and across, landscapes. Bivalves integrate isotopes over time and can thus reveal resource contributions in relation to proximity of resource inputs (Chanton and Lewis 2002, Fry 2002, Kasai and Nakata 2005). Suspension feeders such as the soft-shell clam (*Mya arenaria*) are widespread in estuaries of the Pacific Northwest and have recently been shown to assimilate terrestrial-derived resources (Sakamaki and Richardson 2008a). Similar to the river continuum concept of Vannote et al. (1980), we hypothesize that estuarine organisms, such as the soft-shell clam, are influenced by resources derived from both upstream and marine landscapes, and that the importance of these resources will vary spatially with landscape traits. We further hypothesize that responses of sedentary consumers can vary based on their proximity to resource subsidies and local habitat conditions.

Here, we test hypotheses on how terrestrial and salmon resource subsidies, in addition to individual traits, explain the diet (inferred from stable isotopes of nitrogen and carbon), size, and percent nitrogen of soft-shell clams (Tables 3.1 and 3.2). We test for the effects of these covariates across 14 estuaries that span natural gradients in watershed size, spawning salmon density and other attributes (Table 3.3). Prior to our main analyses we tested metrics of chum (*Oncorhynchus keta*), pink (*O. gorbuscha*) and total (chum and pink combined) salmon density for their ability to explain isotope ratios of soft-shell clam muscle tissue. We hypothesized pink salmon may have a disproportionately large effect on bivalves because they spawn further downstream than chum salmon, including upper reaches of estuaries, and thus closer to bivalve habitats.

Table 3.1. Hypotheses for soft-shell clam stable isotope ratios ($\delta^{15}N$ and $\delta^{13}C$).

Variable	Mechanism	Metric	Level	Response	Reference
Salmon density	Salmon tissues are enriched in stable isotopes.	2006-2007 mean pink salmon biomass density (kg m^{-2})	Site	Positive	(Kline et al. 1993, Fujiwara and Highsmith 1997, Gende et al. 2002, Naiman et al. 2002, Kasai and Nakata 2005)
Watershed size	Terrestrial-derived material is depleted in stable isotopes.	Watershed size principal component axis 1 (PC1)	Site	Negative	(Fry 2002, Kasai and Nakata 2005, Galster 2007, Sakamaki and Richardson 2008a, Sakamaki et al. 2010)
Size	Larger individuals grow more slowly and have slower tissue turnover rates, which reflect dietary sources over longer time periods.	Mass (g)	Individual	Positive	(Rossi et al. 2004)
Age	Older individuals have more time to accumulate stable isotope ratios from enriched dietary sources.	Age (years)	Individual	Positive	(Martínez del Rio et al. 2009, Carleton and Martínez del Rio 2010)
Intertidal height	Individuals higher in intertidal will have lower isotopic discrimination as a result of more limited feeding opportunities.	Height above datum depth (m)	Within-site	Positive	(Honkoop and Beukema 1997, Bowes et al. 2014)
Temperature	Energy requirements for maintenance and growth increase with temperature, reducing isotopic discrimination.	Maximum weekly average temperature (MWAT °C)	Site	Positive	(Honkoop and Beukema 1997)
Clam bed zone	1) Moving outward from upper to lower zones (increasing distance from stream outlet) will reduce the effect of both salmon density and watershed size. 2) Moving outward from upper to lower zones will also correspond with increased dominance of marine resources and enrich isotopes.	Upper, middle and lower clam bed locations.	Within-site	1) Negative (in interaction with salmon and watershed size. 2) Positive as main effect.	(Fujiwara and Highsmith 1997, Fry 2002, Kasai and Nakata 2005, Cak et al. 2008)

Variable	Mechanism	Metric	Level	Response	Reference
Location	1) The effect of salmon and watershed size will increase going from control to below stream locations. 2) Clams below streams will experience increased influx of terrestrial resources, and therefore have depleted isotopes, compared to control locations.	Below stream and control sites.	Within-site	1) Positive (in interaction with salmon and watershed size). 2) Negative as main effect	(Fujiwara and Highsmith 1997, Fry 2002, Kasai and Nakata 2005, Cak et al. 2008)

Table 3.2. Hypotheses for soft-shell clam size and tissue %N.

Variable	Mechanism	Metric	Level	Response	Reference
Salmon density	Salmon tissues are higher quality than other sources, resulting in larger individuals and higher N content in tissues.	2006-2007 mean pink salmon biomass density (kg m^{-2})	Site	Positive	(Weiss et al. 2002, Bilby et al. 2003, Gende et al. 2004a, Carmichael et al. 2004, Hocking and Reynolds 2011, Carmichael et al. 2012)
Watershed size	Terrestrial-derived material can enhance organic content in estuaries, which could increase clam size and %N in tissues. It is also thought to be of lower quality and may displace higher-quality estuarine resources, reducing size and %N.	Watershed size principal component axis 1 (PC1)	Site	Positive/no effect/ negative	(Deegan and Garritt 1997, MacDonald et al. 1998, Weiss et al. 2002, Alliot et al. 2003, Kasai and Nakata 2005, Sakamaki et al. 2010)
Size (for %N only)	Larger individuals grow more slowly and have slower tissue turnover rates, which will reflect higher-quality dietary sources over longer time periods.	Mass (g)	Individual	Positive	(Carmichael et al. 2004, 2012)
Age	1) Size: Older individuals are larger. 2) %N: Younger individuals grow faster, resulting in higher percentages of nitrogen in their tissues.	Age (years)	Individual	1) Positive (for size) 2) Negative (for %N)	(Brousseau 1979, Carmichael et al. 2004, 2012)
Intertidal height	Individuals located higher in intertidal will have limited feeding opportunities This should result in smaller sizes and reduced N content (energy stores) in tissues.	Height above datum depth (m)	Within-site	Negative	(Honkoop and Beukema 1997, Bowes et al. 2014)

Variable	Mechanism	Metric	Level	Response	Reference
Temperature	Energy requirements for maintenance and growth increase with temperature, reducing opportunity for growth and energy stores.	Maximum weekly average temperature (MWAT °C)	Site	Negative	(Honkoop and Beukema 1997)
Clam bed zone	1) Moving outward from upper to lower zones (increasing distance from stream outlet) will reduce the effect of both salmon density and watershed size on mass and %N. 2) Moving outward from upper to lower zones will correspond with an increase in size and %N as marine resource availability increases.	Upper, middle and lower clam bed locations.	Within-site	1) Negative (in interaction with salmon and watershed size). 2) Positive as main effect	(Shurin et al. 2006, Rip and McCann 2011)
Location	1) The effect of salmon and watershed size will increase going from control to below stream locations. 2) Clams below streams will be smaller and have less %N compared to control locations as a result of shifting from marine- to terrestrial-dominated resources. However, reduced habitat quality in control sites may offset this effect.	Below stream and control sites.	Within-site	1) Positive (in interaction with salmon and watershed size). 2) Positive/ Negative as main effect	(Shurin et al. 2006, Rip and McCann 2011)

Table 3.3. **Site-level covariates used to create watershed size PC1 (catchment area, bankfull, depth and bank height), percent alder, pink salmon density, temperature and distances between clam sampling locations.**

Site	Catchment area (km²)	Mean bankfull width (m)	Mean depth (m)	Mean bank height (m)	Watershed Size PC1	Percent riparian alder	Mean 2006-07 pink salmon adult biomass density (kg/m²)	Maximum weekly average temperature (°C)	Distance between clam bed zones below streams (m)	Distance between zones in control locations (m)	Lateral distance between control and below stream locations (m)	Latitude	Longitude
Ada	10.1	11.1	0.12	0.34	-0.91	3.26	0.047	16.00	1 location	NA	NA	52.0553	-128.0507
Bullock Main	3.3	10.9	0.08	0.26	-2.18	3.31	0.078	19.93	35	70	140	52.4029	-128.0785
Clatse	32.1	22.8	0.16	0.30	0.53	26.08	0.264	23.38	102.5	205	280	52.3455	-127.8476
Codville	2.4	3.3	0.18	0.24	-2.50	0.00	0.004	18.92	15.5	NA	NA	52.0790	-127.8633
Fannie Left	35.0	12.8	0.16	0.39	0.39	1.74	0.090	18.57	57.5	115	60	52.0426	-128.0668
Fell Creek	7.0	10.9	0.19	0.41	-0.38	1.16	0.229	21.41	1 location	1 location	74	52.4336	-128.0790
Hooknose	18.4	16.9	0.18	0.46	0.67	3.08	0.057	18.88	56.5	113	155	52.1249	-127.8370
Kunsoot Main	5.7	13.1	0.04	0.22	-2.20	0.00	0.259	17.16	35	NA	NA	52.1569	-128.0435
Mosquito Bay	5.2	9.7	0.11	0.21	-1.84	6.33	0.081	20.48	10	1 location	70	52.3968	-128.1660
Neekas	17.6	17.7	0.16	0.40	0.33	13.35	0.413	22.84	85	170	70	52.4509	-128.1569
Quartcha	40.9	34.1	0.24	0.55	3.28	17.95	0.010	18.77	82	1 location	375	52.5155	-127.8421
Rainbow	13.7	15.1	0.23	0.47	0.77	20.34	0.001	24.86	35	NA	NA	52.4512	-127.7280
Roscoe Main	33.6	23.5	0.28	0.56	2.70	54.77	0.000	24.63	62.5	125	240	52.4696	-127.7448
Sagar	36.6	15.5	0.25	0.43	1.34	0.21	0.013	18.13	1 location	NA	NA	52.0959	-127.8388

3.3. Methods

3.3.1. Study Area

We studied estuaries within 45 km of Bella Bella (52°9’N, 128°8’W) on the central coast of British Columbia, Canada (Figure 3.1). This region lies within the Coastal Western Hemlock-biogeoclimatic zone and receives some of the highest levels of precipitation on the continent (Pojar et al. 1991). Although selective logging occurred in many areas during the first half of the 20th century, this region remains relatively intact due to its remoteness, restricted access and strengthening First Nations governance and conservation coalitions (Price et al. 2009). This remote region provides access to a wide range of relatively pristine watersheds that are ideal systems to test for the effects of terrestrial and salmon resource subsidies in estuaries.

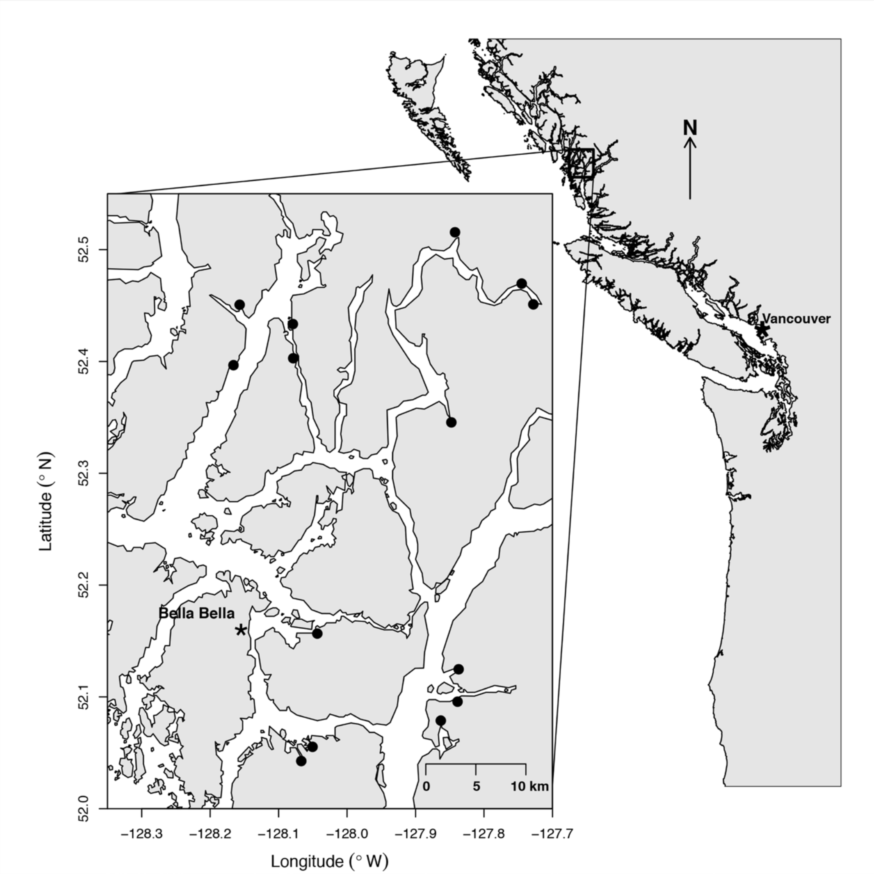

Figure 3.1. Study area in the vicinity of Bella Bella, on British Columbia’s central coast.

We sampled 14 small to medium estuaries, which hosted soft-shell clam populations and varied in upstream catchment area, stream channel size, estuary area, upstream salmon spawning density, and red alder (*Alnus rubra*) dominance (Table 3.3). All streams were dominated by chum (*O. keta*) and pink (*O. gorbuscha*) salmon, which accounted for 90-100% of total adult salmon spawners, with much smaller numbers of coho (*O. kisutch*) and a limited presence of sockeye (*O. nerka*) and Chinook salmon (*O. tshawytscha*). Salmon spawn in streams throughout BC's central and north coasts, which can produce over half of the wild salmon stocks in this region, and account for over 30% of total populations within BC and the Yukon (Slaney et al. 1996).

3.3.2. Sampling

We collected soft-shell clams during the summers of 2008 and 2009 prior to salmon spawning. Samples were collected during tide heights less than, or equal to 1m above chart datum depth (0 m tidal height). Depths of sample locations ranged between 0.47 and 2.1 m above chart datum. At each site three systematic locations were sampled representing upper, middle, and lower zones of the clam bed spanning the vertical width of the clam bed (Figure 3.2). These three zones were sampled directly below stream outlets and adjacent to the main channel within each estuary tidal flat. At each location, 5 soft-shell clams were sampled haphazardly by digging to a depth of 30 cm at each sample location and piling the sediment on the beach surface. The excavated sediment was then searched where we retained the first 5 clams encountered. This method helped reduce depth biases in sampling smaller clams in surficial sediments. Additional holes were excavated adjacent to the original if fewer than 5 clams were present. For each clam collected, we immediately recorded shell length, width, depth and wet weight. Clams were then wrapped in aluminum foil and frozen at -20°C in sealed containers until processing. Sampling time and height above water were recorded for each location to enable depth corrections to chart datum. Height above water was measured by viewing a metre stick, located at the water's edge, through a clinometer from each sample location. The height above water was equal to the height on the metre stick, at zero degrees, minus the height of the observer's viewpoint. In 2009, additional within-site control locations were sampled laterally down shore from steam outlets and outside the depositional deltas of each estuary (Table 3.3). These control locations were located in 9 of our 14 study sites and limited to the upper and lower clam bed zones (Figure 3.2). Age data were collected by sectioning shell chondrophores (encased in Loctite Hysol epoxy) using a Buehler Isomet Low-speed saw with diamond wafering blades. Chondrophore sections were mounted on glass slides and polished sequentially with 30, 9 and 3 micron lapping film. Sections were aged by counting annual growth lines following the methods of MacDonald and Thomas (1980) using light manipulations and a digital camera mounted to a dissecting microscope.

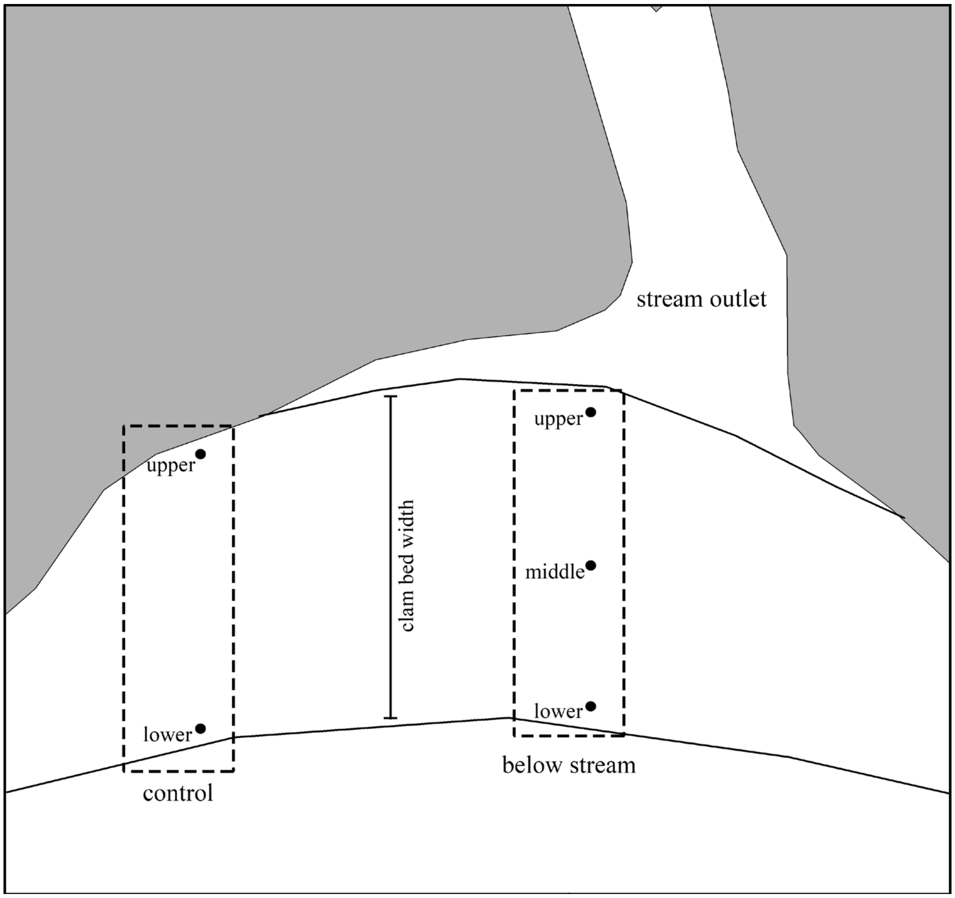

Figure 3.2. Sampling design. Upper, middle and lower clam bed zones were sampled below streams in 2008 and 2009, upper and lower zones were sampled in control locations in 2009.

3.3.3. Watershed Data

Stream and riparian canopy (% alder) data were collected during the summer of 2007 as part of an extensive survey in the region. Temperature was measured continuously using waterproofed temperature loggers (iButtons DS1922L) anchored to rebar below chart datum depth (0m tide) and set to record every 2 hours spanning the study period. Stream measurements occurred at 12 randomly selected transects along a study reach equal to 30 times the mean bankfull width of each stream (Bain and Stevenson 1999). Alder basal area was estimated by measuring the diameter at breast height of all trees greater than 5 cm in diameter within six belt transects that extended perpendicular from each stream and were 35 m long by 10 m wide (Hocking and Reynolds 2011). Percent alder was calculated for each site as:

$$\%A = \frac{B_{alder}}{B_{total}} \times 100 \qquad (1)$$

where $\%A$ is the percent alder for each site, B_{alder} is total basal area of all alder measured in a given site and B_{total} is the total basal area of all tree species measured in that site. Watershed catchment areas were estimated using the Government of British Columbia's mapping website *iMap*BC (Government of British Columbia 2006).

Principal components analysis (PCA) was used to generate a composite variable to describe watershed size to approximate the magnitude of stream discharge and amount of terrestrial-resource influx into estuaries. Component variables included total catchment area (km^2), mean stream bankfull width (width of the stream channel at its highest point before flooding), mean stream depth, and mean stream bank height (maximum stream depth before flooding). Pearson correlation coefficients of component variables ranged between 0.7 and 0.9. The first principal component axis (PC1) described 80% of component variable variances and variables all loaded positively on this axis ranging between 0.48 and 0.52. The PC1 axis values reflect both the capacity of streams to transport nutrient subsidies into estuaries (stream channel measurements) and the amount of terrestrial-derived nutrient sources upstream (catchment area).

3.3.4. Salmon Population Data

The federal Department of Fisheries and Oceans, the Heiltsuk Integrated Resource Management Department, and Simon Fraser University cooperatively conducted all salmon enumeration and spawning reach measurements. We considered upstream salmon biomass density estimates from 2006 to 2009 as potential proxies for salmon carcass availability in estuaries downstream (Harding and Reynolds 2014a). We determined this from data limitations (data collection began in 2006 and we did not want to consider years beyond 2009). Salmon biomass density indices were calculated for chum salmon, pink salmon and chum and pink salmon combined, for year combinations 2006-2007, 2006-2008 and 2006-2009 for each site:

$$SBD_{ij} = \frac{\sum (N_{ij} \times W_j)}{A} \tag{2}$$

where SBD_{ij} = average kg of salmon biomass per m^2 of spawning area per stream for year combination i and species j, N_{ij} = the mean number of returning adult salmon for year combination i and species j, W_j = average salmon mass for each species j, and A = the estimate of spawning area (m^2) within each stream. Spawning area was estimated by multiplying the mean bankfull width by the total spawning reach length for each stream. We accounted for variation in salmon body mass among populations by measuring the weight of 5 dead adult salmon of each sex for each species in a subset of study streams covering our study area. These average salmon masses were applied to the remaining study sites sharing island groups, channels or mainland inlets. We limited our analyses to chum and pink salmon because these species account for 90-100% of total adult salmon in our study region.

We conducted an initial exploratory analysis to identify the best salmon density metric that explained stable isotope ratios of clam foot muscle tissue. We constructed univariate linear models with chum, pink or total (chum and pink) salmon density for each selected year combination explaining $\delta^{15}N$ or $\delta^{13}C$. We compared these models using Akaike Information Criterion corrected for small sample sizes (AICc) that selects for the most parsimonious model given the data. We log transformed all salmon density metrics in all analyses to reduce the leverage of high salmon density values on slope estimates.

3.3.5. Stable Isotope Analysis

Foot muscle tissue samples for isotope analysis were removed from thawed samples and placed in a drying oven at 58°C for up to 96 hours. Each sample was homogenized into a fine powder using a heavy duty Wig-L-Bug grinder (Pike Technologies Ltd).

Sample weights ranging between 0.8-1.2μg were packaged in standard pressed tin capsules (3.5 x 5 mm) and sent to the UC Davis Stable Isotope Facility for analysis of nitrogen and carbon abundance using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Stable isotopes are expressed as the difference between the sample and a known standard, or δ, in parts per thousand (‰):

$$\delta^{15}N \; or \; \delta^{13}C = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000 \tag{3}$$

where R is the ratio of the heavy isotope to the light isotope ($^{15}N/^{14}N$ or $^{13}C/^{12}C$). Standards for nitrogen and carbon analysis are derived from N_2 in air and Pee-Dee Belemnite (PDB) limestone, respectively.

Percent nitrogen of soft-shell clam muscle tissue was calculated as:

$$\%N = \frac{N}{T} \times 100 \tag{4}$$

where N is the mass of nitrogen in the sample and T is the total mass of the sample.

3.3.6. Statistical Analyses

Bivalve mass was chosen as the most ecologically meaningful metric representing an individual's size (Peters 1983). We used the open source statistical software R for all analyses (R Core Team 2012). Variance inflation factors (VIF) of all covariates were less than 2.2 and thus indicated low multicolinearity (Zuur et al. 2009). Pearson correlation coefficients between individual covariates were 0.6 or less and not of great concern (Zuur et al. 2010). The only exception was % alder, which had a VIF of 4.3 and Pearson correlation coefficients of approximately 0.8 with both watershed size and temperature. Due to this high collinearity % alder was removed from all analyses.

For all analyses (isotopes, mass and %N) we used linear mixed-effects modeling to account for the hierarchical structure of the data (Pinheiro et al. 2012). This method allowed regression intercepts to vary by site (site as random intercept), accounted for potential correlation of individuals from the same site between sample years (correlation structure of site within year for all analyses), and accounted for heterogeneity in the residual variance structure (Zuur et al. 2009). Correlation and variance structures were established from residuals of the global models, or models including all variables considered, and AICc selection of the most parsimonious structures with the global model using restricted maximum likelihood (REML) estimation (Zuur et al. 2009). Variance structures on datum depth and control/below stream covariates improved the likelihood of the global models and satisfied the assumptions of residual normality and equal variance for mass and %N analyses respectively (Zuur et al. 2009). No variance structures were required for isotope analyses as the assumptions of equal variance were already met. We include a pseudo-R^2 value for the averaged model from each analysis. This is the R^2 value for a linear model between the fitted values of the averaged model and the observed data. We conducted an additional analysis on an approximation of clam growth that we calculated as individual clam mass divided by age, or the average mass acquired per year. Results were very similar to our analysis of clam mass so we chose to not include it to avoid redundancy.

We wanted to test how the effects of salmon and watershed subsidies could vary by distance from stream outlets (upper, middle and lower clam bed zones) and by location (control vs. below stream). We therefore constructed our models to include the following interactions in all analyses; salmon and zone, salmon and location, watershed size and zone and watershed size and location. We competed models of all combinations of covariates in addition to the specified interactions because we did not have any *a priori* reason to exclude any models from the analyses (Burnham and Anderson 2002). For each analysis we conducted two model competitions, first using centered covariates (subtracting the mean) and again using scaled covariates (centering and dividing by 2 standard deviations). All covariates were centered to avoid inaccuracies in slope estimates for main effects as they can vary considerably depending on the presence of interaction terms (Schielzeth 2010). We also analyzed models with scaled covariates to enable direct comparison of effect sizes amongst variables (Gelman 2008, Grueber et al. 2011). In all analyses, *k*-1 binary dummy variables were created for the three-level zone factor (upper, middle, lower) and 2-level location factor (control, below stream), where *k* is the number of levels in a factor following the methods of Schielzeth (2010). In standardized models, dummy variables were not divided by 2 standard deviations as slope estimates from binary variables already relate to 2 standard deviations (comparisons of 0 and 1) (Gelman 2008). Model competition using AICc revealed that top model weights in all analyses were less than 0.22. We accounted for this model uncertainty using a multi-model approach (Barton 2012). Candidate models used in multi-model inference were limited to the subset of models with a ΔAICc less than 4 (Burnham and Anderson 2002) and estimates for each covariate and interaction term were averaged across candidate model sets using the natural average method. Intercepts, slopes, scaled coefficients and standard errors for the combined effects of salmon and watershed size at each zone and location level were calculated from averaged model outputs. The equations used to calculate these combined effects from interactions are presented in the supplemental information.

3.4. Results

3.4.1. Sampling

A total of 154 and 243 soft-shell clams were sampled in 2008 and 2009 respectively, from 14 sites each year. Clam mass ranged between 1.3-116.9 g and 3.2- 126.6 g in 2008 and 2009, respectively. In 2009, control samples were collected from 9 of the 14 sites (Figure 3.2). Bedrock and small estuary sizes prevented control sampling from the remaining sites. Table 3.3 provides a summary of site-level covariates and distances between sampling locations.

3.4.2. Salmon Metric Pre-selection

The 2006-07 mean pink salmon density explained the most variation in both $\delta^{15}N$ and $\delta^{13}C$ of soft-shell muscle tissue with model weights exceeding 0.8. This salmon metric was used in all subsequent analyses. Model rankings are presented in Table B.1 in Appendix B.

3.4.3. Clam Isotopes

$\delta^{15}N$

The pseudo-R^2 of the averaged model was 0.66. Following our predictions, clams in estuaries with higher upstream salmon densities had enriched δ^{15}N. In addition, the effect of salmon decreased going from upper to lower clam beds (Figure 3.3A). Clams below streams with large watersheds were more depleted in δ^{15}N, but this was only detected in the lower zones (Figure 3.3B). Clams that were higher on shore (higher above chart datum), and those that were larger and older had enriched δ^{15}N, following our predictions (Figures 3.3C-E). Temperature did not describe δ^{15}N. The standardized effects of salmon were positive at all zone and location levels with confidence intervals well above 0 (Figure 3.4A). The effects of watershed size were more variable, with confidence intervals crossing 0 with the exception of lower clam beds (Figure 3.4A). Age, mass and height above chart datum were all positive and highly certain while the effects of temperature were small and high a higher degree of uncertainty (Figure 3.4A). The averaged δ^{15}N model and candidate set are presented in Tables B.2 and B.3 in Appendix B

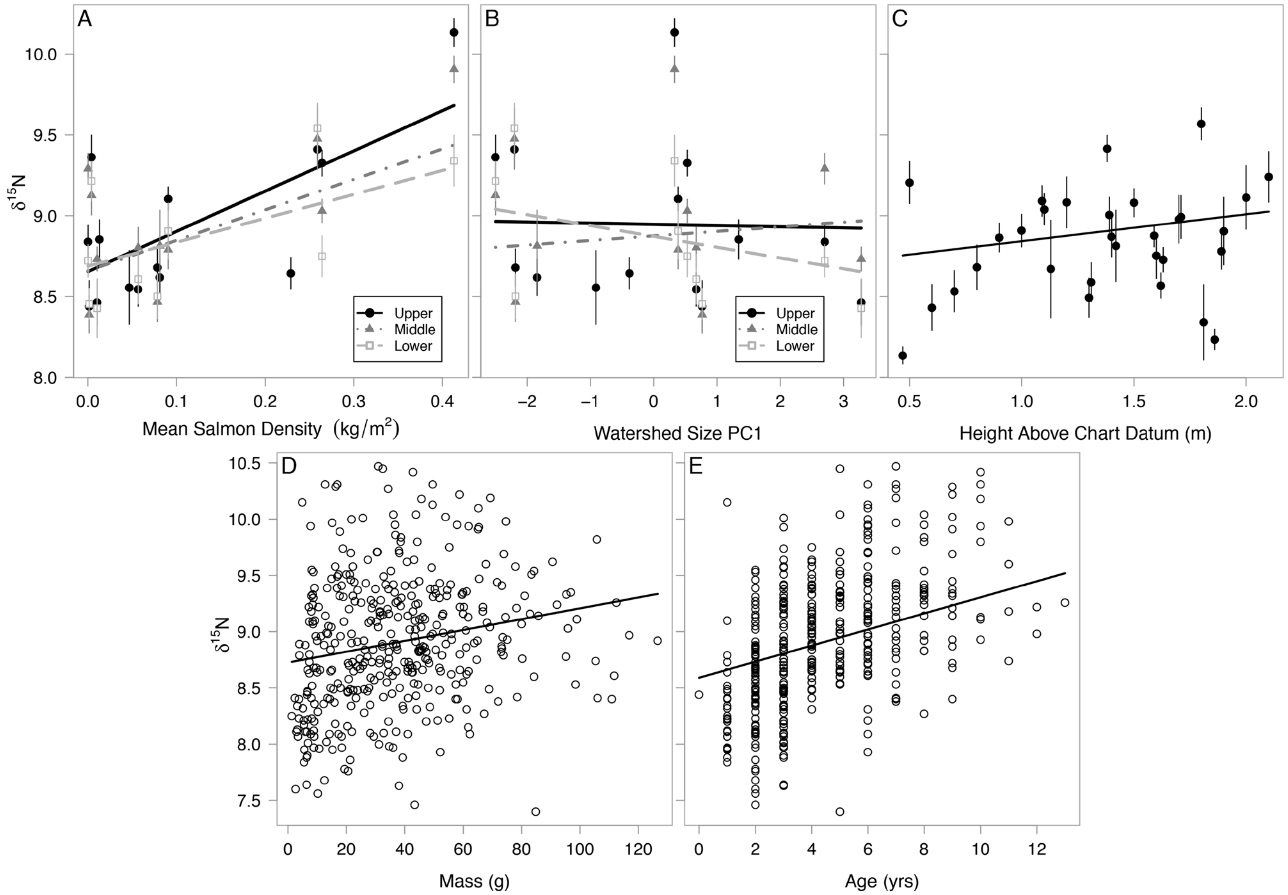

Figure 3.3. **Correlates of soft-shell clam muscle tissue δ^{15}N. (A) Pink salmon density at each clam bed zone, (B) Watershed size PC1 at each clam bed zone, (C) Height above datum depth, (D) Clam mass, and (E) Clam age. Each data point in panels A-C represents mean values with standard error bars. Data points in panels D-E represent individual clams. All trend lines represent relationships using intercept and coefficients from multi-model output; thus they represent the relationships for the x-axis variable that accounts for the effects of other variables, rather than fitting the univariate data shown in each graph.**

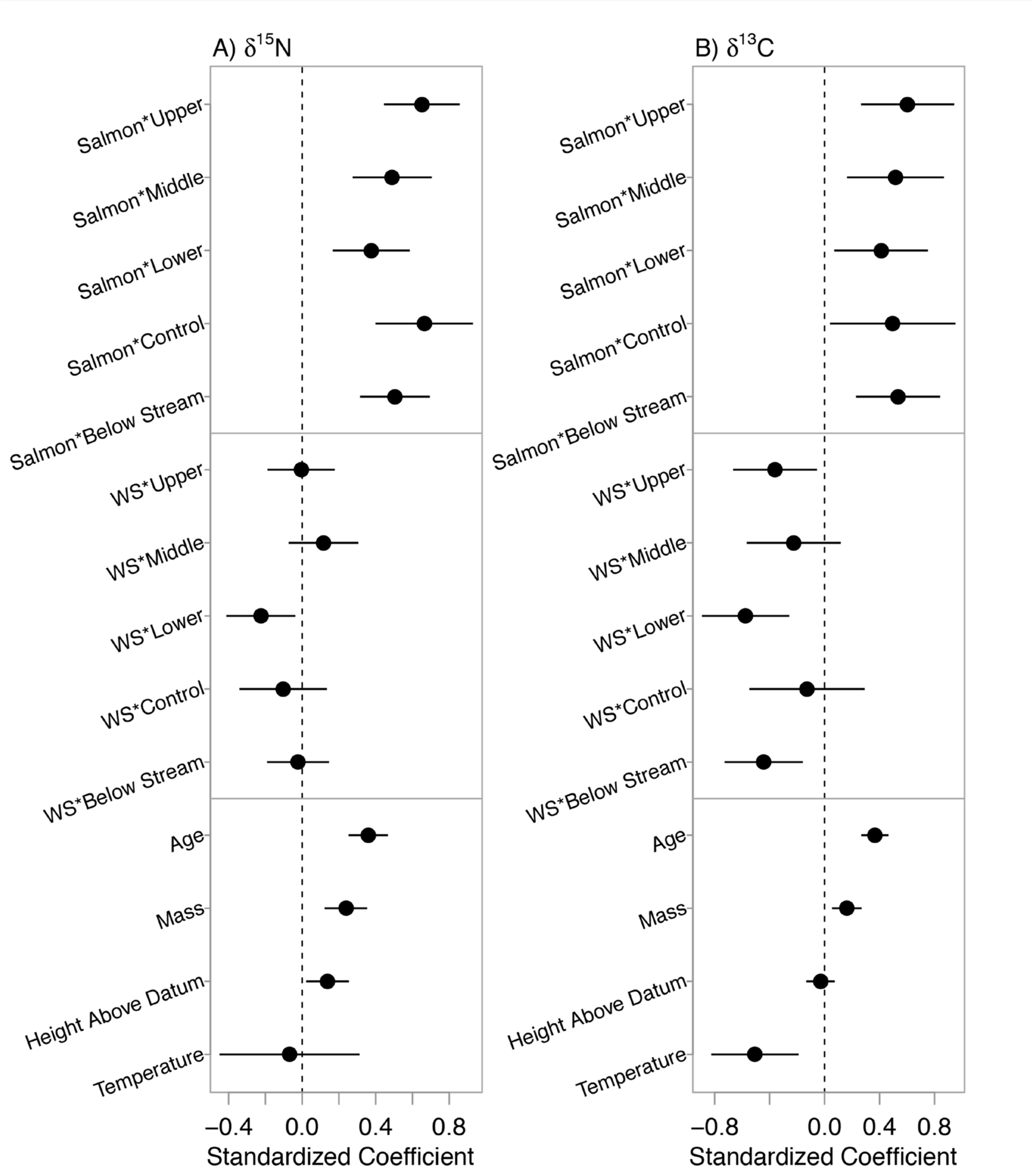

Figure 3.4. **Standardized coefficients (mean = 0, standard deviation = 2) with 95% confidence intervals for covariates considered in the (A) δ^{15}N candidate model set and (B) δ^{13}C candidate model set. Salmon = 2006-07 mean pink salmon density; WS = watershed size PC1. Coefficient values indicate the change, on average, in δ^{15}N or δ^{13}C as the associated covariates increase by 2 standard deviations.**

$\delta^{13}C$

The pseudo- R^2 of the averaged model was 0.23. Clams below large watersheds were more depleted in δ^{13}C and, as we predicted, this depletion was strongest in the locations below streams (Figure 3.5A) but also in the lower zones compared to the upper and middle zones (Figure 3.5B), which did not support our predictions. Clams were enriched in δ^{13}C below streams with higher pink salmon densities and this effect was strongest in the upper and middle zones (Figure 3.5C). Contrary to our predictions, warmer estuaries had clams with more depleted δ^{13}C (Figure 3.5D). Large old clams were enriched in δ^{13}C (Figures 3.5E-F) but height above chart datum had no effect (Figure 3.4B). Similar to δ^{15}N, the standardized effects of salmon on δ^{13}C were positive at all zone and location levels with confidence intervals above 0 (Figure 3.4B). The standardized effects of watershed size were strongest in the upper and lower zones, and below stream locations but less certain in middle zones and control locations (Figure 3.4B). The effects of age, mass and temperature had a high degree of certainty around coefficient estimates (Figure 3.4B). The averaged δ^{13}C model and candidate set are presented in Tables B.4 and B.5 in Appendix B.

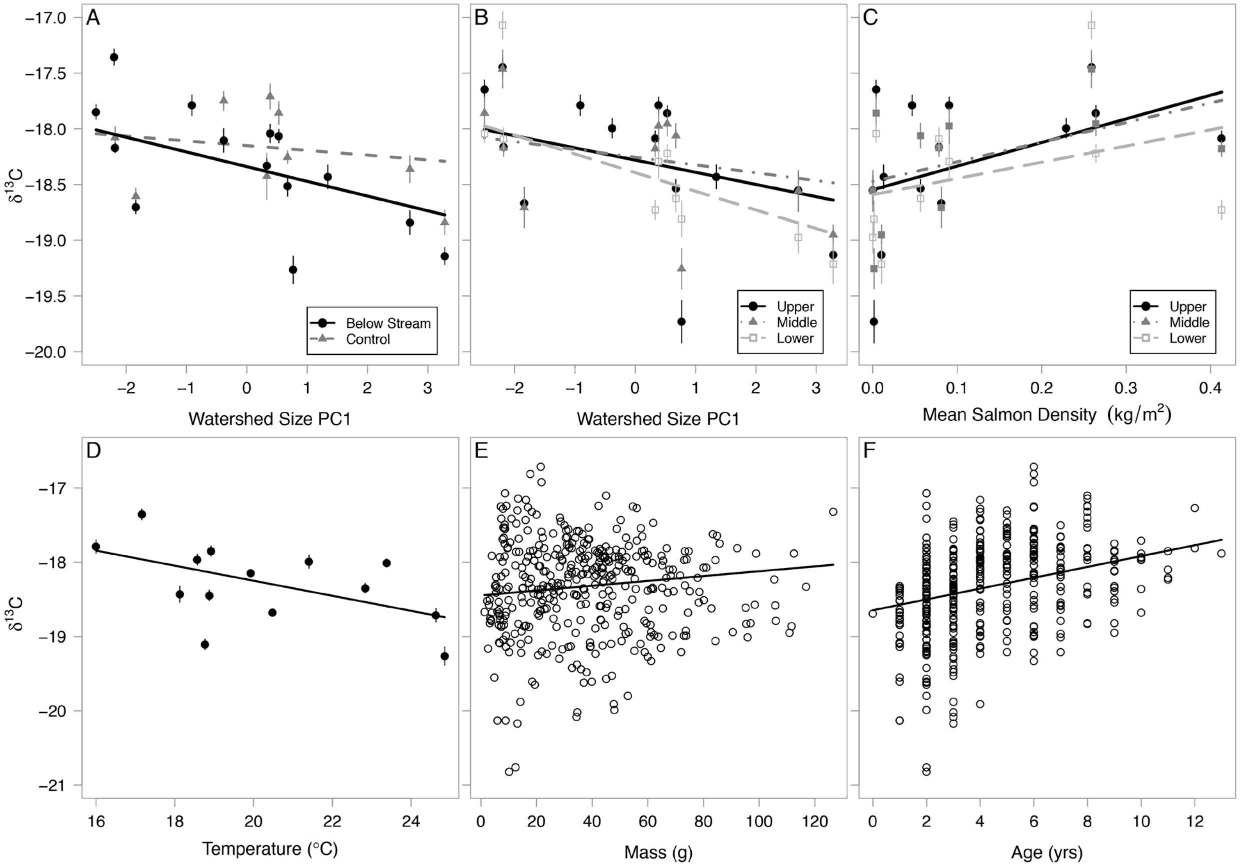

Figure 3.5. **Correlates of soft-shell clam muscle tissue δ^{13}C. (A) Watershed size PC1 at below stream vs. control locations, (B) Watershed size PC1 at each clam bed zone, (C) Pink salmon density at each clam bed zone, (D) Temperature (maximum weekly average temperature), (E) Clam mass, and (F) Clam age. Each data point in panels A-D represents mean values with standard error bars. Data points in panels E-F represent individual clams. All trend lines represent relationships using intercept and coefficients from multi-model output; thus they represent the relationships for the x-axis variable that accounts for the effects of other variables, rather than fitting the univariate data shown in each graph.**

3.4.4. Size

The pseudo-R^2 of the averaged model was 0.62. There were larger clams below larger watersheds but this effect was restricted to below stream locations (Figure 3.6A). Watershed size showed the opposite, and negative, correlation with size in control locations (Figures 3.6A and 3.7A). The positive correlation between clam size and watershed size was strongest in lower clam beds, and below stream locations where confidence intervals did not cross 0 (Figure 3.7A). The effect of location (below stream vs. control) was not an important descriptor of clam mass on its own. Surprisingly, salmon correlated negatively with clam size, opposite to our predictions, though the correlation with salmon in the below stream locations was less negative (Figure 3.6B, 3.7A). This negative relationship was observed at all zone and location levels, where most of the confidence intervals did not cross 0 (Figure 3.7A). Clams were also slightly smaller in the upper, compared to middle and lower clam beds (Figure 3.6C), and clams that were higher above chart datum and younger were smaller (Figures 3.6D-E). The effects of age and height above chart datum were positive and negative respectively, with a higher degrees of certainty, while the effects of temperature were negligible. The averaged clam size model and candidate set are presented in Tables B.6 and B.7 in Appendix B.

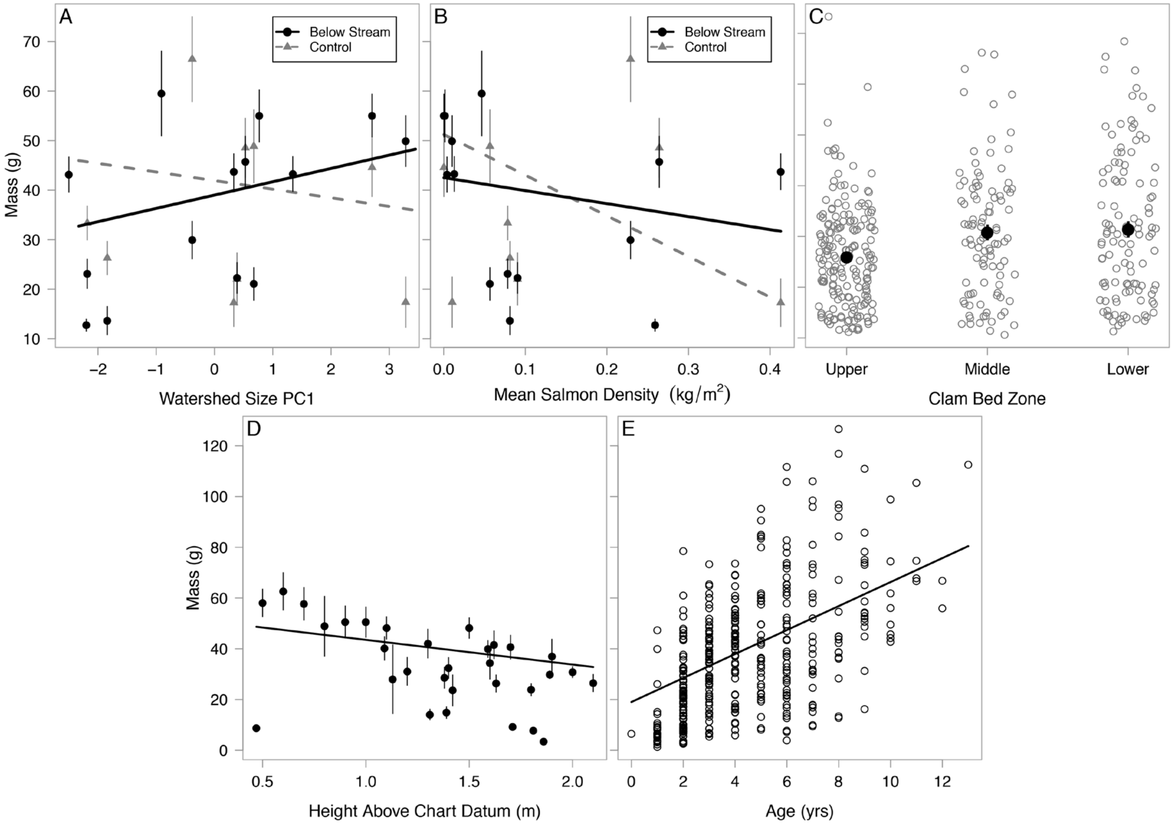

Figure 3.6. **Correlates of soft-shell clam size. (A) Watershed size PC1 at below stream vs. control locations, (B) Pink salmon density at below stream vs. control locations, (C) Clam bed zone, (D) Height above chart datum, and (E) Clam age. Each data point in panels A, B and D represents mean values with standard error bars. Data points in panels C and E represent individual clams. Solid circles in panel C indicate mean mass for each zone with standard error bars. A jitter function was used in panel C for better visualization. All trend lines represent relationships using intercept and coefficients from multi-model output; thus they represent the relationships for the x-axis variable that accounts for the effects of other variables, rather than fitting the univariate data shown in each graph.**

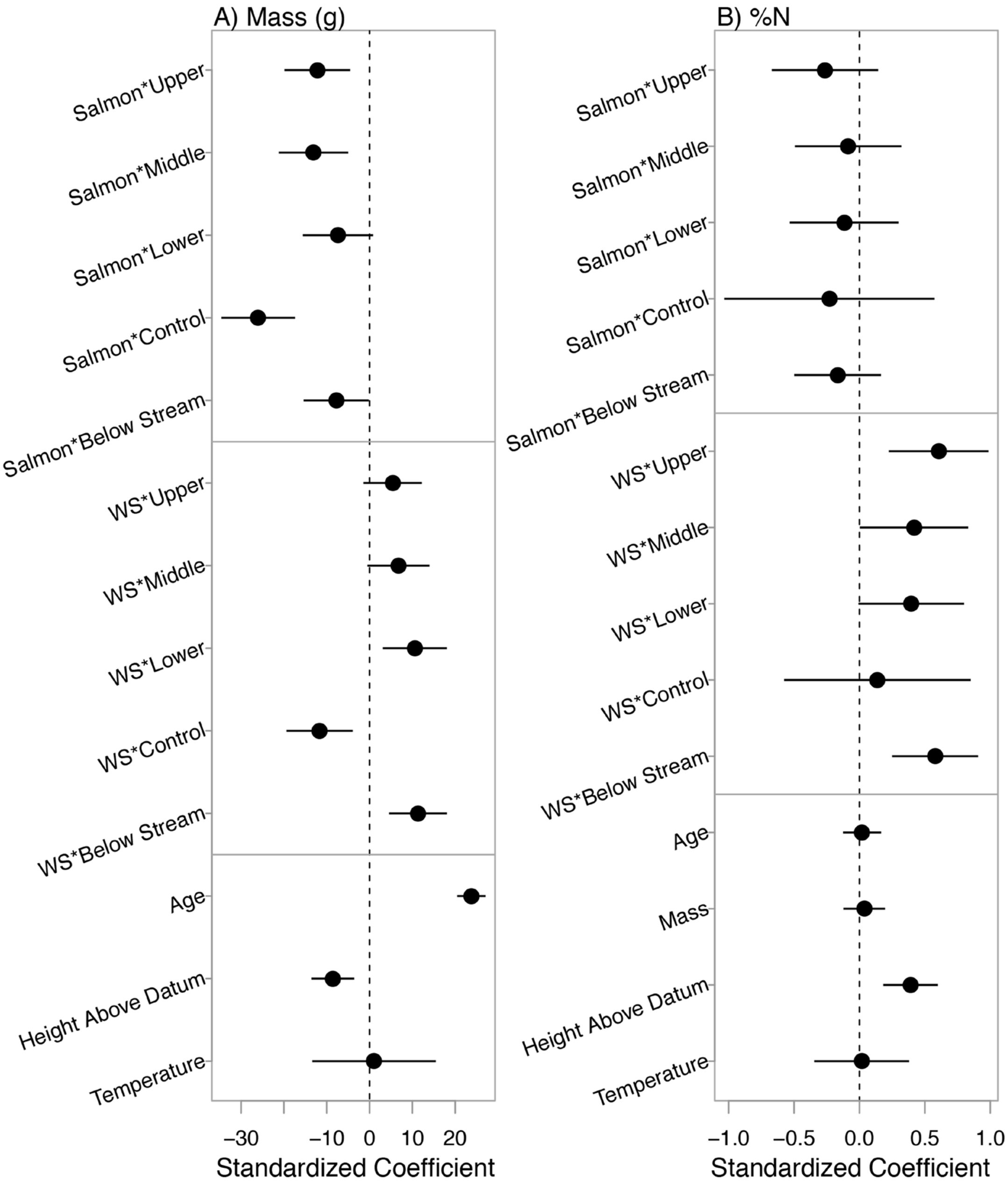

Figure 3.7. Standardized coefficients (mean = 0, standard deviation = 2) with 95% confidence intervals for all covariates considered in the (A) Soft-shell clam size candidate model set and (B) Soft-shell clam %N candidate model set. Salmon = 2006-07 mean pink salmon density; WS = watershed size PC1. Coefficient values indicate the change, on average, in clam size or %N as the associated covariates increase by 2 standard deviations.

3.4.5. Percent N

The pseudo-R^2 of the averaged model was 0.21. Clams below larger watersheds had higher percentages of N in their muscle tissues (Figure 3.8A). Contrary to our predictions, clams in upper zones contained higher %N in their tissues than their counterparts (Figure 3.8B). Analysis did not detect an influence from any other covariates including salmon density, temperature, clam size and age. Although zone and location did not have any interaction effects with salmon density or watershed size, clams below streams had higher %N than those in control locations (Figure 3.8C) and this disparity was most apparent in lower clam beds (Figure 3.8D). The standardized effects of salmon on %N were negative but highly uncertain at all zone and location levels with confidence intervals crossing 0 (Figure 3.7B). The effects of watershed size were positive, particularly in upper clam beds and below streams and confidence intervals did not cross 0, with the exception of control locations. Clams higher above chart datum had elevated %N with confidence intervals well above 0 while all remaining covariates had undetectable effects (Figure 3.7B). The averaged %N model and candidate set are presented in Tables B.8 and B.9 in Appendix B.

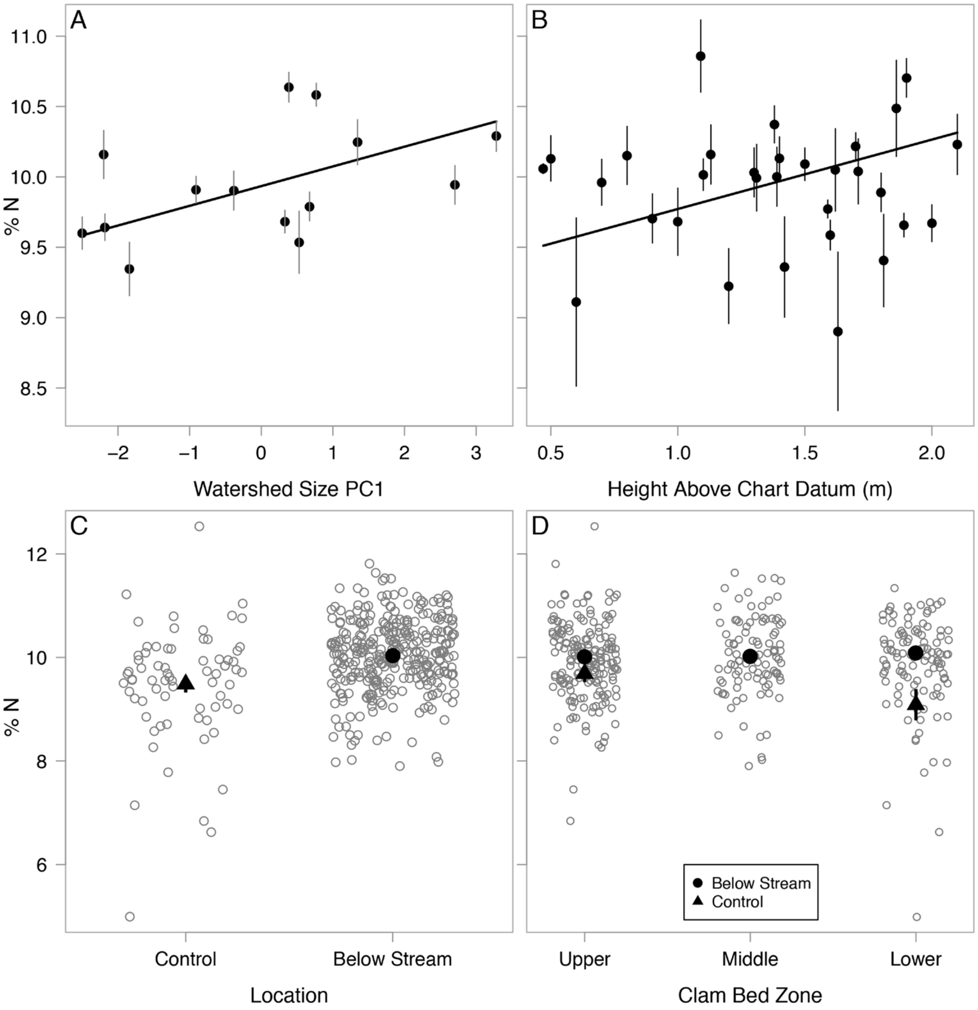

Figure 3.8. **Correlates of soft-shell muscle tissue %N. (A) Watershed size PC1, (B) Height above chart datum, (C) Below stream vs. control locations, and (D) Clam bed zones. Data points in panels A and B represent mean values with standard error bars. Hollow data points in panels C and D represent individual clams; points were dispersed using a jitter function for better visualization. Solid symbols in panels C and D indicate mean values with standard error bars (control locations were not sampled at middle zones). All trend lines represent relationships using intercept and coefficients from multi-model output; thus they represent the relationships for the x-axis variable that accounts for the effects of other variables, rather than fitting the univariate data shown in each graph.**

3.5. Discussion

This study demonstrates the complex relationships between terrestrial and marine resource subsidies and traits of sedentary estuarine consumers. It highlights how cross-ecosystem resource linkages can vary both within and across landscapes. Watershed size and salmon density, individual traits, and habitat characteristics described, to varying degrees, stable isotope ratios of soft-shell clam muscle tissue. The effects of watershed size and salmon subsidies on isotope ratios generally decreased from upper to lower zones of clam beds. Clams size and percent nitrogen increased as the size of upstream watersheds increased. However the effect on clam size was only observed in tidal flats below streams and not in control locations. We were surprised to find that upstream salmon density had a negative relationship with clam size, though this negative effect was weaker below streams compared to control locations. To our knowledge, this is the first study to simultaneously test for terrestrial- and salmon-derived subsidies between and within sites across a broad spatial scale.

Watershed size explained isotope ratios and correlated positively with both size and %N of soft-shell clams. These results support other studies that have demonstrated the importance of terrestrial-derived resource subsidies to estuaries (Darnaude et al. 2004a, Sakamaki and Richardson 2008a, Connolly et al. 2009), which can scale directly with watershed size (Sakamaki et al. 2010, Harding and Reynolds 2014a). In this case the quantity of terrestrial resource influx into estuaries, as explained by watershed size, appears to be more important than higher-quality pulsed inputs such as salmon-nutrients. Although watershed nutrient exports may be lower quality than salmon or estuarine resources, total energy export from upstream may overwhelm other sources and make it a more influential resource (Jonsson and Jonsson 2002, Marczak et al. 2007).

The considerable depletion effect of watershed size on stable isotope ratios in soft-shell clams suggests that terrestrial-derived resources are consumed in proportion to their availability, as also found in a study of Dungeness crabs, *Metacarcinus magister*, (Harding and Reynolds 2014a). Stream exports are dominated by terrestrial-derived organic material (Harmelin-Vivien et al. 2010), which have low proportions of nitrogen and carbon heavy isotopes. These inputs into estuaries also increase in proportion to watershed size (Darnaude 2005, Sakamaki et al. 2010). Thus as influx of terrestrial-derived resources increases, soft-shell clams become more ‘terrestrial’ in their isotopic ratios. Although the effects of watershed size on $\delta^{13}C$ were clear, the effects on $\delta^{15}N$ were less so, with a strong effect only in lower clam beds. This could be a result of settlement dynamics of particulate organic matter, which could favour deeper individuals (Darnaude et al. 2004a). However, as watershed sizes increase, there can also be a shift from heterotrophic nitrogen inputs to autotrophic production in streams, while maintaining a reliance on terrestrial-derived carbon (Sakamaki and Richardson 2013). Therefore, terrestrial-derived nitrogen subsidies could be displaced by freshwater algal nitrogen exports as watershed size increases (Vannote et al. 1980). Because $\delta^{15}N$ in stream algae enriches with watershed size (Harding and Reynolds 2014a), and thus becomes more similar to enriched estuarine sources (Deegan and Garritt 1997), any relationships between watershed size and $\delta^{15}N$ could be masked.

Clams in estuaries below large watersheds were also larger, with higher percentages of nitrogen in their tissues. Bivalves have the ability to consume terrestrial-derived particulate organic matter directly (Kasai and Nakata 2005, Sakamaki and Richardson 2008a). They may also benefit indirectly, through subsidized abundances of diatoms, bacteria and microphytobenthos (Yamanaka et al. 2013). Because growth and %N of soft-shell clams are known to increase with nutrient loading and water flow (Emerson 1990, Carmichael et al. 2012), elevated resource imports into estuaries from larger watersheds (Sakamaki et al. 2010) could allow individuals to grow larger, faster and with higher nitrogen content in tissues (Carmichael et al. 2012). Soft-shell clams are well-suited to these types of resource subsidies, relative to other species, as they can maintain growth at higher nutrient and particulate matter concentrations (MacDonald et al. 1998, Weiss et al. 2002). Although watershed size appears to increase soft-shell %N throughout estuaries, the positive effect on size appears to be limited to the depositional zones below streams. A possible explanation could be sub-optimal habitat limitations to clam growth in control locations as we observed more coarse substrates such as cobble and gravel in these areas. Observed trends in clam size could also be influenced by differences in sediment grain sizes between sampling locations and estuaries, which did not measure in this study. However, clam bed locations below river outlets consisted of sand, mud and fine crushed shell mixtures which do not inhibit growth to the degree of larger substrate sizes (Newell and Hidu 1982). Because growth in bivalves is known to be density dependent, lower clam densities below larger watersheds could also explain the positive correlation between watershed size and clam size (Beal and Gayle Kraus 2002). Unfortunately we were unable to properly assess clam densities due to time constraints with low tides, which is a limitation to this study. However qualitative observations did not reveal any noticeable correlations between clam availability and watershed size. It is also possible that more established and mature populations and higher stream flows below large watersheds could hinder larval recruitment success and bias size distributions towards larger individuals (André and Rosenberg 1991, Morse and Hunt 2013).

Pink salmon density was a strong correlate with soft-shell clam isotope ratios compared to chum salmon. Pink salmon tend to spawn closer to estuaries than chum salmon in our study region, which increases habitat overlap with bivalves. This effect also decreased moving from upper to lower clam bed zones.

Much to our surprise, salmon density had a negative correlation with clam size. One possible explanation is that bivalves require smaller particle sizes such as sand while salmon require coarser gravel for spawning (Groot and Margolis 1991), so sites favourable for pink salmon could be less favourable to clams (de la Huz et al. 2002). The timing of salmon resource subsidies, just before dormant winter periods, could also result in the routing of any energetic benefits from salmon nutrients to metabolic maintenance instead of tissue growth. Salmon can also play a dual role in stream ecosystems as sources of both nutrient subsidies and disturbance (Moore et al. 2004, Harding and Reynolds 2014a). Pink salmon spawning in upper reaches of estuaries may exert similar disturbances to bivalves as they disrupt the substrate while digging and defending nests (Hunter 1959, Neave 1966b).

Both size and age of soft-shell clams were strongly correlated with stable isotopes. Few studies consider individual-level traits when using isotopes as an ecological tool and this study underscores the importance of their consideration (Martínez del Rio et al. 2009, Swain et al. 2014, Harding and Reynolds 2014a). In addition, local habitat conditions can influence isotope ratios, particularly for sedentary organisms such as bivalves. Clams higher in the intertidal were enriched in $\delta^{15}N$, likely reflecting a reduction in isotope discrimination as a result of more limited feeding opportunities. Higher estuary temperatures also correlated with more depleted $\delta^{13}C$, which was contrary to our expectations. Higher water temperatures upstream could elevate exports of isotopically depleted terrestrial detritus from watersheds as a result of faster decomposition of organic matter. Alternately, this relationship could reflect the positive correlation of temperature with the percentage of alder trees upstream, which we dropped from our analyses (see Methods). Alder trees can provide substantial inputs of isotopically depleted detritus (Wipfli and Musslewhite 2004, Sakamaki and Richardson 2008b), which could also deplete soft-shell clam isotope ratios.

As expected, larger clams were found deeper in the intertidal, suggesting higher survival or growth. These clams also had reduced %N in their tissues compared to shallower individuals, contrary to our prediction. Terrestrial-derived nitrogen subsidies could be more concentrated higher in the intertidal and diluted lower down where clams are tidally submerged for longer periods of time. However, because %N of clam tissues is known to increase with growth rates (Carmichael et al. 2004), this result may reflect the fact that larger, and thus slower growing clams are concentrated deeper in the intertidal while smaller and faster growing clams dominate shallower locations.

Our work demonstrates the importance of connectivity amongst coastal landscapes and that this connectivity can vary with landscape traits. Our results, and other work, also suggest that the effect of watershed size can broaden food web connectivity, through increased inputs of upstream resources (Sakamaki and Richardson 2008a, Harding and Reynolds 2014a). Harding and Reynolds (2014a) observed increases in Dungeness crab size in response to terrestrial resource influx within the same region, implying these subsidies may have broader effects within estuarine food webs. Animal movement, such as spawning salmon migrations, also provides substantial resource inputs into these ecosystems. Due to the open nature of estuaries, resource subsidies have the potential to stabilize these communities, increase productivity, and increase resilience to disturbance and periods of resource scarcity (Huxel and McCann 1998, Anderson and Polis 2004). Natural flow regimes are an essential component to the maintenance of subsidy dynamics (Poff et al. 1997), providing resource linkages and passage for animal movement between terrestrial, freshwater and marine landscapes (Palardy and Witman

2014). These considerations have direct implications for estuarine productivity in intact ecosystems such as the central coast of British Columbia, which faces increasing industrial development pressures that can disrupt discharge regimes and alter resource dynamics (Fulweiler and Nixon 2005, Valiela et al. 2014). Estuaries buffer coastlines and produce resources crucial to coastal First Nations and commercial and recreational fisheries. Recognizing the importance of cross-ecosystem resource linkages in maintaining ecosystems can better enable us to understand how they might respond to human-driven pressures such as resource extraction and climate change (Sakamaki and Richardson 2008a). Broader-scale studies such as this can also shed light on how cross-ecosystem processes vary across space and thus can promote realistic resource management and conservation frameworks that acknowledge the inherent heterogeneity in natural systems.

Chapter 4. From earth and ocean: investigating the importance of cross-ecosystem resource linkages to a mobile estuarine consumer[3]

4.1. Abstract

Externally-derived resources often contribute to the structuring of ecological communities. Estuaries are one of the most productive ecosystems in the world and provide an ideal system to test how communities may be shaped by resource subsidies because they occur at the intersection of marine, freshwater and terrestrial habitats. Here we tested the effects of both terrestrial- and salmon-derived subsidies, in addition to other factors such as habitat area, on the diet (inferred from stable isotopes), abundance and size of a mobile estuarine consumer, the Dungeness crab (*Metacarcinus magister*). Crab trap surveys encompassed 19 watersheds over 2 seasons in the central coast of British Columbia, Canada, which spanned natural gradients in estuary size, watershed size, riparian tree composition, and Pacific salmon spawning density. Stable isotope ratios of crab tissue confirmed the predictions that estuarine nutrient regimes can be strongly affected by upstream watershed size, salmon density, and the dominance of nitrogen-fixing red alder (*Alnus rubra*). There were more crabs in larger estuaries and the largest crabs were found in estuaries below the largest watersheds. The proportional contributions of terrestrial- and salmon-derived subsidies to the diet of Dungeness crabs increased with watershed size and salmon density, respectively. These results confirmed that resource subsidies constituted large proportions of the Dungeness crab's diet, that crab abundance is determined by habitat size, but that crab size is affected by the magnitude of terrestrial resource influx.

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4.2. Introduction

The movement of resources between ecosystems can exert strong effects on ecological processes (Polis et al. 1997, Anderson et al. 2008). Externally-derived nutrients can influence the productivity and structure of ecosystems ranging from oceanic islands to freshwater ecosystems (Stapp and Polis 2003, Anderson et al. 2008, Moore et al. 2008, Richardson et al. 2009, Wipfli and Baxter 2010). However, responses vary depending on the nature of a subsidy, the physical characteristics of donor and recipient systems, and the mechanisms or capacities of connectivity between them (Yang et al. 2008, Hocking and Reynolds 2011, Marcarelli et al. 2011). Nutrient subsidies can further be mediated by the traits of individuals or species in recipient habitats such as mobility, spatial distribution, phenology, feeding ecology and body size (Polis et al. 1997, Anderson et al. 2008, Hocking et al. 2013).

The potential for subsidies is especially high between hydrologically-linked habitats (Correll et al. 1992, Yang et al. 2008). Aquatic systems are inherently better equipped to ‘metabolize’ pulsed resources over compressed time periods than terrestrial habitats because the size structure of aquatic food webs can allow energy to flow more efficiently (Hairston and Hairston 1993, Persson et al. 1999, Nowlin et al. 2007). Pelagic primary producers can also respond more rapidly to fluctuations in nutrient conditions as a result of reduced energy allocation to structural tissues and defense (Shurin et al. 2006). The movement of material between aquatic systems is also considerable (Leroux and Loreau 2008), and interface ecosystems, such as estuaries, act as a conduit through which terrestrial nutrient inputs enter the marine environment. This gives estuaries a high capacity to assimilate nutrients and concentrate the effects of upstream watersheds (Correll et al. 1992, Brion et al. 2008, Brookshire et al. 2009). Although estuaries are well studied for the effects of eutrophication from intensive land-use (Carpenter et al. 1998), relatively little is known about the importance of terrestrial-derived subsidies in more intact estuarine systems. A small body of research has shown that terrestrial resource exports from rivers can drive diet and condition in pelagic and benthic estuarine communities and increase the amount of labile organic matter in the benthos (Alliot et al. 2003, Darnaude 2005, Bănaru and Harmelin-Vivien 2009). However, the importance of this subsidy is not known relative to other resources, nor how its effect may vary across landscapes.

The life cycle of Pacific salmon (*Oncorhynchus* spp.) provides an example of 'counter-flow' nutrient transport through estuaries. These fish import large quantities of marine-derived material into freshwater and terrestrial communities. Salmon are born in freshwater streams but spend most of their life at sea, where they accumulate the majority of their body mass (Groot and Margolis 1991). Thus, when they return to natal streams as adults, they are essentially marine organisms enriched in nutrients from offshore feeding grounds. Most Pacific salmon species are semelparous, whereby all adults die after spawning. Their carcasses are spread throughout watersheds by water movement and carnivores, releasing high concentrations of nitrogen in addition to other nutrients such as carbon and phosphorous. Because the sea is enriched in stable isotopes relative to most terrestrial systems (Fry 2006), and salmon occupy high trophic positions within marine food webs, salmon subsidies can be quantified using stable isotope ratios of nitrogen and carbon ($\delta^{15}N$ and $\delta^{13}C$) to trace salmon signatures within terrestrial and freshwater ecosystems (Peterson and Fry 1987). A considerable body of research has investigated the effects of the salmon's unique life history, which couples offshore marine productivity to coastal ecosystems (Gende et al. 2002, Naiman et al. 2002). However, the net effects of spawning salmon can vary (Harding et al. 2014); salmon can subsidize freshwater and riparian habitats through excretion and egg and carcass deposition (Kline et al. 1990, Cederholm et al. 1999, Janetski et al. 2009), and can export nutrients with juvenile emigration and disturbance as adults dig and defend nests (Moore et al. 2007, Kohler et al. 2013). Although considerable amounts of salmon-derived nutrients imported into coastal watersheds are retained, large proportions are also exported downstream to estuaries (Gende et al. 2004a, Mitchell and Lamberti 2005, Cak et al. 2008). The influence of salmon nutrients in estuaries has received some mention (Reimchen 1994, Wipfli et al. 1998, Cederholm et al. 1999, Lessard and Merritt 2006, Field and Reynolds 2013), but research on the topic is limited (Fujiwara and Highsmith 1997, Jauquet et al. 2003, Cak et al. 2008). However, the potential for estuaries to be affected by salmon nutrient subsidies is considerable.

Opportunistic consumers, such as the Dungeness crab (*Metacarcinus magister*) provide an ideal opportunity to investigate the importance of cross-ecosystem processes in estuaries. They are highly mobile, generalist consumers and cover broad depth ranges of benthic habitats thus making them well suited to benefit from a diverse resource base and periods of high resource availability (Stone and O'Clair 2001, Anderson et al. 2008, Bănaru and Harmelin-Vivien 2009). The Dungeness crab is one of the largest, and most economically valuable invertebrates in estuaries of the north-eastern Pacific (Jensen and Asplen 1998). They are distributed along the western continental shelf of North America, from central California to the Gulf of Alaska, and can inhabit estuaries in high densities (Stevens and Armstrong 1984, Jensen and Armstrong 1987, McCabe et al. 1987). They support valuable commercial and recreational fisheries and are a very important traditional resource for Coastal First Nations (Beacham et al. 2008). An extended larval period enables them to disperse substantial distances prior to settlement. Individuals can live for 8-10 years and adult movement can be extensive in open coastal areas but is thought to be more localized in fjord-type channels (Stone and O'Clair 2001, Hildenbrand et al. 2011). Dungeness crabs are opportunistic omnivores, with ontogenetic diet shifts ranging from decomposing organic matter, microalgae, and diatoms to bivalves, shrimp, and fish as individuals mature (Stevens et al. 1982, Jensen and Asplen 1998). They are poor osmoregulators but can venture into upper estuaries during periods of high food abundance, which has been observed to coincide with the presence of spawning salmon (Sugarman et al. 1983, Stevens et al. 1984, Curtis and McGaw 2012). Individuals have been observed scavenging on salmon carcasses in estuaries during fall salmon runs (Harding, *personal observation*) and Dungeness crab stable isotope ratios can be enriched relative to salmon (Christensen et al. 2013). This suggests salmon could provide a substantial dietary contribution to Dungeness crabs.

In this study we test hypotheses for how resource subsidies and individual crab traits explain diet, inferred from nitrogen and carbon stable isotopes, relative abundance, and body size of Dungeness crabs across a natural gradient of 19 coastal watersheds that vary in size, riparian tree composition, estuary area and adult salmon density. First, we test for effects of watershed size (as a proxy for the magnitude of terrestrial- derived resource flux into estuaries), upstream red alder (*Alnus rubra*, a nitrogen fixing tree that can provide nutrients to forest soils and streams) (Helfield and Naiman 2001), estuary area, and spawning salmon density on $\delta^{15}N$ and $\delta^{13}C$ isotopic ratios in crab muscle tissue. We also test these landscape metrics against crab size and shell age to control for potential variability at the individual level. We predicted that large watersheds and high alder cover would deplete $\delta^{15}N$ and $\delta^{13}C$ due to increased influx of terrestrial-derived nutrients (Compton 2003, Page et al. 2008, Connolly et al. 2009). Conversely, we predicted that increases in estuary size and salmon density would enrich $\delta^{15}N$ and $\delta^{13}C$ from higher contributions of estuarine production and salmon nutrient inputs to the resource base (Deegan and Garritt 1997, Fujiwara and Highsmith 1997). We predicted that larger individuals would have enriched $\delta^{15}N$ and $\delta^{13}C$ as they shift diet towards higher trophic levels (Stevens et al. 1982). We also predicted shell age (time since last moulting) would correlate with an enrichment in heavy isotopes. Although Dungeness crabs moult throughout their lives, this frequency decreases with age (Wainwright and Armstrong 1993). Therefore older shells could indicate older individuals, which may feed at higher trophic levels (Stevens et al. 1982).

We also tested for effects of the same covariates on crab size and catch per unit effort (CPUE), which we used as a proxy for relative crab abundance amongst sites. We predicted that watershed size and alder cover would have no effect on crab size or CPUE since terrestrial nutrients are thought to be lower quality than marine or estuary-derived sources (Deegan and Garritt 1997). We predicted that estuary size would increase the size and CPUE of crabs due to increased habitat availability and local resource production (Deegan and Garritt 1997, Vander Zanden and Fetzer 2007). Adult salmon spawner density could increase crab size and CPUE but this seasonal subsidy could also be overwhelmed by estuarine production and the influx of terrestrial resources that occur throughout the year.

We then calculated the relative dietary contributions of terrestrial-, salmon-, and estuarine- derived resources to Dungeness crabs using a simple three-source linear isotope-mixing model. We predicted the relative contributions of terrestrial- and salmon-derived resources would be substantial and in proportion to their availability, as described by upstream watershed size and salmon spawning density.

Our study is the first to test for the effects of terrestrial and salmon-derived subsidies on an estuarine consumer across a gradient of natural landscape settings. Broad-scale studies such as this can highlight the importance of cross-ecosystem processes that drive ecological communities and also describe how these relationships can change across space. Integrating cross-ecosystem processes into land-use frameworks can better complement resource use with conservation as progressive efforts shift towards more ecosystem-based approaches. They can also highlight potential threats facing highly connected habitats as the pressures of large-scale resource development and climate change intensify.

4.3. Methods

4.3.1. Study area

Research was conducted on the central coast of British Columbia, Canada, within the Great Bear Rainforest (Figure 4.1). This region lies within the Coastal Western Hemlock biogeoclimatic zone and receives some of the highest levels of precipitation on the continent (Pojar et al. 1991). Although selective logging occurred in many areas during the first half of the 20th century, this region remains relatively intact due to its remoteness, restricted access and strengthening First Nations governance and conservation coalitions (Price et al. 2009). This remote region has a wide range of relatively pristine watersheds that are ideal systems to test for the effects of terrestrial and salmon resource subsidies in estuaries across space.

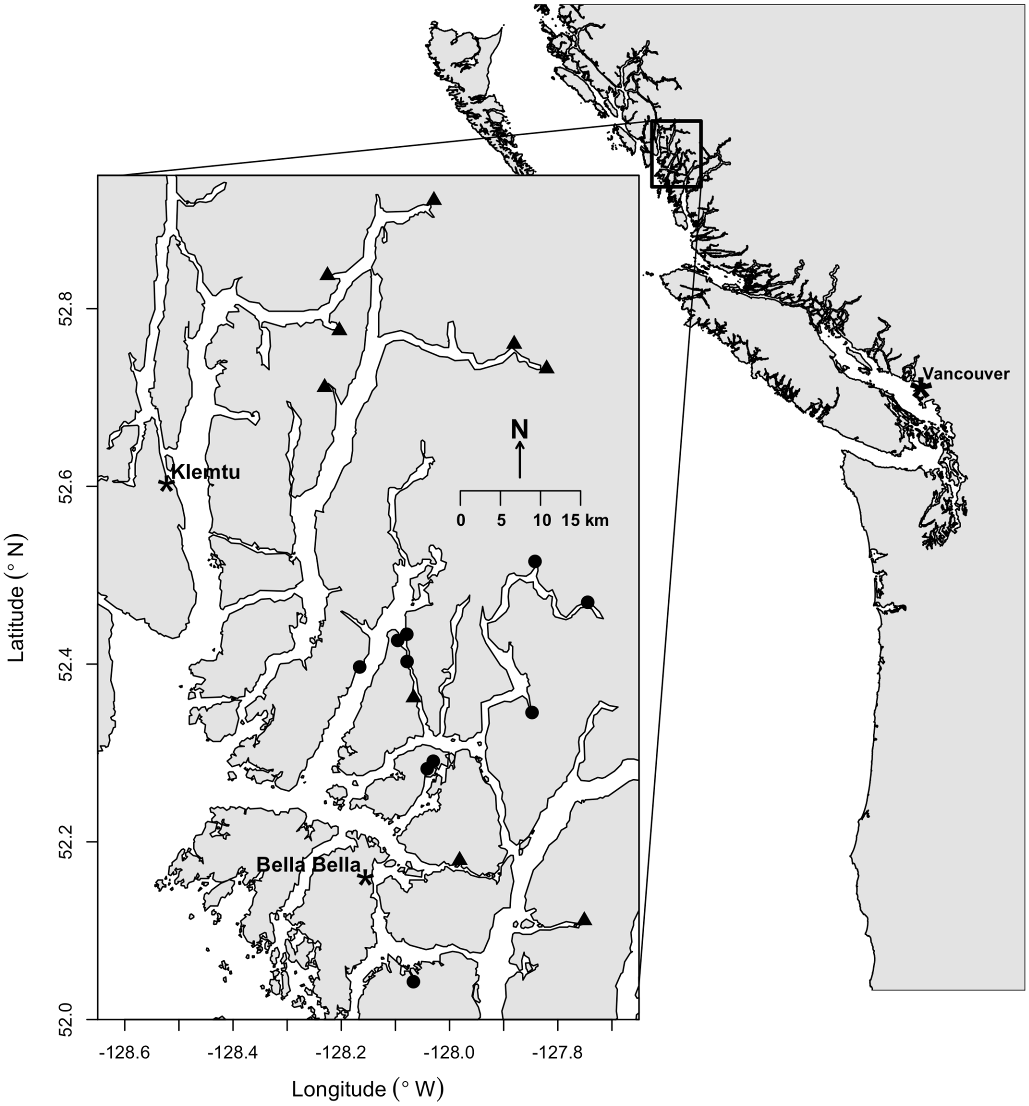

Figure 4.1. **Study site locations. Circles indicate sites sampled in both 2007 and 2008 and triangles indicate sites sampled only in 2007. Asterisks show locations of the Coastal First Nations communities of Bella Bella and Klemtu, British Columbia.**

We sampled 19 estuaries that varied in upstream catchment area, stream channel size, estuary area, upstream salmon spawning density, and red alder dominance (Table 4.1). All streams were dominated by chum (*O. keta*) and pink (*O. gorbuscha*) salmon, with smaller numbers of coho (*O. kisutch*) and a limited presence of sockeye (*O. nerka*) and chinook (*O. tshawytscha*).

Table 4.1. Summary of site-level covariates used in models to describe $\delta^{15}N$ and $\delta^{13}C$ of Dungeness crab muscle tissue, mass and catch per unit effort (CPUE).

Site Code	Catchment Area (km²)	Mean Bankfull Width (m)	Mean Depth (m)	Mean Bank Height (m)	Estuary Area (km²)	Mean Salmon Biomass Density (kg/ m²)	Percent Alder	Fishing Intensity †
1	13.9	20.5	0.12	0.52	0.10	0.88	11.05	2
2	17.7	17.9	0.21	0.37	0.59	0.30	42.07	4
3	3.3	10.9	0.08	0.26	0.04	1.32	3.31	2
4	2.8	8.4	0.09	0.39	0.02	0.60	5.54	1
5	32.1	22.8	0.16	0.30	0.81	1.13	26.08	2
6	22.9	13.3	0.19	0.56	0.84	0.71	5.12	2
7	35.0	12.8	0.16	0.39	0.28	0.46	1.74	2
8	7.0	10.9	0.19	0.41	0.18	1.99	1.16	1
9	30.2	17.1	0.20	0.37	1.10	0.26	2.66	5
10	1.0	3.5	0.04	0.16	0.08	0.92	11.02	1
11	64.8	30.8	0.27	0.42	0.65	0.80	25.48	1
12	49.6	25.5	0.29	0.62	1.30	0.20	19.80	1
13	5.2	9.7	0.11	0.21	0.09	1.15	6.33	1
14	166.5	45.4	0.41	0.61	0.63	0.60	31.75	1
15	40.9	34.1	0.24	0.55	0.84	0.13	17.95	2
16	47.3	38.6	0.26	0.52	2.00	0.31	38.71	2
17	1.6	4.4	0.10	0.23	0.27	0.01	0.00	3
18	1.8	4.1	0.11	0.23	0.20	0.15	0.00	3
19	12.0	13.1	0.11	0.34	2.30	0.04	20.15	4

† An ordinal variable assigned to each site based on interviews with local resource managers (refer to Table 4.2).

4.3.2. Survey

Surveys were conducted in the summers of 2007 and 2008 prior to salmon spawning. We deployed up to 10 collapsible coated-metal traps at each site ranging between 5-15 m datum depth (relative to 0 m tide), each measuring 61 x 61 x 30.5 cm. The mesh size was approximately 7 cm and escape ports were blocked to prevent escape of smaller individuals. Each trap was baited with commercial crab pellet bait soaked in fish oil, and deployed for up to 24 hours before retrieval. For each crab caught, we recorded sex, carapace width, mass, and shell age using protocols adapted from the Department of Fisheries and Oceans (Dunham et al. 2011). Shell age was an ordinal value assigned to each individual depending on carapace traits where values ranged between 1 (moulting) to 7 (very old) (Table C.1). The lower half of one of the most posterior legs was removed to collect muscle tissue samples from up to five adults per site from each year. Crabs were then released and tissue samples were frozen at -20°C in sealed containers until processing. All trap depths were corrected to datum depth for analysis.

4.3.3. Watershed data

Stream and riparian tree canopy (% alder) data were collected between May and July 2007 during an extensive survey of 50 watersheds in the region. Stream measurements were collected from 12 random transects along a study reach. Each study reach length was determined by multiplying the mean stream bankfull width by 30 (Bain and Stevenson 1999). Alder basal area was calculated from the diameter at breast height for each tree greater than 5 cm in diameter in six 35 m long by 10 m wide belt transects that extended perpendicular from each stream into the riparian zone (Hocking and Reynolds 2011). Percent alder was calculated for each site as:

$$A = \frac{B_{alder}}{B_{total}} \times 100 \tag{1}$$

where A is the percent alder for each site, B_{alder} is total basal area of all alder measured in a given site and B_{total} is the total basal area of all tree species measured in that site. Watershed catchment and estuary areas were calculated using the Government of British Columbia's mapping website *iMap*BC (Government of British Columbia 2006). To reflect the mobility and potential habitat use of Dungeness crabs, estuary boundaries were defined by the high tide mark landward and the boundary between the enclosing bay or inlet and the adjacent fjord or channel seaward.

A composite variable for watershed size was calculated using principal components analysis (PCA). Variables included were total catchment area (km^2), mean stream bankfull width (mean width of the stream channel at its highest point before flooding banks), mean stream depth, and mean stream bank height (the mean maximum stream depth before flooding banks). Pearson correlation coefficients between these variables ranged between 0.7 and 0.8. The first principal component axis (PC1) described 86% of variable variances. Variable loadings for PC1 were all positive, and very similar, ranging between 0.49 and 0.51. This means that as the value of PC1 increases, all component variables increase correspondingly. Therefore PC1 was retained for all analyses as it explained the majority of variance and was a descriptor of 'watershed size'. This technique was chosen to account for variation among watersheds in ratios of stream channel size to catchment area. This method reflects both the magnitude of upstream terrestrial-derived nutrient sources (catchment area) and the potential for stream channels to convey these nutrients downstream into estuaries (stream channel measurements).

To control for the effects of fishing in our study sites, we collected information from managers with local resource authorities: The Heiltsuk Integrated Resource Management Department in Bella Bella and The Kitasoo Fisheries Program in Klemtu. These managers have lived all their lives in the region, and are deeply familiar with local fisheries. Managers were asked to assign each estuary to one of a series of ordinal numbers representing combinations of local, recreational and commercial crab fishing intensity (Table 4.2).

Table 4.2. Description of fishing intensity categories assigned to study sites by local resource authorities from the Heiltsuk Integrated Resource Management Department in Bella Bella, and the Kitasoo Fisheries Program in Klemtu, British Columbia.

Code	Description
1	Rare to occasional local or recreational fishing (traps observed 1-5 times per year) + No commercial fishing
2	Rare to occasional local or recreational fishing + Rare commercial fishing (commercial sets observed once every year)
3	Frequent local or recreational fishing (traps observed >5 times a year) + Rare commercial fishing
4	Frequent commercial fishing (commercial sets observed more than once a year) + Rare to occasional local or recreational fishing
5	Frequent local or recreational fishing + Frequent commercial fishing

4.3.4. Salmon Population Data

Salmon counts and spawning reach lengths for all sites came from cooperative stock assessment efforts by the federal Department of Fisheries and Oceans, the Heiltsuk Integrated Resource Management Department, the Kitasoo/ Xai'xais Fisheries Program, and Simon Fraser University. A salmon density index was calculated using the average number of spawning chum and pink salmon from 2006 to 2009 for each site:

$$\text{Salmon Density} = \frac{\sum (N_i \times W_i)}{A} \tag{2}$$

where *Salmon Density* = average kg of salmon biomass per m^2 of spawning area per stream from 2006 to 2009, N_i = the mean number of returning adult salmon for the given years for each species i, W_i = average salmon mass for each species i, and A = the estimate of spawning area (m^2) within each stream. We accounted for variation in body size among populations by using sub-region specific average salmon masses from watersheds that share island groups and mainland inlets. We limited our analyses to chum and pink salmon because these species account for 90-100% of total adult salmon spawners within study sites. Detailed descriptions of salmon enumeration and estimates of population sizes can be found in Hocking and Reynolds (2011).

In this study we used upstream salmon biomass density as a proxy for salmon carcass availability in estuaries downstream. The mean salmon biomass density from 2006-2009 provided the most representative metric for salmon nutrient availability to Dungeness crabs. We determined this from data limitations (data collection began in 2006 and we did not want to consider years beyond 2009) and by competing indices for all individual years and year combinations between 2006-09 for a subset of five study sites that also have historical salmon count data. Because Dungeness crabs can live up to 10 years, they have the potential to benefit from salmon returns over time. We therefore constructed univariate linear models using the year combinations described above, with each explaining a historical salmon index spanning the previous ten years (1996-2005), which we assumed to be an optimal salmon metric if the data existed for all sites. We competed these models using Akaike Information Criterion corrected for small sample sizes (AICc) to see which years, or year combinations, between 2006 and 2009 had the highest likelihood explaining the historical index for these 5 sites. The 2006-09 index had the highest likelihood with a model weight approaching 1 (Table C.2). We log transformed the 2006-09 salmon density index for analysis of $\delta^{15}N$ to better describe the asymptote observed in the raw data.

Muscle tissue samples were removed from the exoskeleton and placed in a drying oven at 58°C for up to 96 hours. Each sample was homogenized into a fine powder using a heavy duty Wig-L-Bug© grinder (Pike Technologies Ltd). A set amount of sample (0.8-1.2µg) was packaged in standard pressed tin capsules (3.5 x 5 mm) and sent to the UC Davis Stable Isotope Facility for analysis of nitrogen and carbon abundance using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Stable isotopes are expressed as the difference between the sample and a known standard, or δ, in parts per thousand (‰):

$$\delta^{15}N \ or \ \delta^{13}C = \left(\frac{R_{\mathrm{sample}}}{R_{\mathrm{standard}}} - 1 \right) \times 1000 \tag{3}$$

Where *R* is the ratio of the heavy isotope to the light isotope ($^{15}N/^{14}N$ or $^{13}C/^{12}C$). Standards for nitrogen and carbon analysis are derived from N_2 in air and Pee-Dee Belemnite (PDB) limestone, respectively.

4.3.5. Statistical Analyses

The open source statistical software R was used for all analyses (R Core Team 2012). Multicollinearity amongst all variables was generally low, with all variance inflation factors less than 3 (Zuur et al. 2010). Correlation coefficients between all covariates were 0.6 or less, which is not of great concern (Zuur et al. 2009). The only exception was watershed size and percent alder, which were moderately correlated (0.7). However, given the potential importance of these covariates, both were retained for analyses as the statistical methods we employed are known to be generally robust to collinearity (Freckleton 2010). Also, results revealed that parameter estimates for watershed size and percent alder did not change drastically between models that had only one of these covariates, versus models that had both, suggesting that they were explaining largely unique variation in the data. We also tested for (but did not find) regional differences between clusters of northern and southern sites in all analyses.

For isotope analysis, we used linear mixed-effects modeling to account for the hierarchical structure of the data (Pinheiro et al. 2012). This also allowed us to let regression intercepts vary between sites to account for extraneous site-level differences that may have influenced trends, to control for the correlation of individuals from the same site between sample years, and to account for heterogeneity in the variance structure (Zuur et al. 2009). Random, correlation, and variance structures were established from residuals of the global model, or models including all variables considered, and by using AICc selection of the most parsimonious structures with the global model using restricted maximum likelihood (REML) estimation (Zuur et al. 2009, Hocking and Reynolds 2011). For both $\delta^{15}N$ and $\delta^{13}C$ analyses, the random effect of site, the auto-correlation structure of site within year, and the variance structure of estuary size, accounted for pseudo-replication, satisfied the assumptions of residual normality and equal variance, and improved the likelihood of the global model (Zuur et al. 2009). We had strong hypotheses about all covariates considered and did not assume the importance of any particular variable over another. Consequently we competed all possible model combinations of variables in the global set using AICc. Top model weights were less than 0.25 so we accounted for model uncertainty using a multi-model approach (Barton 2012). We standardized our raw covariates with a mean of 0 and standard deviation of 2 to enable direct comparison of effect sizes amongst variables (Grueber et al. 2011). Candidate models were limited to the subset of all combinations of models with a ΔAICc less than 4 (Burnham and Anderson 2002). Parameter estimates for each variable were averaged across the candidate model set using the natural average method.

For crab abundance and size analyses we used site-level means from each sample year as all explanatory variables were also at the site-level. Crab mass was chosen as the best representation of an individual's size over any linear measurement of morphology (e.g. carapace width) because it is the most ecologically meaningful metric (Peters 1983). Unlike the isotope analyses of individuals, our covariates in CPUE and size analyses were not hierarchical (all were at the site-level) so we employed generalized least squares modeling with a nested correlation structure of site within year to address the lack of independence of the same sites between years (Zuur et al. 2009, Pinheiro et al. 2012). Top model weights were less than 0.35 so we used multi-model inference using the same methods described previously to account for model uncertainty. In addition, we limited models to those containing three or fewer covariates due to limited degrees of freedom. Additional analyses, using alternative model structures, did not reveal any support for interactions among the covariates considered.

We used a simple three-source linear isotope-mixing model to estimate the dietary contributions of terrestrial, salmon and estuarine sources to Dungeness crabs at each of our study sites (Phillips 2001). This model assumes equal partitioning of both C and N for all three sources, that crab diet consisted of these sources in proportion to their availability, and that the isotope ratios for these sources was consistent across all study sites (Verspoor et al. 2010). For terrestrial sources we used mean δ^{15}N and δ^{13}C values of stream particulate organic matter (POM) at 20 watersheds in our study region (3 random replicate samples per site over 2 seasons) (Darnaude 2005, Harmelin-Vivien et al. 2010). For salmon sources we used mean δ^{15}N and δ^{13}C values of dorsal muscle tissue from spawning chum and pink salmon at 8 watersheds in our study region (5 samples of each species per site). For estuarine sources we used mean δ^{15}N and δ^{13}C values of eelgrass (*Zostera marina*) collected from 20 estuaries within our study region (5 random samples from each site over 2 seasons). Terrestrial POM isotope samples were attained by vacuum filtering 500 ml of stream water through pre-combusted glass fibre filters (Whatman GF/F, 47 mm, 0.7 μm). Filters used for δ^{13}C POM analysis were acid fumigated following the protocol of Harris et al. (2001) to eliminate inorganic carbon content prior to analysis. Eelgrass samples were thoroughly cleaned and rinsed with deionized water prior to processing. All samples were processed and analyzed using the same methods described previously. We accounted for isotopic fractionation using a value of 2.54 per TL for δ^{15}N from Vanderklift and Ponsard (2003) and 0.4 per trophic level (TL) for δ^{13}C from Post (2002). We assumed that crabs can consume salmon sources directly (1 TL), or indirectly by consuming prey that assimilate this source (2 TL), so we multiplied fractionation values for salmon by an intermediate factor of 1.5 TL. We postulated that it was less likely for Dungeness crabs to consume terrestrial POM or

Zostera directly, so we multiplied fractionation values for these sources by a factor of 2 TL. The proportional contribution of each source was calculated for each estuary as:

$$p_A = \frac{(\delta^{13}\overline{C}_C - \delta^{13}\overline{C}_B)(\delta^{15}\overline{N}_D - \delta^{15}\overline{N}_B) - (\delta^{15}\overline{N}_C - \delta^{15}\overline{N}_B)(\delta^{13}\overline{C}_D - \delta^{13}\overline{C}_B)}{(\delta^{13}\overline{C}_C - \delta^{13}\overline{C}_B)(\delta^{15}\overline{N}_A - \delta^{15}\overline{N}_B) - (\delta^{15}\overline{N}_C - \delta^{15}\overline{N}_B)(\delta^{13}\overline{C}_A - \delta^{13}\overline{C}_B)} \tag{4}$$

$$p_{B=} \frac{(\delta^{15}\overline{N}_D - \delta^{15}\overline{N}_C) - (\delta^{15}\overline{N}_A - \delta^{15}\overline{N}_C)p_A}{\delta^{15}\overline{N}_B - \delta^{15}\overline{N}_C} \tag{5}$$

$$p_C = 1 - p_A - p_B \tag{6}$$

Where p_A, p_B and p_C represent the proportional dietary contributions of sources *A, B* and *C* (salmon, POM and eelgrass respectively) corrected for fractionation to Dungeness crabs *D*. $\delta^{15}\overline{N}_i$ and $\delta^{13}\overline{C}_i$ represent the overall mean isotopic ratios for sources *A, B* and *C* or the site-level mean isotopic ratios for *D*.

4.4. Results

4.4.1. Survey

Dungeness crabs were sampled from 19 sites in 2007 and 10 of those sites again in 2008. A total of 164 and 98 individual crabs were measured in 2007 and 2008, respectively. Of these, 78 and 46 were sampled for isotopes in 2007 and 2008, respectively (Table 4.3).

Table 4.3. Summary of Dungeness crab surveys in 2007 and 2008 on the central coast of British Columbia.

Site Code	Year	Number of Traps	Mean Trap Depth (m)	Total Trap Hours	Total Crabs	CPUE †
1	2007	10	5.1	225.6	5	0.532
2	2007	5	10.3	100.1	6	1.439
3	2007	5	10.7	49.5	5	2.423
3	2008	9	10.4	197.4	2	0.243
4	2007	5	8.7	48.2	4	1.992

Site Code	Year	Number of Traps	Mean Trap Depth (m)	Total Trap Hours	Total Crabs	CPUE †
5	2007	10	5.8	159.3	4	0.603
5	2008	9	13.0	199.2	9	1.084
6	2007	5	7.7	99.0	4	0.970
7	2007	4	7.9	76.4	3	0.943
7	2008	10	7.5	246.2	1	0.097
8	2007	5	10.0	35.5	4	2.703
8	2008	10	10.0	530.9	10	0.452
9	2007	10	10.9	86.6	4	1.109
10	2007	5	5.6	36.6	1	0.657
10	2008	9	7.1	233.3	11	1.132
11	2007	10	7.7	175.2	22	3.014
12	2007	10	12.2	206.9	16	1.856
13	2007	10	14.2	95.3	2	0.504
13	2008	9	13.4	219.7	2	0.218
14	2007	5	9.2	50.3	9	4.294
15	2007	5	12.8	98.9	11	2.670
15	2008	9	15.4	191.0	17	2.136
16	2007	10	12.2	247.1	32	3.108
16	2008	9	15.9	303.9	28	2.211
17	2007	5	5.7	49.5	3	1.454
17	2008	10	5.4	421.5	7	0.399
18	2007	5	5.8	89.3	6	1.612
18	2008	10	6.7	472.3	11	0.559
19	2007	5	10.9	107.5	23	5.136

† The number of crabs caught per trap day of fishing.

4.4.2. Crab isotopes

$\delta^{15}N$

Watershed size, salmon density and percent alder all correlated strongly with δ^{15}N of crab muscle tissue. As predicted, crab δ^{15}N was depleted in estuaries below larger watersheds and with higher percentages of alder (Figure 4.2A & C). Also as predicted, crab δ^{15}N enriched with increasing salmon density (Figure 4.2B). Both watershed size and salmon density had the highest relative importance (Figure 4.2D) and were present in every model of the candidate set. Confidence in the effects of watershed size, salmon density, and percent alder were particularly high because the 95% confidence intervals

(CI) did not cross zero (Figure 4.2D). Crabs that were large or had older shells had slightly enriched δ^{15}N, as predicted, but these effects were uncertain with CI crossing zero. Contrary to our prediction, estuary size had no effect on δ^{15}N and was associated with large CI that spanned zero, indicating high variability amongst individuals and sites. The full candidate model sets for these and other analyses are summarized in appendix Tables C.3-6 in Appendix C.

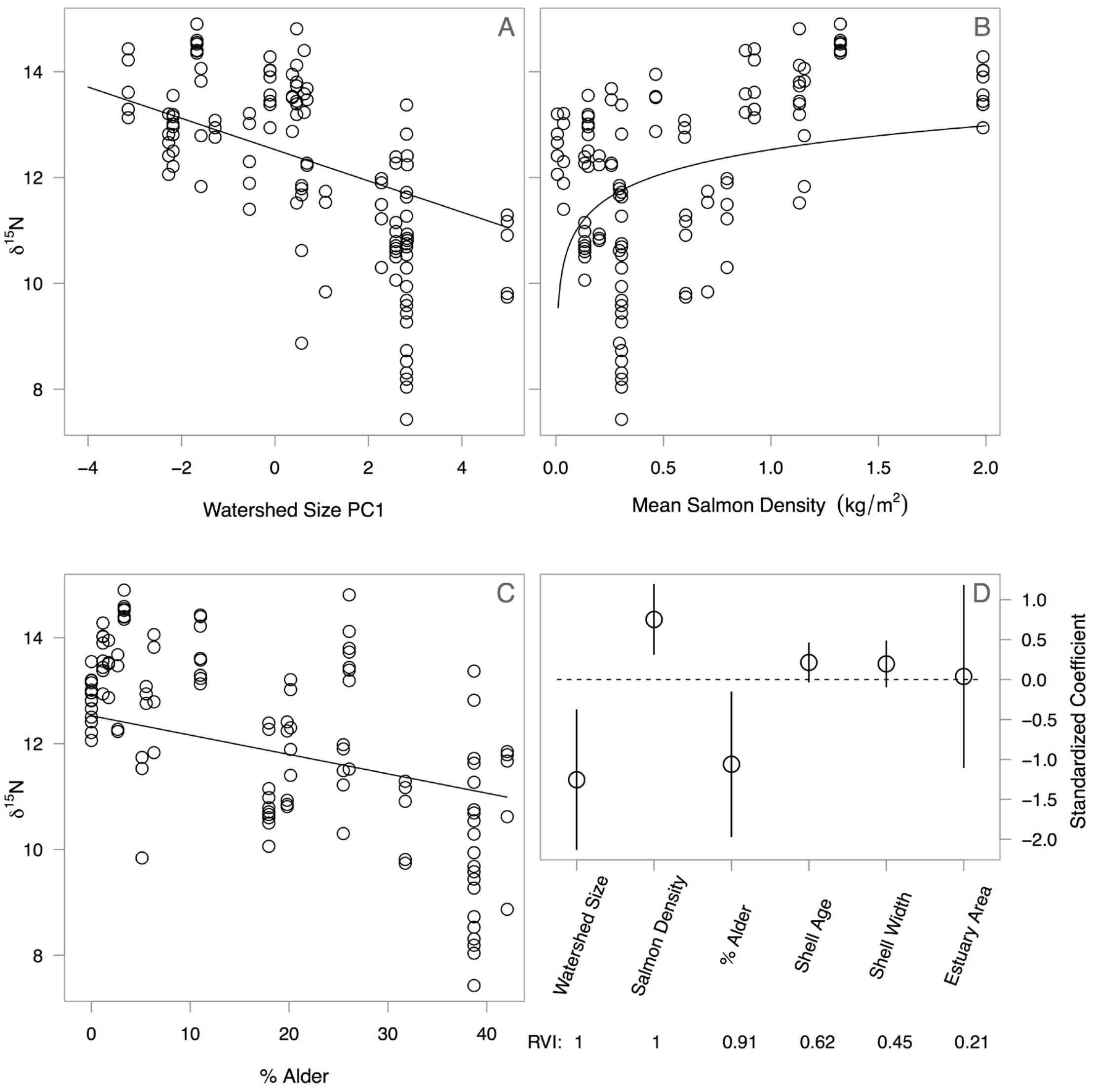

Figure 4.2. A) Dungeness crab muscle tissue $\delta^{15}N$ vs. watershed size principal component 1. B) $\delta^{15}N$ vs. mean salmon density with trend line based on log-transformed salmon density. C) $\delta^{15}N$ vs. percent alder basal area upstream relative to total basal area of all tree species. Each data point represents an individual crab and data points stacked vertically indicate individual estuaries. All trend lines represent univariate models using intercept and coefficients from multi-model output; thus they represent the relationships for the x-axis variable while accounting for other variables, rather than fitting the univariate data shown in each graph. D) Standardized coefficients (mean = 0, standard deviation = 2) with 95% confidence intervals for all covariates considered in the $\delta^{15}N$ candidate model set in order of relative variable importance (RVI), which is the sum of weights for all models in which each covariate is present.

δ^{13}C

Watershed size had the strongest effect on δ^{13}C of crab muscle tissue (Figure 4.3C). As predicted, crabs with older shells had more enriched δ^{13}C and those below larger watersheds had more depleted δ^{13}C (Figure 4.3A-B). Both shell age and watershed size had CI that did not cross zero and were present in the majority of candidate models with cumulative weights of 0.96 and 0.86 from the candidate model set, respectively (Figure 4.3C). The effects of both estuary size and salmon density were contrary to our predictions but the results were highly uncertain with large CI that spanned zero considerably. Correlations with carapace width and percent alder followed our predictions but were highly uncertain and displayed low levels of support with low cumulative weights from the candidate model set.

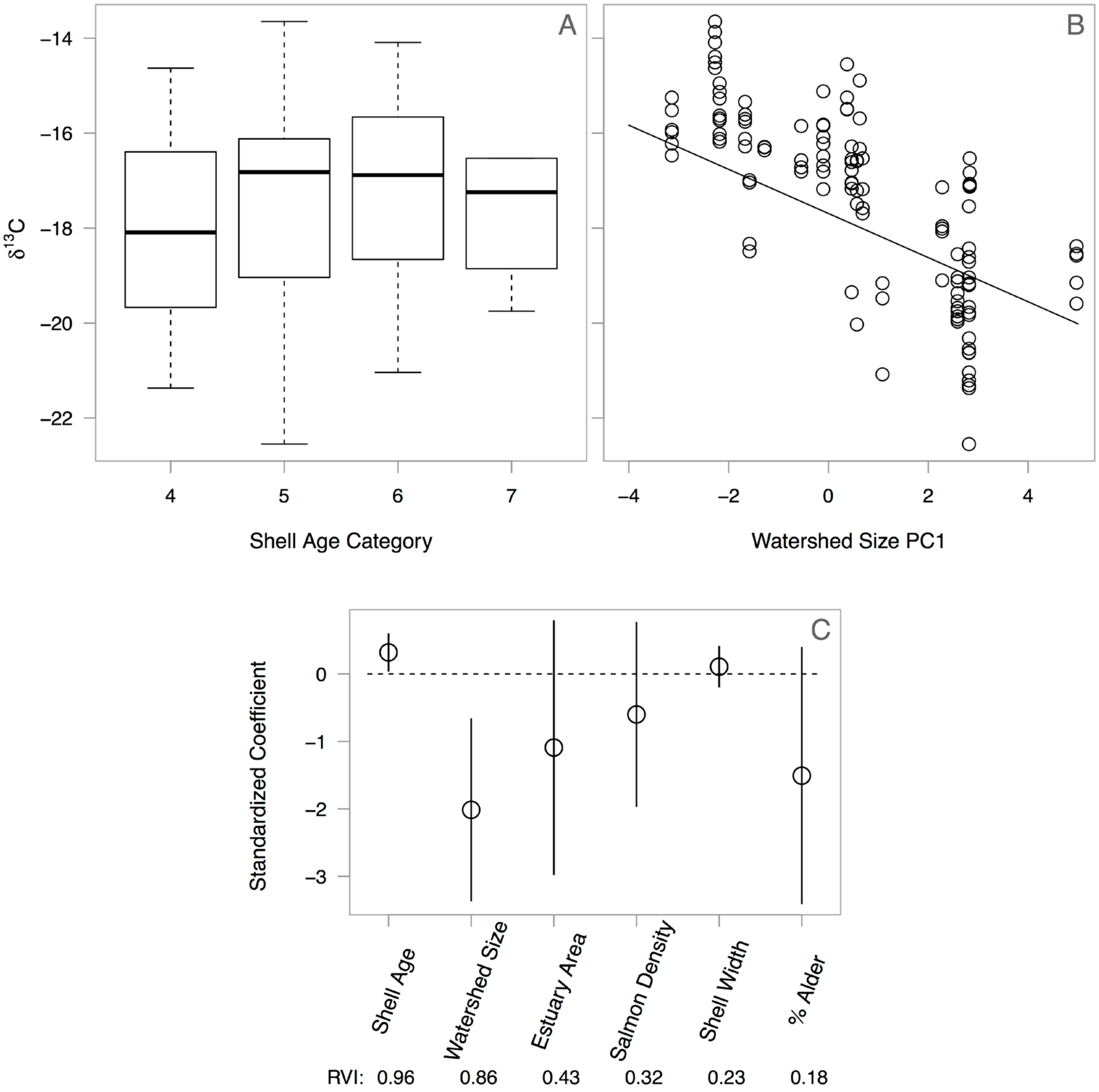

Figure 4.3. **A) Dungeness crab muscle tissue δ^{13}C vs. shell age category, from younger to older (see Table S2). B) δ^{13}C vs. watershed size principal component 1. Trend line for B represents univariate model using intercept and coefficient from multi-model output (see explanation of data fitting in caption of Figure 2). C) Standardized coefficients (mean = 0, standard deviation = 2) with 95% confidence intervals for all covariates considered in the δ^{13}C candidate model set in order of relative variable importance, RVI, i.e. the sum of weights for all models in which each covariate is present.**

Catch Per Unit Effort

As predicted, catch per unit effort (CPUE) of Dungeness crabs was highest in the largest estuaries (Figure 4.4A-B). No other variable correlated strongly with CPUE, which supported our predictions for watershed size and percent alder, but not for salmon. Although watershed size had a positive effect, the result was highly uncertain and had limited support with a cumulative weight of 0.25 from the candidate model set. Fishing intensity correlated negatively but, as with trap depth and percent alder, it had very weak support (Figure 4.4B). Salmon density had a negligible relationship with CPUE, with a cumulative weight of only 0.08 from the candidate set.

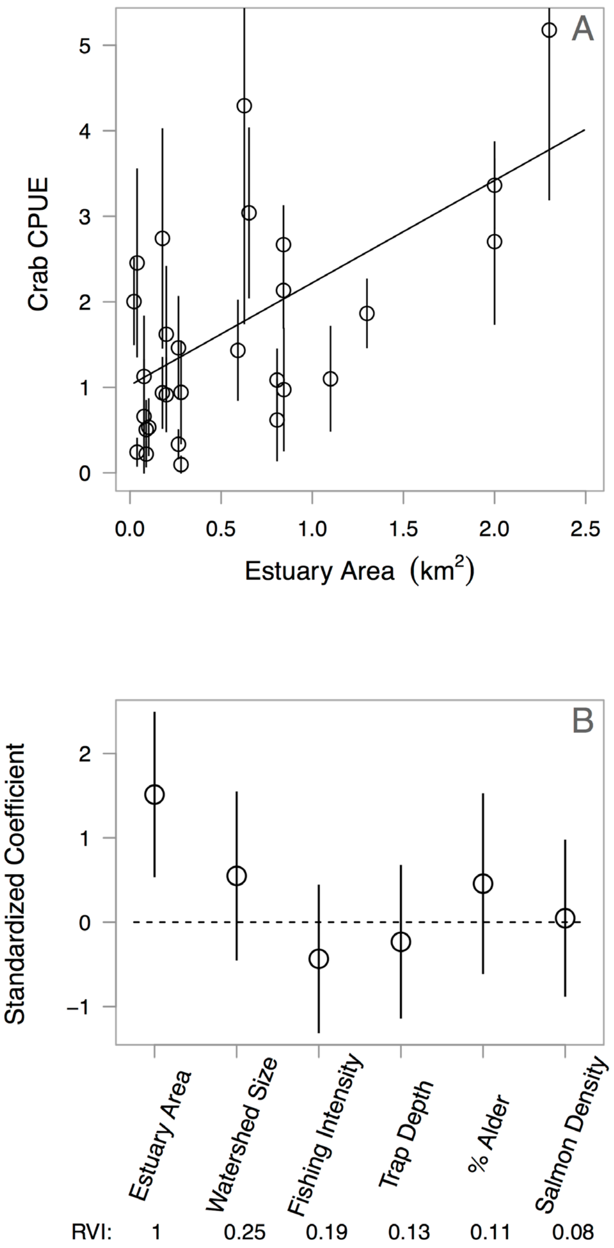

Figure 4.4. A) Mean Dungeness crab catch per unit effort (CPUE) vs. estuary area, with standard error bars. CPUE was calculated as the number of crabs caught per individual trap day fished. The trend line represents univariate model using intercept and coefficient from multi-model output (see explanation of data fitting in caption of Figure 2). B) Standardized coefficients (mean = 0, standard deviation = 2) with 95% confidence intervals for all covariates considered in the CPUE candidate model set in order of relative variable importance, RVI, i.e. the sum of weights for all models in which each covariate is present.

Crab Size

Crabs were heavier in estuaries located below larger watersheds. This was not one of our predictions but was strongly supported (Figure 4.5A-B). All other covariates had highly uncertain effects with confidence intervals spanning zero and very low levels of support, which did not support our predictions for estuary size or salmon (Figure 4.5B).

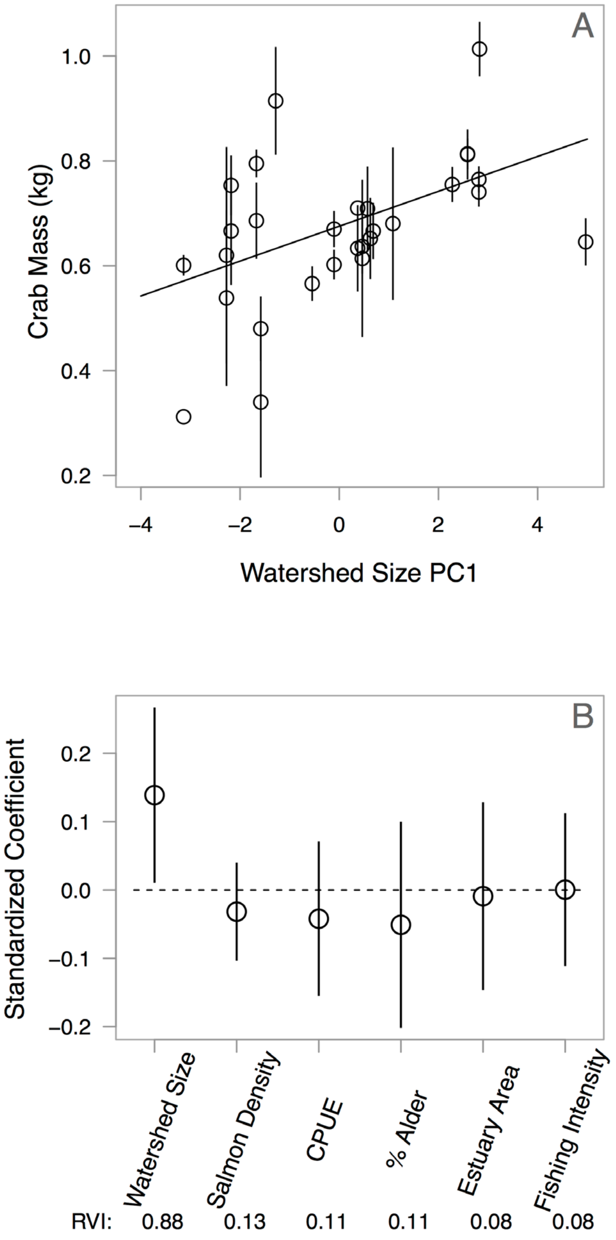

Figure 4.5. A) Mean Dungeness crab mass vs. watershed size principal component 1. The trend line was constructed from a univariate model using the intercept and coefficient from multi-model output (see explanation of data fitting in caption of Figure 2). B) Standardized coefficients (mean = 0, standard deviation = 2) with 95% confidence intervals for all covariates considered in mass candidate model set in order of relative variable importance, RVI, i.e. the sum of weights for all models in which each covariate is present.

Isotope Mixing Model

Source isotope ratios fully encompassed the range of individual Dungeness crab isotope ratios (Figure 4.6). Source dietary contributions ranged between 0.25 to 0.67 for salmon, -0.02 to 0.40 for terrestrial POM, and 0.28 to 0.58 for estuarine sources. As predicted, the contributions of external resources scaled positively with metrics of their availability. Salmon dietary contributions scaled positively with upstream salmon density, and terrestrial contributions scaled positively with watershed size, with R^2 values of 0.39 and 0.55 respectively (Figure 4.7).

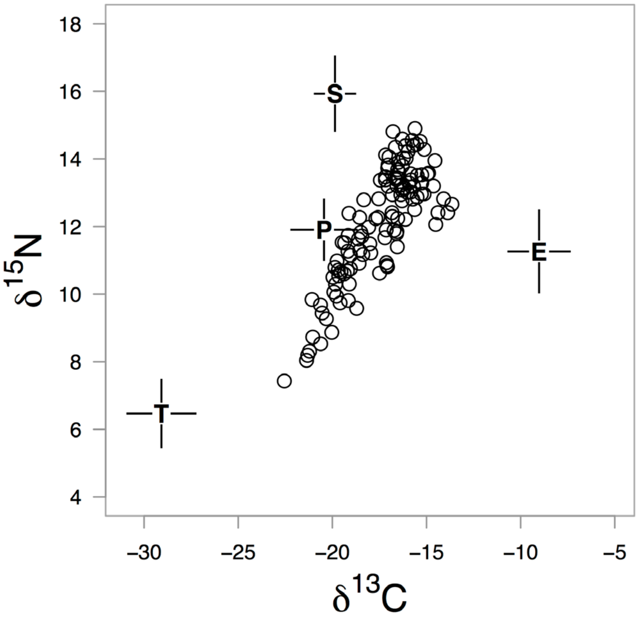

Figure 4.6. Isotope bi-plot of individual crabs and three sources used in isotope-mixing model analysis: 'S', 'T', and 'E' which indicate salmon, terrestrial, and estuarine sources, respectively. Terrestrial sources are stream particulate organic matter and estuarine sources are *Zostera marina*. Error bars represent the standard deviation of isotope ratios for each source. Plankton, 'P', is included for visual reference but was not used in the isotope-mixing model. All mean source and plankton isotope values are corrected for 2 trophic levels of fractionation except for a 1.5 trophic level correction for salmon.

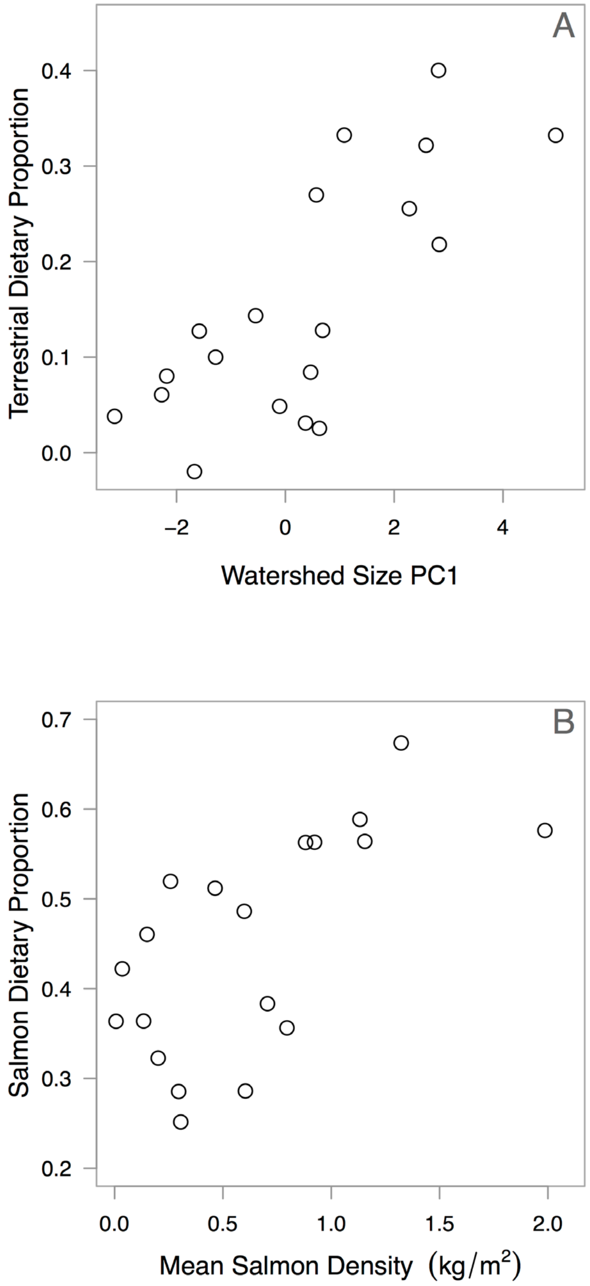

Figure 4.7. **A) Proportional contribution of terrestrial resource subsidies to the diet of Dungeness crabs vs. watershed size principal component 1. B) Proportional contribution of salmon resource subsidies to the diet of Dungeness crabs vs. mean upstream salmon density. Proportional dietary contributions were calculated in isotope-mixing models that considered terrestrial, salmon and estuarine dietary sources. Watershed size and salmon density were covariates tested in isotope, CPUE and size analyses.**

4.5. Discussion

These analyses provide novel insight into the importance of resource subsidies in estuarine ecosystems and how this can vary among landscapes. Results supported our predictions that watershed size, salmon density, percent alder and the shell age of individuals explained stable isotope ratios of Dungeness crab muscle tissues. Crabs were also more abundant in larger estuaries but were heavier in estuaries below larger watersheds. Results from the isotope-mixing models confirmed that the proportions of terrestrial and salmon sources contributing to crab diet increased with upstream watershed size and salmon density, suggesting that crabs are assimilating these resources in proportion to their availability. This is the first study to evaluate the effects of terrestrial- and salmon-derived nutrients, amongst other factors, on estuarine invertebrates using stable isotopes and individual- and population-level responses across a broad range of watersheds. Below we interpret our results in the context of stable-isotope ecology and cross-ecosystem dynamics, before concluding with a brief comment on the importance of integrating landscape connectivity into conservation and management.

Watershed size had strong depletion effects on both δ^{15}N and δ^{13}C of crab muscle tissue. This was shown in both AICc model selection and isotope-mixing model analyses. Terrestrial-derived material is depleted in heavy isotopes of carbon and nitrogen as a result of remineralization of organic material through detrital pathways. Thus, as terrestrial nutrient contributions to estuaries increase, we find a more ‘terrestrial’ or depleted signature in Dungeness crabs (Chanton and Lewis 2002, Connolly et al. 2009). Higher prevalence of alder trees also depleted crab δ^{15}N. Alders fix nitrogen directly from the atmosphere as a result of symbiotic bacterial associations and can saturate forest soils with nitrogen, which can leach δ^{15}N-depleted nitrates into streams (Naiman et al. 2002, Compton 2003). Because alders shed their leaves annually, they can also increase the amount of organic material exported from watersheds into streams and estuaries (Wipfli and Musslewhite 2004, Richardson et al. 2009).

We partially confirmed our prediction that crabs with older shells (i.e. time since last moult) would have enriched δ^{13}C but this was not observed for δ^{15}N. It is also possible this $\delta^{13}C$ enrichment is a result of shifts in the dissolved organic carbon pool (Gillikin et al. 2006) experienced by crabs showing habitat preferences during moulting.

In contrast to watershed size and red alder, upstream adult salmon density had a strong enrichment effect on Dungeness crab $\delta^{15}N$. This confirms our observation that crabs feed on salmon carcasses and our prediction that the density of salmon upstream can mediate this effect.

The isotope-mixing model results complemented the inference from isotope AICc analyses; as availability of both terrestrial sources and salmon increased among watersheds, so did their contributions to the diets of crabs relative to estuarine sources (Figure 4.7). Although AICc analyses did not detect an effect of salmon on $\delta^{13}C$ ratios, we believe this is because $\delta^{13}C$ values for salmon occupy the mid-range between $\delta^{13}C$ for terrestrial POM and eelgrass (Figure 4.6). Therefore, models competed in AICc analyses would be most affected by depleted (terrestrial particulate organic matter, POM) and enriched (other sources) isotope values while not detecting any salmon effect. The isotope-mixing model approach addressed this issue and showed that salmon are indeed influencing both the $\delta^{15}N$ and $\delta^{13}C$ of crab muscle tissue. One limitation of isotope-mixing model analysis is the assumption that diet consists only of the sources considered. There are many other dietary sources for Dungeness crabs, such as other fish species. In addition, our use of eelgrass as an estuarine end member is also a simplification, as many other sources, such as benthic algae and sedge plant species, likely contribute to this source in reality. Additional uncertainty around these dietary contributions from variation in fractionation rates between sources, and amongst individual crabs, must also be recognized (Phillips and Gregg 2001).

While freshwater ecosystems are known to be supported by both terrestrial- and locally-derived resources (Post 2002, Thorp and Delong 2002, Marcarelli et al. 2011), there is conflicting research on the importance of terrestrial-derived subsidies in estuarine productivity. We found much stronger effects of terrestrial resources than some studies (Deegan and Garritt 1997, Chanton and Lewis 1999, 2002). Our results support those of Connolly et al. (2009), who detected considerable isotopic shifts towards terrestrial resources in detritivorous invertebrates occupying river plumes of estuaries. In addition, Darnaude et al. (2004a) and Bănaru et al. (2007) detected increased terrestrial contributions to benthic invertebrates in larger systems, which suggests that the effects of terrestrial subsidies scale with river discharge. Our broad cross-system research unifies these previous studies by demonstrating how contributions of terrestrial-derived subsidies scale with watershed size, and can increase the size of estuarine consumers.

There are many potential pathways through which terrestrial- and salmon-derived resource subsidies could propagate through estuarine food webs to Dungeness crabs. Nutrient loading from rivers can elevate organic content in estuaries (Mayer et al. 1998, Hopkinson et al. 1999, Alliot et al. 2003) and has been shown to increase production of oysters (Oczkowski et al. 2011) and the abundance (Hoffman et al. 2007) and condition (Bănaru and Harmelin-Vivien 2009) of fish. Increased terrestrial particulate organic matter (POM) could be consumed directly by crabs, elevate benthic diatom production, and increase productivity of prey such as polychaetes, crustaceans and molluscs. Although plankton can provide substantial nutrient inputs to benthic habitats (Chester and Larrance 1981), sediment organic matter below river outlets is dominated by terrestrial POM (Darnaude et al. 2004a). This can be seen in our mixing model results, when comparing our terrestrial POM end member to the mean isotope value of phytoplankton; terrestrial POM fully encompasses the range of Dungeness crab isotope values and describes crab diet, whereas phytoplankton does not (Figure 4.6). It is also possible that the effect of watershed size on crab size could be confounded if lower predation and competitive pressures experienced by crabs are associated with reduced salinities in upper estuaries of larger systems (Oczkowski et al. 2011). However, the extent of this is likely limited as Dungeness crabs are poor osmoregulators and cannot occupy zones of reduced salinity for extended periods of time (Stevens et al. 1984, Curtis and McGaw 2012).

Although we did not find any evidence that salmon nutrients result in more abundant, or larger crabs, there are other potential effects that we did not test for such as increases in adult fecundity, increased larval recruitment success or the persistence of populations in sub-optimal habitats (Marcarelli et al. 2011, Barry and Wilder 2012). In addition, salmon spawning occurs prior to winter months when crabs migrate to deeper habitats and reduce activity (Stone and O'Clair 2001). Therefore any energetic benefits from salmon subsidies could be relegated to maintenance through dormant winter seasons, rather than growth.

Catch-per-unit-effort, which we used as a metric for relative abundance of crabs amongst sites, was best explained by estuary area. This suggests that abundance is limited by the amount of available habitat and not the influx of additional resources. Dungeness crabs commonly cannibalize as adults (Pauley et al. 1986). If cannibalism and competition are density dependent, this could explain why adult abundances are not affected by nutrient subsidies. Future research could investigate whether CPUE approximates total numbers of crabs within a site or whether larger estuaries also host higher densities of individuals. Although the effect of fishing intensity on CPUE was negative, it was highly uncertain. We recognize that the fishing intensity categories employed were very basic, but our intent was to control for fishing effort, not to investigate its effects. Actual capture data, which do not exist for recreational and sustenance fisheries, would be required for any study intending to analyze the effects of fishing on crab abundance.

Although this study found strong evidence of both terrestrial- and salmon-derived subsidies to Dungeness crabs, it was not clear whether the mechanisms were direct, through consumption of terrestrial POM and salmon carcasses, or indirect, where inputs are driven upwards from the bottom of the food web. We suspect that the majority of salmon resources are being consumed directly by crabs, whereas terrestrial subsidies may enter the food web at multiple levels and subsidize crabs indirectly. Further investigation of potential nutrient pathways would be beneficial to decipher whether these subsidy effects are community wide or limited to subsets of likely benefactors (Darnaude et al. 2004b, Anderson et al. 2008).

This study demonstrates how landscape traits can have major effects on adjacent ecosystems and can strengthen ecosystem-based management efforts that aim to incorporate connectivity amongst coastal landscapes (Price et al. 2009). For example, Canada’s Wild Salmon Policy (Fisheries and Oceans Canada 2005), which aims to integrate ecosystem values into management of Pacific salmon, recognizes that salmon nutrients are important in freshwater and riparian ecosystems. Our work suggests estuaries can also benefit directly from these annual nutrient pulses in the Northern

Pacific. These results could also help inform resource management and conservation efforts in intact areas such as BC's central coast, which face increasing industrial development pressures such as forestry, liquid natural gas expansion and potential oil transport infrastructure including pipeline and ocean tanker traffic. The consideration of potential effects from these industries, and their associated land-use management strategies, should expand beyond direct effects and consider how these activities may alter natural nutrient dynamics that could drive productivity in downstream habitats such as lakes and estuaries. Climatic warming can also alter hydrodynamic regimes through reductions in seasonal flow and shifts in peak flow timing (Shrestha et al. 2012). Consequently, the productivity of estuaries may decrease in the future if the influx of terrestrial subsidies depends on river discharge and high-flow events (Salen-Picard et al. 2002, Darnaude 2005). The rapid expansion of hydro-power development within the region also poses potential risks in terms of cutting off sediment and particulate organic matter supplies to estuarine ecosystems (Mayer et al. 1998). Lastly, estuaries support rich ecosystems that host traditional resources utilized by Coastal First Nations and support commercial and recreational fisheries. Therefore, conservation efforts should prioritize areas where industrial land-use activities are being considered upstream of estuaries that are of particular food, social and ceremonial importance to First Nations, support abundant food resources or possess other high conservation values.

Chapter 5. Investigating patterns in resource subsidy contributions to the diets of estuarine consumers[4]

5.1. Abstract

Resource subsidies are widespread but do not always play a crucial role in recipient ecosystems. The importance of a subsidy can be determined by its availability relative to local resources and by consumer life history traits such as feeding ecology. Based on these considerations we investigate how strongly consumer diets are determined by landscape traits that describe resource availability. In addition, we determine whether these relationships vary between sedentary and mobile species with different feeding ecologies, and between cross-ecosystem subsidies and locally derived resources. We examine the proportional dietary contributions of salmon- and terrestrially-derived resource subsidies to blue mussels (*Mytilus edulis*), soft-shell clams (*Mya arenaria*) and Dungeness crabs (*Metacarcinus magister*) in estuaries of the north-eastern Pacific. We compare subsidy contributions to those of other inferred dietary sources using Bayesian isotope mixing models. We then examine variability, and spatial patterns in consumer diets through correlations between the estimates of source dietary contributions and measureable landscape traits. Analyses revealed high variation in the diet of Dungeness crabs at the site level compared to mussels and soft-shell clams. Correlations between Dungeness crab diet and landscape were also much stronger compared to both bivalve species, suggesting the importance of local resource conditions to this mobile consumer. Although bivalve diets also correlated with landscape traits such as watershed size and salmon density, proportional source contributions to their diet did not change to the same degree. We conclude that both terrestrial- and salmon- derived subsidies are an

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[4] A version of this chapter is in preparation for publication with Jennifer N. Harding and John D. Reynolds.

important resource to estuarine consumers, particularly mobile consumers, and this importance can be determined indirectly by measureable landscape traits.

5.2. Introduction

There is increasing recognition that ecological communities, previously studied in isolation, are open systems and depend on externally-derived energy sources (Richardson and Sato 2015). The movement of material and energy across ecosystem boundaries can constitute large proportions of the resource base that drives most communities on Earth (Polis et al. 1997). Responses to such resource subsidies can vary over space and time (Anderson et al. 2008) but generally result in elevated productivity within recipient habitats (Richardson and Sato 2015). However, the quality, timing and magnitude of resource subsidies can influence the extent to which resource inputs bolster productivity (Yang et al. 2008, Marcarelli et al. 2011). Subsidy timing can be controlled by phenology, species migration or abiotic processes such as rainfall events, while the quality and magnitude of resource subsidies can be influenced by the traits of donor landscapes (hereafter referred to as donor traits) and the capacity of resource exchange between ecosystems (Polis et al. 1997, Marczak et al. 2007).

Donor traits such as size and species composition can influence the nutrient quality, extent and duration of spatial subsidies (Yang et al. 2010, Kominoski et al. 2011). For instance, larger watersheds that export more material downstream correlate with larger sizes of estuarine invertebrates (Harding and Reynolds 2014a, Harding et al. 2015) and nitrogen availability in riparian plant communities can be dictated by the density of spawning salmon or the abundance of deciduous alder trees within watersheds (Hocking and Reynolds 2011). Ecosystems that are connected by water have a high capacity to exchange and assimilate resource subsidies (Shurin et al. 2006, Leroux and Loreau 2008, Marcarelli et al. 2011). Consequently, aquatic habitats, especially those that interface between different ecosystems, are ideal systems to investigate how the importance of resource subsidies vary spatially (Richardson and Sato 2015).

In addition to donor traits, individual consumer traits within recipient habitants also govern the effects of subsidies (Yang et al. 2010). Factors such as mobility, feeding ecology and body size will dictate whether a species can effectively access a resource subsidy relative to other resources (Anderson et al. 2008, Nowlin et al. 2008). Therefore the net effects of spatial subsidies can be context dependent, benefitting specific cohorts of communities under certain conditions (Moore et al. 2008), or be very broad, permeating throughout food webs (Spiller et al. 2010).

Estuaries make ideal systems to compare the importance of spatial subsidies to locally derived resources. They are on the ecotone between marine, freshwater and terrestrial ecosystems. In addition to local productivity, estuaries can receive substantial influxes of externally-derived material including terrestrial subsidies (Darnaude et al. 2004a, Connolly et al. 2009, Sakamaki et al. 2010) and salmon nutrients in the Northern Pacific (Fujiwara and Highsmith 1997, Cak et al. 2008, Harding and Reynolds 2014a, Harding et al. 2015). Few studies have investigated how spatial or temporal changes in the availability of resource subsidies affect the dietary composition of consumers, and fewer have examined how dietary contributions correlate with landscape traits or how these relationships might vary among organisms within the same habitat.

Here, we applied Bayesian isotope mixing models of stable isotopes to calculate posterior estimates of inferred dietary contributions from resource subsidies to sedentary consumers; the soft-shell clam (*Mya arenaria*) and the blue mussel (*Mytilus edulis*), and a mobile estuarine consumer, the Dungeness crab (*Metacarcinus magister*). Stable isotope ratios of consumer tissues can provide insight into resource assimilation (DeNiro and Epstein 1978, Deniro and Epstein 1981) and are increasingly used as a tool to estimate the dietary composition of consumers (Phillips 2001).We compared proportional dietary contributions of salmon- and watershed-derived subsidies to other resources across multiple coastal watersheds of the north-eastern Pacific. We then assessed relationships between dietary contributions and three simple and measureable watershed traits; salmon density, watershed size, and low-tide mudflat area in estuaries to determine how strongly diet correlates with local habitat traits or whether consumer life history traits override resource heterogeneity between sites. We hypothesized that dietary contributions would vary substantially among watersheds in our study region. We also predicted that dietary contributions would correlate with landscape traits but the correlations would be stronger, and dietary composition would change most, with the Dungeness crab due to its mobility and opportunistic feeding behaviour. We expected the diets of sedentary soft-shell clams and mussels to also be altered by local resource availability but to a lesser degree as a result of passive filter feeding and diet homogenization from planktonic contributions. Dietary shifts of clams may also differ from those of mussels due to differences in habitat type. For example, nutrient exports from watersheds may subsidize clams more than mussels because clams occupy soft substrate depositional zones where influxes of terrestrial organic material are most likely to settle. For all analyses salmon muscle tissue and stream particulate organic matter (POM) were each collected to represent spatial subsidies from spawning salmon and upstream terrestrial landscapes respectively (Harding and Reynolds 2014a, Harding et al. 2015). Specifically, we hypothesized that dietary proportions of salmon and terrestrial subsidies would increase with salmon density and watershed size respectively while accounting for other dietary sources within estuaries. We also predicted that increased terrestrial resource influx from larger watersheds could bolster local plankton productivity in estuaries, thus increasing availability to filter feeders (Chanton and Lewis 1999, Coffin and Cifuentes 1999). From the same logic we also postulated that epiphytic growth, and resultant contributions to the resource base, would also scale with watershed size due to elevations in dissolved nutrient influx (Frankovich and Fourqurean 1997). We predicted that sediment organic matter (SOM) assimilation by soft-shell clams would increase below larger watersheds as a result of larger contributions of organic particulate matter (Sakamaki et al. 2010). We also anticipated that larger watersheds would facilitate larger proportions of soft-shell clams in the diet of Dungeness crabs because larger clams exist below larger watersheds (Harding et al. 2015) in addition to potential increases in clam abundance.

5.3. Methods

5.3.1. Study sites

We selected sites that span natural gradients in spawning salmon density and watershed size on the central coast of British Columbia (Figure 5.1). This area is in the Coastal Western Hemlock-biogeoclimatic zone and receives some of the highest levels of precipitation on the continent (Pojar et al. 1991). Watersheds within this region are relatively intact due to their remoteness, First Nations governance and conservation efforts (Price et al. 2009).

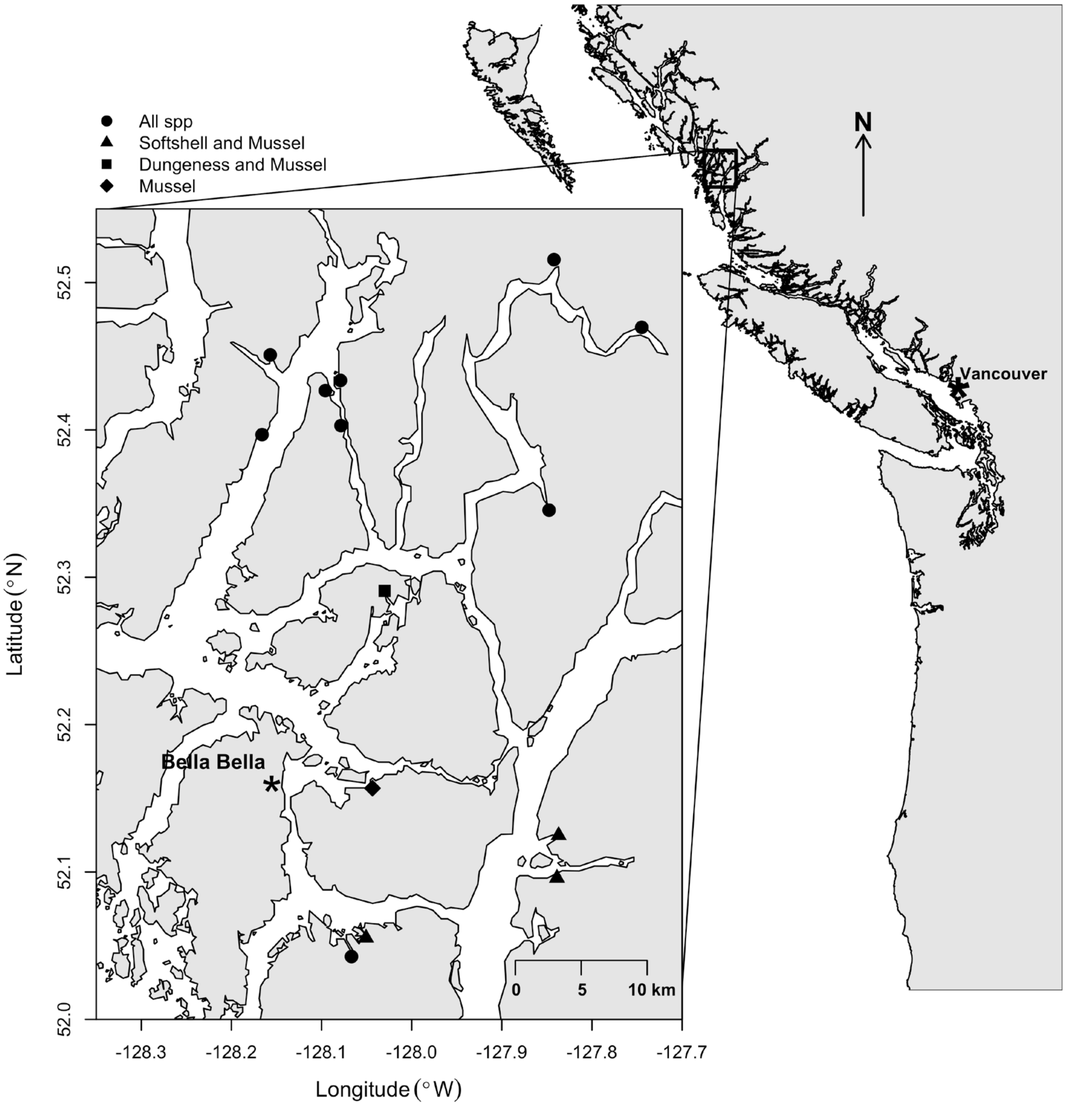

Figure 5.1. **Sample locations of mussels (14 sites), soft-shell clams (12 sites) and Dungeness crabs (10 sites).**

5.3.2. Consumer Sample Collections

Mussels

Mussels were collected from 14 watersheds during the summer (210 mussels) and fall (204 mussels) of 2008 to enable a seasonal comparison. Samples were collected during low summer tides and by free diving during the fall salmon-spawning season. The first five individuals encountered were collected from three systematically chosen locations that spanned the length of the intertidal zone occupied by mussels below stream outlets.

Soft-shell Clams

Clams were collected from 12 watersheds during summer low tides of 2008 (124 clams) and 2009 (132 clams). Fall samples were not collected because high tides prevented collection during daylight hours. Clams were collected from up to three locations (depending on beach size) per watershed that spanned the length of clam beds below stream outlets. For each sample location, five individuals were collected from the sediment by digging to a depth of 30 cm and retaining the first five clams from the sediment pile (Harding et al. 2015).

Dungeness crabs

Crabs were collected with traps from 10 watersheds during the summers of 2007 (32 crabs) and 2008 (36 crabs) using up to 10 traps at a time each measuring 61 × 61 × 30.5 cm. Depths ranged between 5 and 15 m datum depth (relative to 0 m tide). Traps were baited with crab pellet and fish oil and set for up to 24 hours. The lower half of one of the most posterior legs of each crab was removed to collect muscle tissue samples from up to five adults per site from each year. The crabs were then released (Harding and Reynolds 2014a).

All samples were wrapped immediately in aluminum foil and frozen at -20°C in sealed containers until processing. See Table 5.1 for sample totals.

Table 5.1. Sample totals for consumers collected by site and sampling period.

Site	Mussel Summer 2008	Mussel Fall 2008	Soft-shell 2008	Soft-shell 2009	Crab 2007	Crab 2008
Ada	15	15	5	5		
Bullock Main	15	15	12	15	5	2
Clatse	15	15	13	14	3	5
Fannie Left	15	15	15	15	3	1
Fell Creek	15	10	6	5	4	5
Hooknose	15	15	13	15		

Site	Mussel Summer 2008	Mussel Fall 2008	Soft-shell 2008	Soft-shell 2009	Crab 2007	Crab 2008
Kill Creek	15	15	8	5	1	5
Kunsoot Main	15	15				
Mosquito Bay	15	15	5	10	2	2
Neekas	15	15	15	14	1	3
Quartcha	15	14	14	15	5	5
Roscoe Main	15	15	13	14	5	5
Sagar	15	15	5	5		
Troupe North	15	15			3	3

5.3.3. Source Sample Collections

For salmon sources we used regional mean $\delta^{13}C$ and $\delta^{15}N$ values of dorsal muscle tissue from spawning chum and pink salmon collected from eight watersheds in our study region where five samples of each species were collected per site. We limited our analyses to chum and pink salmon because these species account for 90–100% of total adult salmon in our study region. For terrestrial sources we used site-specific mean $\delta^{13}C$ and $\delta^{15}N$ values of POM (collected from 3 random replicate samples per site in each season) (Darnaude 2005, Harmelin-Vivien et al. 2010). Freshwater POM consists mostly of terrestrial organic matter (Harmelin-Vivien et al. 2010, Sakamaki et al. 2010). POM isotope samples were collected by vacuum filtering 500 ml of stream water through pre-combusted glass fibre filters (Whatman GF/F, 47 mm, 0.7 lm). Filters used for $\delta^{13}C$ POM analysis were acid fumigated following the protocol of Harris et al. (2001) to eliminate inorganic carbon content prior to analysis.

In addition, we selected potential direct and indirect dietary sources from within estuaries. This included eelgrass (*Zostera marina*), epiphytes that grow on the surface of eelgrass, plankton, sediment organic matter (SOM; for clams only) and soft-shell clams (for crabs only). Eelgrass, epiphytes and plankton are major contributors of estuarine organic matter (Fry et al. 1977, Frankovich and Fourqurean 1997). Sediment organic matter was considered as a potential source for infaunal soft-shell clams (Sakamaki et al. 2010), which are a prey item of Dungeness crabs (Stevens et al. 1982, Jensen and Asplen 1998).

5.3.4. Isotope Sample Processing

The adductor muscle of mussels, the foot muscle of clams and the leg muscle of crabs were dissected and dried at 58°C for up to 96 hours. We used site- and season-specific mean δ^{13}C and δ^{15}N values of eelgrass and epiphytes (five random samples from each site in summer and fall of 2008). Eelgrass and epiphyte samples were cleaned thoroughly and rinsed with de-ionized water prior to processing. Season-specific regional plankton isotope values were used as we assumed variation to occur seasonally, not between estuaries. Plankton samples were collected from five offshore locations within our study region during summer and fall seasons of 2008 and 2009 using vertical plankton tows to a depth of 8 m. Plankton within 20-200 μm were retained for processing to reflect phytoplankton and protozooplankton dietary contributions (Sieburth et al. 1978). Site-specific isotope values for soft-shell clams (see previous methods) and SOM were also collected in the summers of 2008 and 2009. For each site, SOM samples were collected from each of the three clam sampling locations by taking sediment cores down to 15 cm. Each sediment sample was rinsed with deionized water through 100 μm mesh and this liquid was vacuum filtered through two pre-combusted glass fibre filters for nitrogen and carbon analysis. All carbon SOM samples were acid fumigated and analyzed following the above protocols.

After excluding filtered POM and SOM samples, each sample was pulverized into a fine powder using a heavy duty Wig-L-Bug grinder (Pike Technologies). All dried samples were packaged into standard pressed tin capsules (3.5 X 5 mm; 5 X * mm for SOM; 10 X 10 mm for POM filters) and analyzed at the UC Davis Stable Isotope Facility for natural abundance of nitrogen and carbon using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon, Cheshire, UK). Acid-fumigated samples were packaged in silver capsules. Stable isotopes are expressed as the difference between the sample and a known standard, or δ, in parts per thousand (‰):

$$\delta^{15}N \text{ or } \delta^{13}C = (\frac{R_{sample}}{R_{s\tan dard}} - 1) \times 1000 \tag{1}$$

where R equals the ratio of the heavy isotope to the light isotope ($^{15}N/^{14}N$ or $^{13}C/^{12}C$). Standards for nitrogen and carbon analysis are derived from N_2 in air and Pee-Dee Belemnite limestone, respectively.

5.3.5. Landscape Traits

Watershed Size

We used principal components analysis (PCA) to generate a composite variable describing watershed size to approximate the amount of terrestrial-resource influx into estuaries via stream discharge. Component variables included total catchment area (km^2), mean stream bankfull width (width of the stream channel at its highest point before flooding), mean stream depth, and mean stream bank height (maximum stream depth before flooding) from each site. Pearson correlation coefficients of these metrics ranged between 0.7 and 0.9. The first principal component axis (PC1) described over 80% of component variances, which all loaded positively (ranged between 0.48 and 0.52). The PC1 axis represents the magnitude of nutrient transport downstream into estuaries (stream channel measurements) and the amount of terrestrial-derived nutrient sources upstream (catchment area).

Estuary Low Tide Area

The area of exposed intertidal mud flat at low tide was measured by sketching the mudflat extents on air photos during low tides approximately 1 m above chart datum. Areas were calculated using the Government of British Columbia's mapping website *iMap*BC (Government of British Columbia 2006).

5.3.6. Salmon Population Data

The federal Department of Fisheries and Oceans, the Heiltsuk Integrated Resource Management Department, and Simon Fraser University cooperatively conducted all salmon population counts and spawning area measurements. We considered upstream salmon biomass density estimates between years 2006 and 2009 as metrics for salmon nutrient inputs into estuaries (Harding and Reynolds 2014a, Harding et al. 2015). These years were considered because data collection began in 2006 and we did not want to consider years beyond 2009. Salmon biomass densities were calculated for chum, pink, and both species of salmon combined, for year combinations 2006–2007, 2006–2008 and 2006–2009 for each study site:

$$SBD_{ij} = \frac{\sum (N_{ij} \times W_j)}{A} \tag{2}$$

where SBD_{ij} = average kg of salmon biomass per m^2 of spawning area per stream for year combination i and species j, N_{ij} = the mean number of returning adult salmon for year combination i and species j, W_j = average salmon mass for each species j, and A = the estimate of spawning area (m^2) within each stream.

We used previously selected salmon metrics for Dungeness crabs (2006-09 combined salmon biomass density) and soft-shell clams (2006-07 pink salmon biomass density) (Harding and Reynolds 2014a, Harding et al. 2015) and conducted additional analyses to select the most appropriate salmon density metric for mussels (described below). Spawning area was calculated by multiplying the mean bankfull stream width by the total length of spawning reach for each stream. We accounted for variation in salmon body mass among populations by measuring the weight of the same salmon from which we collected isotope samples within our study region. Average salmon masses from these sites were extrapolated to the remaining study sites sharing island groups, channels or mainland inlets.

We determined the best salmon density metric that described stable isotope ratios of mussel adductor muscle tissue by competing univariate linear models with chum, pink or total (chum and pink) salmon density for each selected year combination explaining $\delta^{15}N$. We competed these models using Akaike Information Criterion corrected for small sample sizes (AICc). We log transformed all salmon density metrics in all analyses to reduce the leverage of high salmon density values on slope estimates.

5.3.7. Statistical Analyses

Isotope Mixing Models

MixSIAR (v1.2), a Bayesian stable isotope mixing model, was used in R to generate posterior probability distributions of the proportional dietary contributions of salmon-, terrestrial- and estuarine-derived sources to each consumer (Semmens et al. 2009, R Core Team 2012, Stock and Semmens 2013). Separate model runs were conducted for crabs, clams, summer mussels and fall mussels. For crabs and clams, separate sampling years were considered as random effects. For all consumers, sites and individuals were also considered as random effects. Each model run consisted of three parallel chains of 50,000 iterations with a burn in phase of 25,000. Every 25th sample of the remaining 25,000 iterations was retained to generate posterior distributions. Site- and season-specific source values were used where possible and source concentration dependence was considered in all models (Phillips and Koch 2002). Each source value was the mean ± 1 SD from each site or a regional mean value (Table 5.2). Trophic fractionation was assumed to be 2.3 ± 1.6 ‰ (mean and SD) for δ^{15}N and 0.4 ± 1.2 ‰ for δ^{13}C per trophic level (TL) (McCutchan et al. 2003). The Gelman-Rubin, Heidelberger-Welch and Geweke diagnostic tests were used to confirm convergence on a posterior distribution (Stock and Semmens 2013). Although mixing models are powerful and informative tools, they are a simplification of actual consumer diets and multiple assumptions must be made; fractionation is constant between trophic levels; all potential dietary sources are considered in the models; everything consumed is assimilated and homogenized into the consumer tissues analyzed; consumers within each analysis have the same potential sources of diet; and all source contributions are beta-distributed (Moore and Semmens 2008, Hopkins and Ferguson 2012, Phillips et al. 2014).

Table 5.2. Sampling period and spatial resolution of dietary sources. POM = terrestrial particulate organic matter; SOM = estuarine sediment organic matter.

	Consumer Analyses			
Inferred Sources	**Mussel Summer**	**Mussel Fall**	**Soft-shell Clam Summer**	**Dungeness Crab Summer**
Salmon	Regional mean 2009	Regional mean 2009	Regional mean 2009	Regional mean 2009

	Consumer Analyses			
Inferred Sources	**Mussel Summer**	**Mussel Fall**	**Soft-shell Clam Summer**	**Dungeness Crab Summer**
POM	Site mean summer values 2008	Site mean fall values 2008	Site mean summer values 2008	Site mean summer values 2008
Eelgrass	Site mean summer values 2008	Site mean fall values 2008	Site mean summer values 2008	Site mean summer values 2008
Plankton	Regional mean summer values 2008	Regional mean fall values 2008	Regional mean summer values 2008	NA
Epiphytes	NA	NA	NA	Site mean summer values 2008
SOM	NA	NA	Site mean summer values 2008-09	NA
Soft-shell Clams	NA	NA	NA	Site mean summer values 2008-09

Mussel dietary sources included salmon, POM, eelgrass and plankton. Soft-shell clam sources included salmon, POM, eelgrass, SOM and plankton. Crab sources included salmon, POM, eelgrass, epiphytes, soft-shell clams and eelgrass. Fractionation was assumed across one trophic level for mussels and clams. Crab fractionation was assumed to occur across 2 TL for POM and eelgrass, 1.5 TL for salmon and epiphytes (an average of direct and indirect consumption) and 1 TL for soft-shell clams (Harding and Reynolds 2014a).

Beta regression

Median posterior estimates of the proportional dietary contribution of each source from mixing models were regressed against single watershed traits (watershed size, salmon density or estuary low-tide mudflat area) using a beta model framework with a logit link function. We considered upstream salmon density and watershed size as predictors of the contributions of salmon and terrestrial POM to consumer diets, respectively (Harding and Reynolds 2014a, Harding et al. 2015). Dietary contributions of eelgrass were regressed against the area the mudflat in each estuary at low tide, which we assumed to be an indirect proxy for eelgrass habitat availability. Watershed size was also used as a predictor for the contributions of plankton, epiphytes, SOM and soft-shell clams. For dietary contributions of soft-shell clams to crab diets, we competed watershed size models against models with estuary mudflat as the predictor, which we assumed to be a proxy for the amount of available intertidal clam habitat. Watershed size PC1 and estuary mudflat area had a Pearson correlation coefficient of 0.6.

Broken-stick regression was tested if visual inspection of raw data suggested a potential break point in relationships. Break points were predetermined using piecewise regression (1,000 bootstrap iterations) in the R package SiZeR (Schwarz 2014). Broken-stick models were competed against duplicate linear models using Akaike Information Criterion for small sample sizes (AICc) and the model with the highest Akaike weight of evidence was selected. To avoid over-fitting broken-stick models, and to make ecological sense, regressions were restricted to prevent both positive and negative relationships in the same trend line. For example, if an overall positive relationship was observed but the first section of the broken-stick was slightly negative, that section was restricted to have a slope of zero (intercept only) until the second positive section. We assumed that small negative deviations from an overall positive relationship were due to factors not considered in the model.

When watershed size had a pseudo-$R^2 > 0.20$ further regressions were conducted using two of the four watershed size PC1 components; catchment area and stream bankfull width. This was done to provide further context in terms of meaningful and measurable metrics that could inform when certain sources would be more important in the diet of these consumers. Catchment area and bankfull width were chosen because they had the lowest Pearson correlation coefficients of the component variables (0.7) and reflected both the size of catchment basins and stream channels. All goodness of fit values are pseudo-R^2 defined as the correlation between a model's fit and the posterior median estimates of source contributions to diet.

5.4. Results

The isotope ratios of dietary sources encompassed those of consumers in all mixing model analyses (Supplemental Figures D.1-4). This confirmed that the sources considered represented the potential dietary range for each consumer in isotope space. Site- and individual-level variability in Dungeness crab diets were considerably higher compared to both clams and mussels in both seasons (Figure 5.2). However, year-level variability was higher for soft-shell clams compared to crabs. For bivalves, site-level mussel diets varied more than soft-shell clams and mussels had slightly higher site-level diet variability in the fall than the summer.

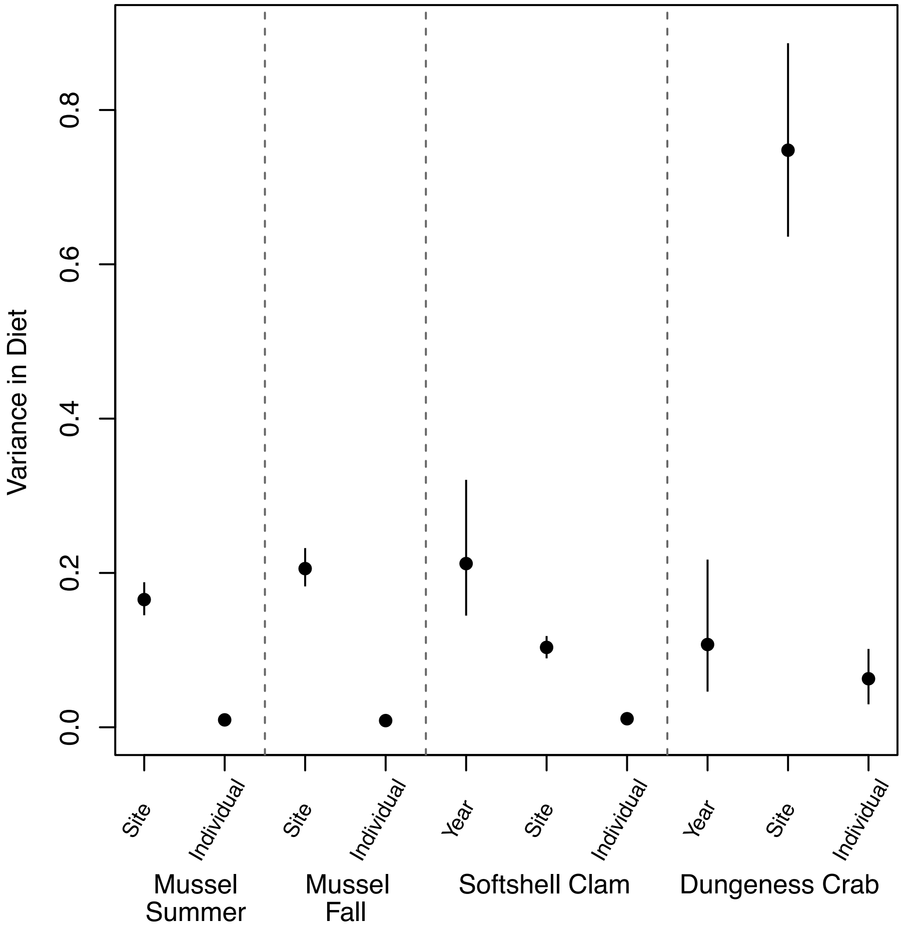

Figure 5.2. **Median posterior estimates of diet variability for mussels, soft-shell clams and Dungeness crabs. Error bars indicate 25-75% credible intervals.**

5.4.1. Mussels

Preliminary analysis indicated that the 2007-08 mean pink salmon density was the best descriptor of mussel $\delta^{15}N$ with an AICc model weight of 0.72. All other salmon metrics had weights less than 0.3. We used the same salmon metric for soft-shell clams in a previous study (Harding et al. 2015)

Mean contributions of each source to the diet of mussels are presented in Table 5.3. Proportional contributions ranged between 0.13 for POM and 0.37 for eelgrass in the summer and 0.13 for POM and 0.50 for eelgrass in the fall. Dietary contributions of plankton decreased from 0.26 in the summer to 0.16 in the fall. Eelgrass contributions increased from 0.37 in the summer to 0.50 in the fall while the contribution of POM and salmon to the diets of mussels did not change substantially between the two seasons.

Table 5.3. Mean proportional contributions of inferred sources to the diet of mussels, soft-shell clams and Dungeness crabs. Numbers in brackets indicate 1 standard deviation. POM = terrestrial particulate organic matter; SOM = estuarine sediment organic matter.

Source	Mussels		Soft-shell Clams	Dungeness Crab
	Summer	Fall		
Epiphytes	-	-	-	0.08 (0.06)
POM	0.13 (0.01)	0.13 (0.01)	0.10 (0.02)	0.03 (0.01)
Plankton	0.26 (0.03)	0.16 (0.03)	0.21 (0.05)	-
Salmon	0.24 (0.02)	0.21 (0.02)	0.21 (0.05)	0.30 (0.08)
Soft-shell Clams	-	-	-	0.35 (0.09)
SOM	-	-	0.22 (0.06)	-
Eelgrass	0.37 (0.02)	0.50 (0.02)	0.26 (0.06)	0.24 (0.06)

Most landscape traits did not effectively describe the diet of mussels during the summer. POM contributions increased in mussel diet below larger watershed sizes but the model fit was poor (Figure 5.3A; Table 5.4). Salmon contributions to mussel diet did not increase notably with salmon density in the summer (Figure 5.3B; Table 5.4). Larger watershed sizes correlated with increased dietary contributions of plankton but this effect was not apparent in watersheds with a PC1 value of less than 0.61 (Figure 5.3C; Table 5.4). Additional broken-stick regressions revealed a stronger relationship between plankton dietary contributions and catchment area (R^2 = 0.18) compared to stream bankfull width (R^2 = 0.07; Table 5.5; Figures D.5 A-B). The contribution of plankton to the diet of mussels in the summer did not increase until watersheds reached a catchment size of 32.1 km^2. Larger low tide mudflat areas reduced the contributions of eelgrass to mussel diet above a threshold of 8.4 ha, but model fit was poor (Figure 5.3D; Table 5.4).

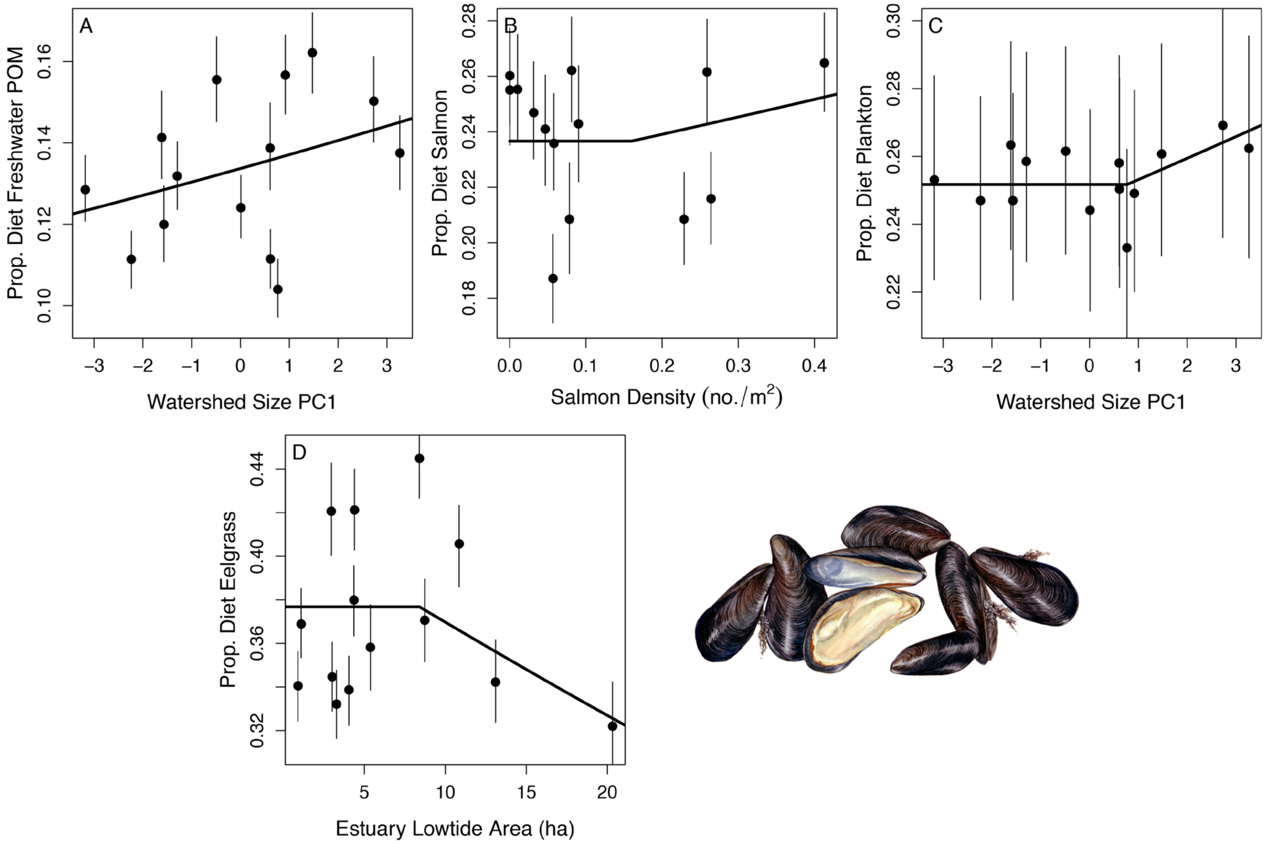

Figure 5.3. **Landscape trait correlations with inferred sources of mussels collected in the summer. Broken-stick regressions of A) Terrestrial particulate organic matter (POM) dietary contributions vs. watershed size, B) salmon contributions vs. 2007-08 mean pink salmon density, C) plankton contributions vs. watershed size, and D) Eelgrass contributions vs. low tide mudflat area. Data points are median posterior estimates from isotope mixing models with 25-75% credible intervals. Mussel image copyright © 1997-2015 Charting Nature/ Brenda G. Gillespie.**

Table 5.4. Model type, AICc weight and pseudo-R^2 for inferred sources considered in mussel diet analysis. POM = terrestrial particulate organic matter.

		Summer			Fall		
Source	Model	Type	AICc Weight	Pseudo-R^2	Type	AICc Weight	Pseudo-R^2
POM	Watershed Size	Linear	0.52	0.12	Linear	0.51	0.29
Salmon	Pink Salmon Density	Broken stick	0.56	0.06	Broken Stick	0.87	0.25
Plankton	Watershed Size	Broken stick	0.86	0.28	Broken Stick	0.53	0.29
Eelgrass	Low-tide Mudflat Area	Broken stick	0.72	0.15	Broken Stick	0.52	0.31

Table 5.5. Additional regressions on individual watershed size PC1 components in mussel diet analysis.

		Summer		Fall	
Source	Model	Type	Pseudo-R^2	Type	Pseudo-R^2
POM	Catchment Area	NA	NA	Linear	0.39
POM	Bankfull Width	NA	NA	Linear	0.41
Plankton	Catchment Area	Broken Stick	0.18	Broken Stick	0.48
Plankton	Bankfull Width	Broken Stick	0.07	Broken Stick	0.02

There were stronger correlations between landscape-level traits and source dietary contributions to mussels in the fall. Relationships were opposite to those in the summer with the exception of salmon density. POM contributions decreased with increasing watershed size (Figure 5.4A; Table 5.4). Further regressions showed stronger, and negative, correlations with both catchment area (R^2 = 0.39) and bankfull width (R^2 = 0.41; Table 5.5; Figures D.6 A-B). Salmon in mussel diet increased with salmon density in streams with more than 0.32 pink salmon/m^2 but these results must be interpreted with caution as this result is highly dependent on a single data point (Figure 5.4B; Table 5.4). Dietary contributions of plankton decreased with increasing watershed size, but there was no effect below smaller watersheds (PC1 values < -0.49; Figure 5.4C; Table 5.4). Additional regressions showed a much stronger relationship with catchment area (R^2 = 0.48) than with bankfull width (R^2 = 0.02; Table 5.5; Figures D.6 C-D). The amount of plankton in the diet of mussels in the fall did not decrease until watersheds reached a catchment size of 17.6 km^2. Eelgrass contributions increased in estuaries with larger low tide mudflat areas (Figure 5.4D; Table 5.4).

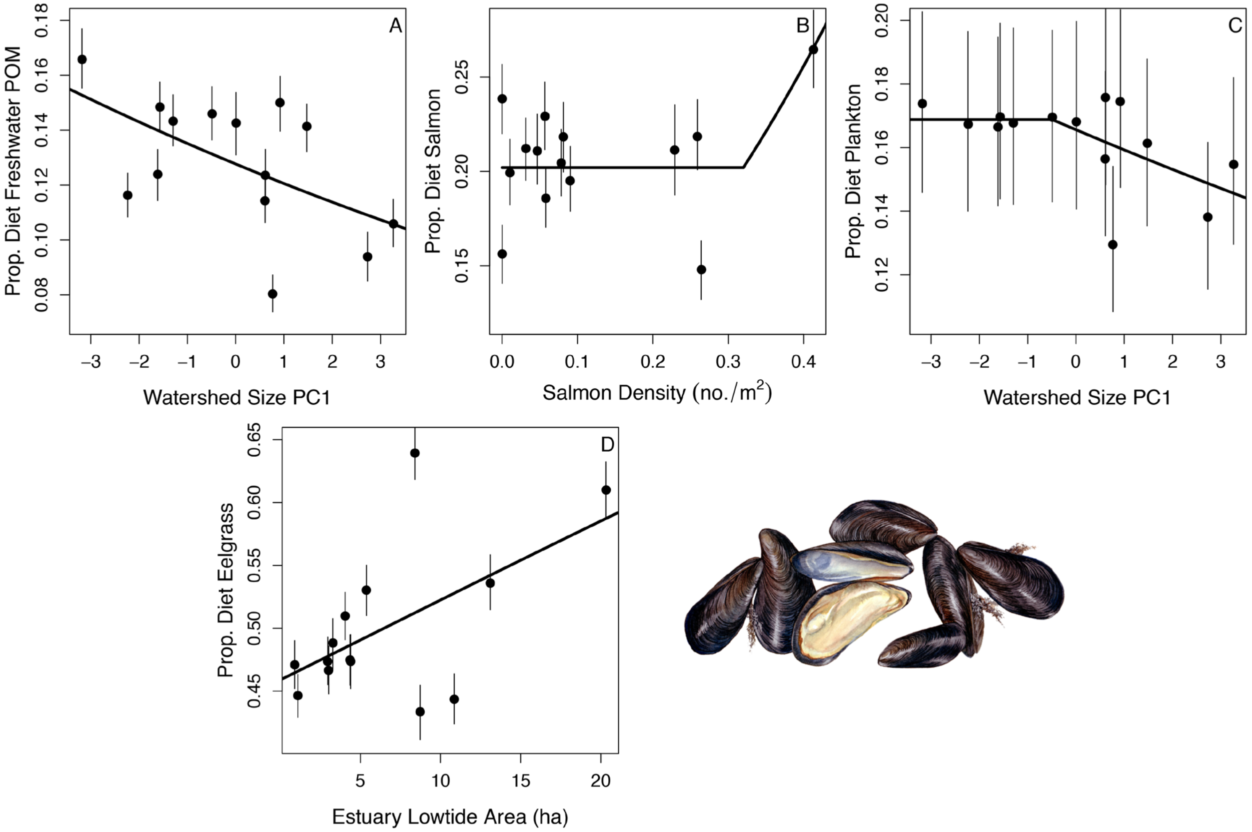

Figure 5.4. Landscape trait correlations with inferred sources of mussels collected in the fall. A) Linear regression of terrestrial particulate organic matter (POM) dietary contributions vs. watershed size, B) broken-stick regression of salmon contributions vs. 2007-08 mean pink salmon density, C) broken-stick regression of plankton contributions vs. watershed size, and D) linear regression of eelgrass contributions vs. low tide mudflat area. Data points are median posterior estimates from isotope mixing models with 25-75% credible intervals. Mussel image copyright © 1997-2015 Charting Nature/ Brenda G. Gillespie.

5.4.2. Soft-shell Clams

Proportional dietary contributions of inferred sources to soft-shell clams ranged between 0.10 for SOM and 0.26 for eelgrass (Table 5.3). Both plankton and salmon had mean dietary contributions of 0.21.

POM contributions increased in estuaries below larger watersheds, but this was not evident in watersheds with PC1 values less than 0.74 (Figure 5.5A; Table 5.6). Further regressions showed a weaker relationship with catchment area (R^2 = 0.07) compared to bankfull width (R^2 = 0.32; Table 5.7; Figures D.7 A-B). The dietary contribution of POM did not increase until streams reached a bankfull width of 16.9 m. Salmon contributions increased with salmon densities above 0.16 pink salmon/m^2 (Figure 5.5B; Table 5.6). There were weaker relationships between watershed size and plankton contributions, low tide mudflat area and eelgrass contributions, and watershed size and SOM contributions (Figures 5.5C-E; Table 5.6). We did not compete models in an AICc framework for plankton, eelgrass and SOM sources, as visual inspection suggested linear relationships.

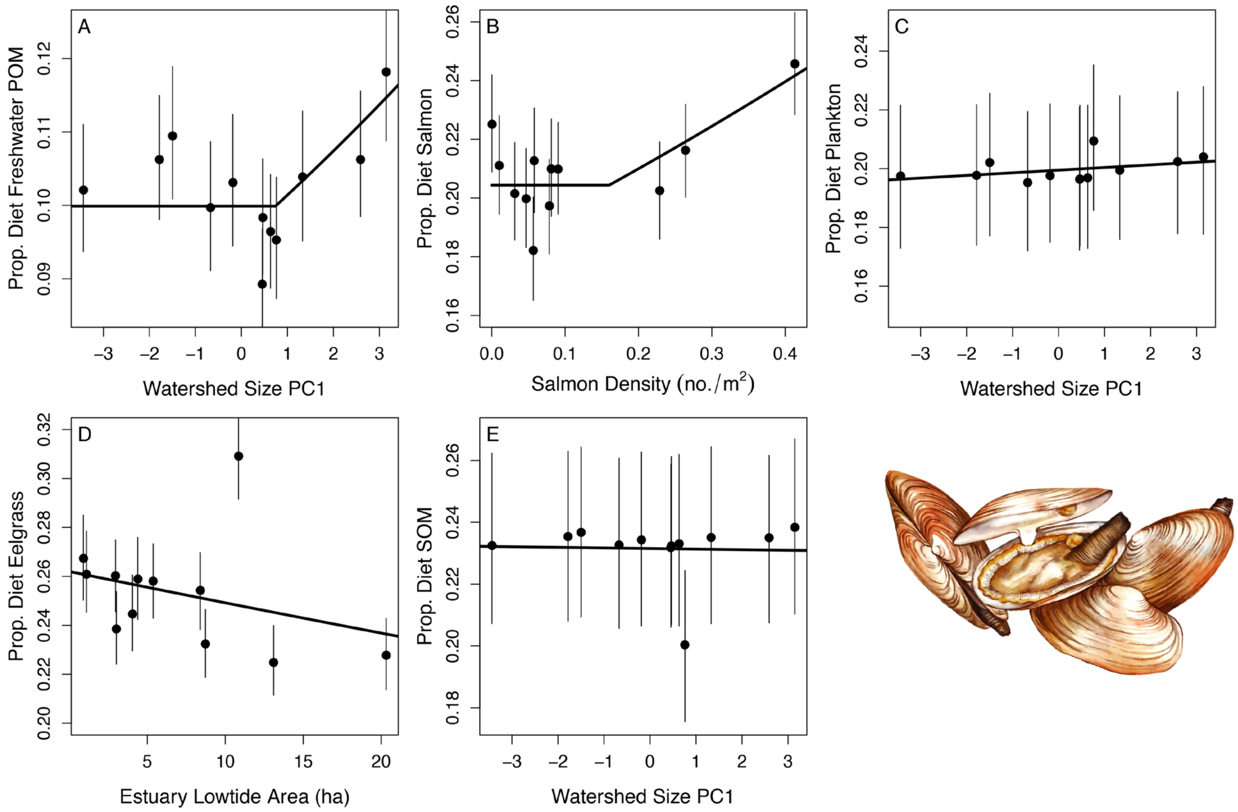

Figure 5.5. Landscape trait correlations with inferred sources of soft-shell clam diet. Broken-stick regressions of: A) Terrestrial particulate organic matter (POM) dietary contributions vs. watershed size; and B) salmon contributions vs. 2007-08 mean pink salmon density. Linear regressions of: C) plankton contributions vs. watershed size, D) eelgrass contributions vs. low tide mudflat area, and E) sediment organic matter (SOM) contributions vs. watershed size. Data points are median posterior estimates from isotope mixing models with 25-75% credible intervals. Soft-shell clam image copyright © 1997-2015 Charting Nature/ Brenda G. Gillespie.

Table 5.6. Model type, AICc weight and pseudo-R^2 for inferred sources considered in soft-shell clam diet analysis. AICc model competition was not used for plankton, eelgrass or SOM sources as data only suggested linear relationships. POM = terrestrial particulate organic matter; SOM = estuarine sediment organic matter.

Source	Model	Type	AICc Weight	Pseudo-R^2
POM	Watershed Size	Broken stick	0.95	0.43
Salmon	Pink Salmon Density	Broken stick	0.85	0.48
Plankton	Watershed Size	Linear	NA	0.16
Eelgrass	Low-tide Mudflat Area	Linear	NA	0.11
SOM	Watershed Size	Linear	NA	<0.01

Table 5.7. Additional regressions with individual watershed size PC1 components for soft-shell clam diet analysis.

Source	Model	Type	Pseudo-R^2
POM	Catchment Area	Broken Stick	0.07
POM	Bankfull Width	Broken Stick	0.32

5.4.3. Dungeness Crabs

Proportional dietary contributions of inferred sources to crabs ranged between 0.03 for POM and 0.35 for soft-shell clams (Table 5.3). Both plankton and salmon had mean dietary contributions of 0.21.

The contribution of POM to the diet of crabs increased in estuaries below larger watersheds (Figure 5.6A; Table 5.8). Although POM contributions increased across the range of watershed sizes sampled, the rate of POM dietary contributions increased at PC1 values > 1.32. Additional regressions revealed strong relationships with both catchment area (R^2 = 0.61) and bankfull width (R^2 = 0.70; Table 5.9; Figures D.8 A-B). There were higher rates of POM contributions in watersheds with catchment areas above 36.6 km^2 and bankfull widths greater than 15.7 m. Salmon dietary contributions increased substantially and then saturated above salmon densities of 1.2 salmon/m^2 (Figure 5.6B; Table 5.8). Dietary contributions of epiphytes increased below larger watersheds but did not change substantially (Figure 5.6C; Table 5.8). We did not compete models for epiphyte contributions for previous reasons stated. Eelgrass contributions were reduced in estuaries with larger low tide mudflats (Figure 5.6D; Table

5.8). Dungeness crabs also had substantially higher proportions of soft-shell clams in their diets below larger watersheds (Figure 5.6E; Table 5.8). Additional regressions showed notable relationships for both catchment area (R^2 = 0.32) and bankfull width (R^2 = 0.49; Table 5.9; Figures D.8 C-D).

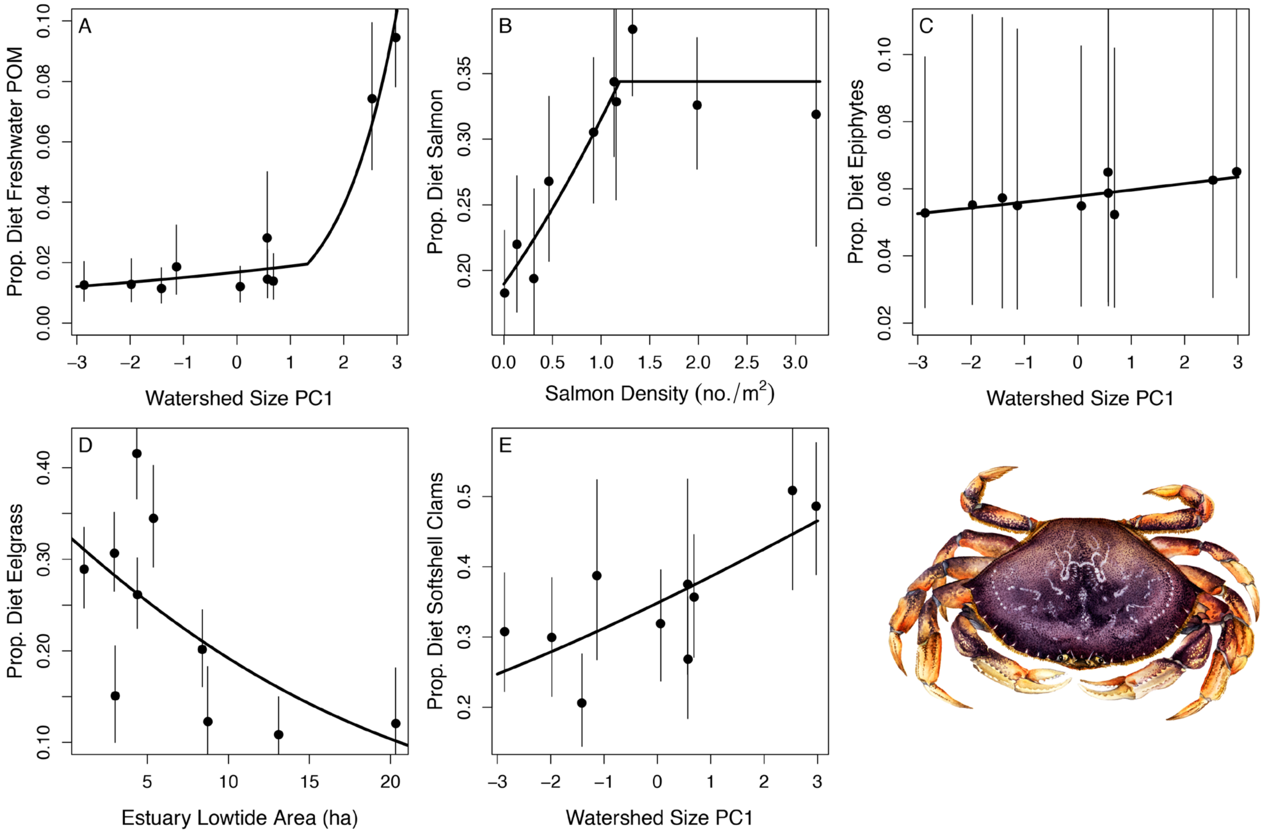

Figure 5.6. **Landscape trait correlations with inferred sources of Dungeness crab diet. Broken-stick regressions of: A) Terrestrial particulate organic matter (POM) dietary contributions vs. watershed size; and B) salmon contributions vs. 2006-09 mean salmon density. Linear regressions of: C) epiphyte contributions vs. watershed size, D) eelgrass contributions vs. low tide mudflat area, and E) soft-shell clam contributions vs. watershed size. Data points are median posterior estimates from isotope mixing models with 25-75% credible intervals. Dungeness crab image copyright © 1997-2015 Charting Nature/ Brenda G. Gillespie.**

Table 5.8. Model type, AICc weight and pseudo-R^2 for inferred sources considered in Dungeness crab diet analysis. AICc model competition was not used for the epiphyte source as data only suggested a linear relationship. POM = terrestrial particulate organic matter. *Lowtide mudflat area models were included in AICc model selection; all other models considered had AICc weights < 0.20.

Source	Model	Type	AICc Weight	Pseudo-R^2
POM	Watershed Size	Broken stick	0.98	0.90
Salmon	Pink Salmon Density	Broken stick	>0.99	0.90
Epiphytes	Watershed Size	Linear	NA	0.51
Eelgrass	Low-tide Mudflat Area	Linear	0.95	0.46
Soft-shell	Watershed Size	Linear	*0.63	0.70

Table 5.9. Additional regressions with individual watershed size PC1 components for Dungeness crab diet analysis.

Source	Model	Type	Pseudo-R^2
POM	Catchment Area	Broken Stick	0.61
POM	Bankfull Width	Broken Stick	0.70
Soft-shell	Catchment Area	Broken Stick	0.32
Soft-shell	Bankfull Width	Broken Stick	0.49

5.5. Discussion

Habitat and life history traits, such as feeding ecology, play a substantial role in assessing dietary contributions to aquatic invertebrates (Benke et al. 1984). Overall, the diets of mussels and soft-shell clams were less variable compared to the diet of Dungeness crabs at the site level. This highlights the importance of local resource conditions for mobile consumers such as crabs. Although dietary shifts in mussel and soft-shell clams were less pronounced, proportional dietary contributions of certain sources did correlate with landscape traits. We assumed that filter feeders would be affected more by larger-scale oceanographic conditions that influence plankton production, but they were also assimilating larger proportions of local resources than expected such as eelgrass, salmon and, to a lesser degree, terrestrial POM. Factors such as the connectivity of resource pools to consumers can determine the effect of spatial subsidies. Although transport of organic matter by water movement will enable all consumers, sedentary or mobile, to exploit a subsidy, mobility enables consumers such as Dungeness crabs to exploit spatially heterogeneous resource pools (Howe and Simenstad 2015a). In addition, differences in feeding ecology will influence dietary composition. Mussels and soft-shell clams are passive filter feeders and dependent on resources available to them in the water column and at their immediate location. In contrast, Dungeness crabs are opportunistic and omnivorous consumers with a broad scope in potential dietary sources; they have the ability to adapt and exploit local resource conditions within specific sites (Stevens et al. 1982, Jensen and Asplen 1998).

5.5.1. Mussels

Proportional contributions of POM and salmon were similar between summer and fall seasons. However, the dietary contributions of plankton and eelgrass changed considerably. The amount of plankton in the diet of mussels decreased from summer to fall, likely reflecting fall reductions in plankton abundance as water temperatures decrease and plankton blooms subside. Interestingly, plankton contributions did not exceed 30% in either season, slightly less than maximum values reported by Howe and Simenstad (2015b). Eelgrass contributions increased from summer to fall and constituted the largest proportions of mussel diet in both seasons. This could be due to an increase in eelgrass abundance in the fall following a full growing season. Fall increases could also be result of more time for eelgrass to senesce and enter the food web through detrital processes (Frankovich and Fourqurean 1997). Nonetheless this result reflects the importance of local organic matter sources such as eelgrass beds (Williams et al. 2009).

Correlations of source contributions to mussel diet with landscape traits had mixed results. Overall, fall correlations were much stronger than those in the summer. This could reflect the increased contrasts between site-level processes, such as higher stream discharges in the fall, which could strengthen resource delivery from upstream landscapes to estuaries. The only exceptions were correlations between watershed size and the dietary proportion of plankton, which had similar pseudo-R^2 values for both seasons. However, most relationships changed direction between seasons with the exception of salmon. For example, the contribution of POM and plankton to the diet of mussels in the summer was elevated in larger watersheds but this relationship was the opposite in the fall. Terrestrial POM export to estuaries is known to increase with watershed size and dissolved nutrient loading is also likely to scale positively, which could bolster POM and localized plankton inputs during the summer (Chanton and Lewis 2002, Sakamaki et al. 2010). Negative relationships in the fall could occur if elevated stream discharges forced POM settlement past intertidal mussel habitat and reduced salinities below plankton requirements. Increased fall contributions of eelgrass in estuaries with larger intertidal mudflats may represent increased eelgrass production in these sites following summer growth periods. It is also possible eelgrass contributions may encompass inputs of marsh detritus with similar isotope ratios. These detrital inputs would likely increase as stream levels rise with the fall rainy season.

5.5.2. Soft-shell Clams

Proportional contributions of sources to the diet of soft-shell clams were more even. POM was the lowest dietary component of soft-shell clams and all remaining sources had similar values, with eelgrass forming the largest dietary component. Soft-shell clams are capable of ingesting a wide variety of organic material including bacteria, diatoms, suspended particulate matter and re-suspended benthic organic matter (Newell et al. 1986). This work suggests that salmon-derived organic matter is an additional dietary component in the northern Pacific; the overall contribution of salmon was equal to that of plankton and salmon are known to contribute to the particulate organic matter content in streams (Johnston et al. 2004, Harding et al. 2015). Similar to mussels, eelgrass was a major dietary component for soft-shell clams. Organic inputs of eelgrass are substantial in many estuaries and can indirectly subsidize consumers by elevating bacterial production (Williams et al. 2009). Correlations with landscape traits were notable for both POM and salmon and low for the remaining three sources. Broken-stick regressions revealed potential thresholds for watershed size (stream bankfull > 16.9 m) and salmon density (> 0.16 pink salmon/ m^2) that correlate with increased assimilation of terrestrial subsidies. The incorporation of POM into soft-shell clam diet increased below larger watersheds although it is possible this relationship could shift seasonally as seen with mussels (Atwood et al. 2011).

5.5.3. Dungeness Crabs

Soft-shell clams, salmon and eelgrass sources dominated the diet of Dungeness crabs with small contributions of epiphytes and POM. Crabs are opportunistic omnivores with a broad dietary scope and have been observed moving across habitat boundaries to exploit resources (Curtis and McGaw 2012, Hübner et al. 2015). Their diet can include detritus, POM, diatoms, soft-shell clams and salmon (Jensen and Asplen 1998, Harding and Reynolds 2014a). Correlations between crab diet and landscape traits were high, particularly for POM and salmon contributions. Broken-stick regression revealed a threshold in watershed size (catchment area > 36.6 km^2; stream bankfull > 15.7 m) where POM became more prominent in crab diets. Interestingly, we also detected a saturation point where salmon stopped contributing to crab diets (> 1.19 $salmon/m^2$). This is likely a result of crabs preferring salmon when they are available, whereas bivalves can only assimilate salmon as a function of particulate matter concentrations in the water column. In addition, salmon are only present for limited windows of time and thus crabs are limited in how much salmon they can consume relative to other dietary sources throughout the year. Unlike bivalve diets, crab source contributions changed substantially across sites with the exception of epiphytes, which remained low and relatively constant.

This study reveals the importance of clams to Dungeness crabs as dietary source. Although crabs eat many species of bivalves, soft-shell clams are easier to access as a result of their more fragile shells compared to other common species such as Pacific littlenecks (*Protothaca staminea*) and butter clams (*Saxidomus gigantea*). Soft-shells were also the most common clam species across our study sites. Although intertidal clam beds may encompass a small area of available crab habitat, they could constitute a disproportional amount of resources available to crabs. Harding and Reynolds (2014a) and Harding et al. (2015) reported that terrestrial-derived subsidies were an important determinant of both soft-shell clam and Dungeness crab size, where larger watersheds corresponded with larger individuals of both species. This study suggests that terrestrial-derived subsidies are also influencing crabs indirectly through soft-shell clams as indicated by the increase in soft-shell clam dietary contributions below larger watersheds.

5.5.4. Conclusion

As with any research using isotope-mixing models, this study has limitations. Potential dietary sources such as benthic macroalgae and marsh plants have not been included. Although macroalgae was limited in the intertidal, bands of *Fucus* and *Ulva spp.* were present in the upper intertidal zone. This could potentially effect the accuracy of source contributions produced by the model if proportions of known sources are attributed to contributions of unknown sources (Phillips et al. 2014). However, there is a trade-off as high numbers of sources can reduce the precision of source contribution estimates (Phillips et al. 2014). For example, our study showed higher dietary contributions of eelgrass than reported by Howe and Simenstad (2015b). Our higher eelgrass contributions could encompass upstream marsh detritus inputs, including C4 sedge plants with similar isotope ratios such as saltgrass (*Distichlis spicata*). Our use of broken-stick regression to identify non-linearity and potential thresholds must also be interpreted with some caution. While broken-stick regressions for crab diet were quite strong, many non-linear regressions for bivalve diet performed only marginally better than a simple linear relationship. While this does provide some support for non-linearity, alternative non-linear relationships that do not force abrupt changes in slope could be more appropriate but no not identify threshold values like broken-stick regression (Chiu et al. 2006).

These findings build on the results of chapters 3 and 4 which demonstrated that terrestrial and salmon subsidies are consumed in proportion to their availability by both soft-shell clams and Dungeness crabs (Harding and Reynolds 2014a, Harding et al. 2015). While these earlier chapters found strong linear relationships between stable isotope ratios of consumer tissues and watershed size and upstream salmon density, they did not account for additional resources available within estuaries. This chapter confirms that both consumers are increasingly assimilating both terrestrial subsidies as watershed increases, and salmon subsidies as upstream densities of salmon increase in the presence of other available dietary resources. In addition, this chapter shows that these relationships are not necessarily linear. Broken-stick regressions suggest that terrestrial subsidies do not increase substantially in their contributions to consumer diets until watersheds reach a certain size. In addition, this chapter has shown that crabs may be indirectly subsidized by terrestrial resources as they consume more soft-shells clams, which are larger, below larger watersheds (Harding et al. 2015).

Similarly, salmon must reach a certain density before salmon subsidy contributions begin to increase in clam diet. However, salmon contributions to crab diet increase even at low salmon densities and then appear to saturate at just over one salmon per square metre. This suggests any further increases in salmon availability beyond this point will not result in crabs eating more salmon. Due to the fact that crabs are most likely selecting and directly consuming salmon carcasses, this saturation point may indicate their maximum capacity to consume salmon. Given that salmon are only present for limited periods of time each year, crabs will be limited in the amount of salmon they can consume overall, in relation to dietary sources that are available throughout the year.

Spatial subsidies form a substantial component of the estuarine resource base. The connectivity of these spatial resource flows, by water and by consumer mobility, can determine how much the diet of an individual correlates with local resource conditions. In this study, bivalve diets varied much less than that of Dungeness crabs. Passive filter feeders such as mussels and soft-shell clams have more limited access to resources depending on passive water transport and sources immediately available to them. Crabs can selectively exploit resources due to their mobility and opportunistic feeding behaviour, migrating into favourable resource pools that can vary over space and time. This results in a more varied diet that strongly reflects specific landscape-level traits. This can enable rough site-specific assessments, based on measureable traits, to determine whether subsidies are more or less important to estuarine consumers.

Chapter 6. General Discussion

Landscape-based approaches are slowly emerging as alternatives to classical forms of ecological study and resource management. Intrinsic to this is placing ecosystems within the wider context of their geographical region and increasing our knowledge about the importance of cross-ecosystem resource linkages (Loreau et al. 2003). This thesis attempts to identify interdependencies between species and habitats that have previously been studied and managed in isolation and provides a broad spatial evaluation of the role of terrestrial- and salmon-resource subsidies in estuarine ecosystems. Through broad spatial comparisons I reveal that resource linkages vary spatially and thus the importance of resource subsidies can be context dependent.

Chapter 2 explores how salmon subsidies to riparian and estuarine habitats can vary spatially as a result of salmon spawner distributions, associations with predators, and watershed traits. In the systems studied, spawning pink salmon always concentrated in lower stream reaches while chum salmon shifted to upper reaches as stream size increased. Hunter (1959) recorded elevated numbers of pink salmon, relative to chum, in lower reaches of one of our larger study streams, suggesting these spawning distribution patterns may be typical for these two species. Wolves and bears transferred pink salmon carcasses to riparian areas in lower stream reaches while chum salmon carcasses were distributed throughout stream reaches, mainly from bear-associated transfers. Habitat characteristics, such as estuary meadow area and stream depth, explained the number of carcasses transferred by wolves, whereas bears transferred more carcasses at high salmon densities and when chum salmon were present. This suggests that wolves select streams to consume salmon based on habitat characteristics while bears follow the highest densities of salmon and show a preference for chum salmon. Overall, salmon have the most potential to subsidize lower reaches of streams from transfers of both salmon species by wolves and bears. As distance upstream increases, bear-chum associations increasingly drive this subsidy potential. However, because the amount of individual salmon carcasses consumed by bears decreases at higher spawning salmon densities, a non-linear relationship between the amount of carcass tissue left by bears and salmon density likely exists (Gende et al. 2001). Future work could therefore examine responses to variability in riparian subsidies as a function of salmon density and salmon species. Our results represent patterns of spatial gradients in salmon subsidies to riparian forests (Hilderbrand et al. 1999) but the use of a 10 m band and our discounting of unknown salmon carcasses are certainly underestimating the total magnitude of subsidies and the total salmon predation within these sites. Our inference is also limited to peak spawning periods, and predation patterns can vary depending on the stage of spawning (Quinn et al. 2003). However, given the dependence of bear predation on salmon density, peaks of salmon carcass transfer by bears would likely occur during peak spawning periods. Wolf-transferred carcasses showed minimal density dependence and may be temporally driven by diurnal patterns or flow conditions (Darimont et al. 2003). Total carcass inputs into estuaries were highly variable between the two years. This could potentially be driven by large differences in pink salmon returns that cycle between even and odd return years. Historically, even-year dominance has occurred in most regions however odd pink years have been dominant in our study region, and this trend may be strengthening coast-wide (Irvine et al. 2014). This chapter reveals some contextual, and spatially explicit relationships that determine the potential of salmon subsidies within coastal watersheds.

In Chapters 3 and 4 I performed a detailed assessment of how sedentary and mobile estuarine consumers respond to resource subsidies across natural landscape gradients. In Chapter 3 I demonstrate that watershed size and upstream salmon density can be used to approximate the amount of terrestrial- and salmon-derived resources that are available in estuaries. Both watershed size and salmon density correlated with stable isotope ratios of soft-shell clams as the availability of these subsidies increased confirming that clams are assimilating subsidies in proportion to their availability. However, the only subsidy metric that explained individual clam size was watershed size. In addition, I show that these effects are contextually dependent on where a clam is located within an estuary. Prior to starting my graduate studies I worked in the central coast of British Columbia for nine years. During this period I often speculated on whether salmon subsidies had any effects on intertidal communities, in particular, sedentary filter feeders. I was surprised to discover bivalves assimilate salmon nutrients and that their stable isotope ratios track the density of salmon spawning upstream. Even more surprising was the more pronounced effects of terrestrial-derived resources which show similar responses in stable isotopes but also correlate with more concrete biological responses such as larger individual clams. Subsequent studies could investigate isotope patterns within shells to look at year-to-year variation in growth responses to variable salmon returns over time. Additional considerations include the effects of variable substrate types on correlations between clam size and watershed size and how autotrophic production from larger streams, such as freshwater plankton exports, contributes to subsidies downstream.

In Chapter 4, I show that Dungeness crab stable isotope ratios also shift in response to subsidy inputs. When I first conceived this study, it seemed “obvious” that salmon carcasses should be a key subsidy, since I have observed crabs moving up into estuaries to scavenge on carcasses for years. I was therefore surprised that terrestrial-derived resources, not salmon, influence the individual size of crabs while habitat area appears to determine crab abundance. While salmon subsidies are clearly an important dietary resource to crabs, the effects may be more short-lived due to their pulsed nature when compared to more constant resource inputs from upstream landscapes. The fall timing of salmon runs, just prior to dormant winter periods for many marine invertebrates, may result in any benefits from salmon subsides not translating to increased crab productivity. Both chapters also consider a broad range of additional factors to strengthen our conclusions that both terrestrial- and salmon-derived subsidies are a substantial contributor to estuarine resources, and that terrestrial subsidies have the most pronounced biological effects. Future work is required to identify the mechanisms by which crabs are being subsidized by terrestrial resource inputs. Are crabs eating elevated levels of microalgae or epiphytic diatoms below watersheds or are they mainly subsidized indirectly via increased productivity of prey such as bivalves?

In Chapter 5, I investigated how the diets of estuarine consumers vary spatially. I considered a wide range of inferred dietary sources including terrestrial and salmon subsidies. I show that the dietary contribution of resources can vary seasonally and that the prevalence of resource subsidies scales with landscape traits. Specifically, terrestrial- and salmon-derived resources scale with watershed size and salmon density respectively. This work also suggests that mobile consumers are most likely to benefit from resource subsidies, as they are able to exploit spatially heterogeneous resources. Future research could test the generality of this statement, since it is based on only a very limited set of species. The benefits of subsidies may also be more complex, as terrestrial subsidies to Dungeness crabs occur both directly through the influx of particulate organic matter, and indirectly through soft-shell clams. Finally, I show that simple watershed-traits can provide valuable information about the importance of resource subsidies within estuarine ecosystems. Future research could integrate additional watershed considerations, such as total deciduous tree content, and estimates of slope or steepness, which would be important determinants of the type and magnitude of resource exports delivered to estuaries. The role of dissolved terrestrial nutrient inputs, and potential influences on bottom-up responses in estuarine communities are also important considerations that I was not able to address directly in this dissertation.

An increasing body of recent research is attempting to examine the role of resource subsidies at broader, and more appropriate spatial scales (Moore et al. 2008, Sakamaki et al. 2010, Verspoor et al. 2011, Harding and Reynolds 2014a) building on ideas proposed by Polis et al. (1997) and others. This thesis contributes to this growing body of work, arguing that subsidy resource flows are an essential component to estuarine ecosystems, but that the importance of these resource linkages is highly variable. This variability is determined by resource availability, specific watershed-level factors and by the traits of estuarine consumers. Placing these considerations within the context of natural landscape variability will better enable us to determine when and where a resource is more important.

Estuaries are ecosystems in their own right but are clearly dependent on the traits of adjacent systems (Elliott and Whitfield 2011). They can therefore exhibit biochemical characteristics ranging from terrestrial to marine based on resource inputs from adjacent terrestrial, and distant offshore systems. Although this work did not find any evidence that salmon nutrients increase productivity in estuaries, salmon do provide substantial resource inputs that are assimilated into food webs. It is commonly known that individuals are attracted to higher quality resources (Marcarelli et al. 2011). Resources containing higher protein content, much like salmon, have been shown to increase mate attraction and female fecundity in terrestrial invertebrates (Barry and Wilder 2012). Similar effects could occur in estuaries where salmon nutrients are more readily available. Future work could shed light on whether estuaries with salmon returns have individuals with higher reproductive potential compared to systems without salmon.

There is a considerable body of research that has shown that salmon are an important resource to freshwater ecosystems, terrestrial predators, and riparian forests (Gende et al. 2002 Figure 6.1, Naiman et al. 2002). It is also widely accepted that salmon depend on intact watersheds, streams and estuaries to complete their life cycle (Reiser and Bjornn 1991, Thorpe 1994, Fisheries and Oceans Canada 2005). What this dissertation has provided is spatially explicit relationships of how associations between species, and species and landscapes, can drive mechanisms that determine how salmon nutrients are dispersed in coastal watersheds (Figure 6.1). This work has also shown that terrestrial and salmon subsidies are assimilated into estuarine ecosystems, that this can vary spatially between and within watersheds and by species, and that terrestrial subsides may be a more important determinant of estuarine productivity in the North-eastern Pacific.

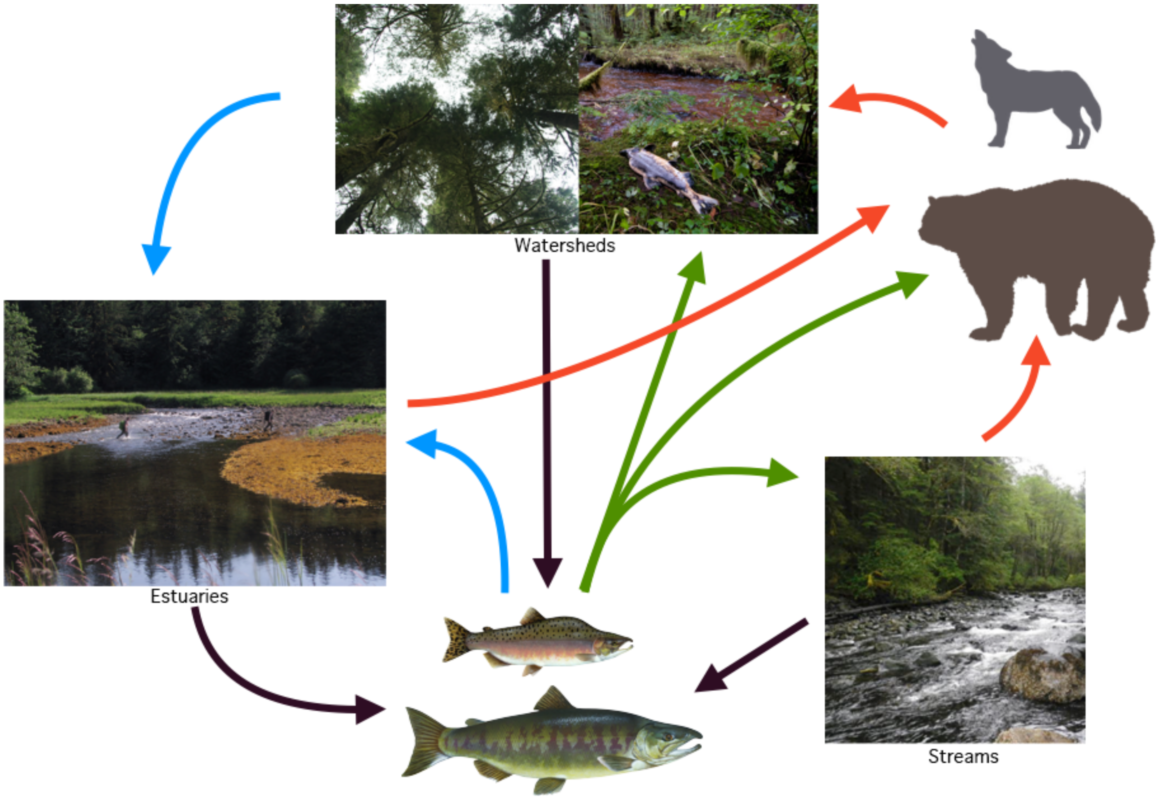

Figure 6.1. **Contributions of this dissertation to what we know about salmon resource subsidies. Green arrows indicate what other research has established about the importance of salmon to freshwater ecosystems, terrestrial predators and riparian forests. Brown arrows indicate the dependence of Pacific salmon on intact watersheds, streams and estuaries to complete their life cycle. Orange arrows indicate what this dissertation has contributed to our understanding of how associations between species, moderated by the landscapes they inhabit, can drive subsidy dynamics of Pacific salmon in coastal watersheds. Blue arrows indicate what this work has determined about the importance of terrestrial and salmon resource subsidies in estuarine ecosystems. Photo credit: Heather Recker (estuaries), Jennifer Harding (streams), Joel Harding (watersheds left image), Conor McCracken (watersheds right image).**

My results demonstrate that landscape traits can have major effects on adjacent ecosystems. This has implications for government policy frameworks such as the Wild Salmon Policy in Canada, which identifies the requirement to integrate ecosystem values into the management of Pacific salmon (Fisheries and Oceans Canada 2005). While it recognizes the substantial evidence that salmon nutrients are important in freshwater and riparian ecosystems, our work provides the necessary scientific rationale that estuaries should also be included in the list of habitats that can directly benefit from these annual nutrient pulses (Irvine 2009). For example, current management of salmon by the Canadian Department of Fisheries and Oceans uses escapement targets based on the total number of fish that reach spawning grounds of streams. Because any resource subsides from salmon are driven by the concentration of this marine resource within recipient ecosystems (i.e. the number of salmon per square metre of riparian area or stream) future management scenarios could shift to using target salmon densities within streams, rather than total numbers. In addition, changes in upstream land cover and disruptions to riparian areas are known to effect salmon populations (Stalberg et al. 2009), but the same activities could also alter terrestrial resource flows into estuaries and have community-level effects. The extent and type of forestry practices would greatly alter the delivery of nutrients to estuaries. Although forestry can cause initial nutrient increases to streams this often correlates with increased levels of suspended solids and decreases in dissolved oxygen (Naiman and Bilby 2001, Ensign and Mallin 2001). In addition, forestry can alter watershed hydrology by reducing stream water supply in dry seasons and increasing stream flows and delivery of sediment and woody debris in wet seasons. This would have the potential to inhibit terrestrial resource delivery during summer months and negate resource subsidies during winter storms via substrate scouring in upper estuaries and promoting anoxic conditions in estuaries via sedimentation and loading of wood in lower zones.

This thesis can also augment ecosystem-based management efforts along the coast of British Columbia and strengthen land-use planning that recognizes the connectivity amongst coastal landscapes (Price et al. 2009). For instance using identified thresholds of watershed size and salmon density where associated resource subsidies become increasingly important could guide management decisions such as where to reduce logging, or strengthen precautionary practices such as buffer zones, and maintain target salmon densities to facilitate these cross-ecosystem resource exchanges. This could be of particular importance in relatively pristine areas such as British Columbia's central coast that face increasing pressures from industrial development (e.g. logging, fossil fuel distribution) and the potential effects these activities could have downstream in estuarine communities. Sustenance economies are an intrinsic part of Coastal First Nation communities in this region and many traditional resources are taken from estuaries including bivalves, crabs and other invertebrate species. Therefore, ecosystem-based initiatives should prioritize these considerations in areas where industrial land-use activities are slated adjacent to estuaries of particular food, social and ceremonial importance.

As resource management and conservation paradigms shift in recognition of the benefits to multi-species, or ecosystem-based approaches, they must also recognize the interconnections between ecosystems. For instance, it has been suggested that Dungeness crabs exhibit different degrees of movement depending on habitat type. Individuals on the open coast are known to range quite widely while those in fjord-type channels are thought to have more restricted ranges (Stone and O'Clair 2001, Hildenbrand et al. 2011). Our findings go a step further and highlight the substantial influence that upstream watershed-scale processes can have on spatially discrete crab populations. Because the Dungeness crab fishery is one of the most valuable invertebrate fisheries on the British Columbian coast, decision makers may want to consider which activities are allowed upstream of commercially important Dungeness crab populations that reside in channelized and fjord-like habitats.

Lastly, this study highlights the importance of ecological research in relatively pristine ecosystems. Given the enrichment effects of pollution on isotope ratios, this research would have been much more difficult, if not impossible, in densely populated regions or areas subject to intensive industrial activity (Brion et al. 2008). The conservation of our natural landscapes is crucial in order to continue research aimed at improving our understanding of what drives ecological processes. To properly steward our natural heritage, make informed management decisions and realize a sustainable economy, we must be able to conduct research in intact systems to use as baselines for proper ecosystem functioning.

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Appendix A.

Supporting material for Chapter 2

Table A.1. Site-level covariate summary. Asterisks indicate sites that were also surveyed for estuary carcasses in 2008 and 2009.

Site	Section Length (m)	Total Length (m)	Estuary Section Length (m)	Stream Bankfull (m)	Spawning Area (ha)	Meadow Area (ha)	Mean Depth (m)	Survey Years
Ada	50	350	30	11.1	0.39	0.24	0.12	2009 to 2013
Beales Left	100	300	100	10.9	0.33	2.06	0.09	2009 to 2013
Bullock Main *	100	550	50	10.9	0.60	0.68	0.08	2012, 2013
Clatse *	100	800	220	22.8	1.82	2.07	0.16	2009, 2010, 2013
Codville	100	300	50	3.3	0.10	0.52	0.18	2009, 2013
Fancy Head	50	165	20	5.5	0.09	0.16	0.06	2009 to 2013
Fancy Right	100	500	60	4.8	0.24	0.45	0.06	2009, 2011 to 2013
Fannie Left *	200	1375	80	12.8	1.76	1.52	0.16	2009, 2010, 2012
Hooknose *	200	1800	45	16.9	3.04	1.02	0.18	2009, 2010, 2012, 2013
Kill Creek *	100	480	40	3.5	0.17	0.22	0.04	2011 to 2013
Kunsoot Main *	100	1000	240	13.1	1.31	1.67	0.04	2013
Lee	100	700	50	12.4	0.87	0.79	0.19	2010, 2011, 2013
Mosquito Bay	100	600	30	4	0.24	0.31	0.15	2012, 2013
Neekas *	200	1800	260	17.7	3.19	1.19	0.16	2010, 2012, 2013
Rainbow	50	250	120	15.1	0.38	1.56	0.23	2009, 2012, 2013
Sagar *	50	150	30	15.5	0.23	1.70	0.25	2009 to 2013

Table A.2. Estuary-carcass site summary.

Site	Year	Pink Dead	Total Pink Live	Pink Density (#/m^2)	Chum Dead	Total Chum Live	Chum Density (#/m^2)	Spawning Length (km)	Stream Discharge (m^3/s)
Bullock Main	2008	10	20	<0.00	112	220	0.04	0.62	1.43
Bullock Main	2009	2317	6300	1.05	399	2100	0.35	0.62	1.93
Clatse	2008	337	2300	0.13	830	1700	0.09	0.90	9.14
Clatse	2009	12429	29000	1.59	998	8000	0.44	0.90	4.70
Fannie Left	2008	28	784	0.04	53	462	0.03	1.50	6.25
Fannie Left	2009	296	12800	0.73	17	1820	0.10	1.50	0.36
Hooknose	2008	0	149	<0.00	8	864	0.03	1.80	2.68
Hooknose	2009	620	4566	0.15	65	1282	0.04	1.80	3.60
Kill Creek	2008	0	0	0.00	122	175	0.10	0.45	0.07
Kill Creek	2009	290	1023	0.61	31	750	0.45	0.45	0.15
Kunsoot Main	2008	9	200	0.02	142	220	0.02	1.28	0.82
Kunsoot Main	2009	8042	23190	1.77	53	567	0.04	1.28	0.04
Mosquito Bay	2008	0	991	0.41	12	567	0.24	0.75	0.09
Mosquito Bay	2009	333	2625	1.09	23	677	0.28	0.75	1.68
Neekas	2008	62	10200	0.32	2133	8200	0.26	2.10	4.84
Neekas	2009	21909	88454	2.78	7820	34000	1.07	2.10	1.26
Sagar	2008	0	50	0.02	65	550	0.24	0.18	16.43
Sagar	2009	194	1601	0.69	163	421	0.18	0.18	6.19

Table A.3. Live salmon top model. NZ=non-zero data points.

Model:		
Covariates	Estimate	SE
Intercept	4.28	0.35
Distance upstream	-1.92	0.32
Spawning area	0.97	0.28
Salmon species	0.51	0.15
Distance X Spawning Area	0.91	0.20
Distance X Salmon species	2.19	0.33
Spawning Area X Salmon species	-0.92	0.14
Neg. binomial dispersion parameter	0.59	0.05
Zero-inflation parameter	0.06	0.02
Random Effects:		
Site	Variance	SD
Intercept	1.14	1.07
Year	Variance	SD
Intercept	0.19	0.43
	Total	NZ
Data points	718	104
Sites	16	
Years	5	

Table A.4. Averaged models for salmon transferred by wolves and bears. NZ=non-zero data points.

Model	**Wolf**		**Bear**	
Covariates	Estimate	SE	Estimate	SE
Intercept	-0.82	0.37	0.52	0.41
Distance upstream	-0.98	0.29	-0.24	0.34
Salmon density	0.38	0.32	2.43	0.39
Spawning area	0.88	0.21	0.43	0.24
Salmon species	-0.02	0.17	1.44	0.15
Distance X salmon species	-0.03	0.39	0.92	0.32
Distance X Spawning area	-0.07	0.27	0.29	0.22
Salmon density X Salmon species	-1.08	0.34	-0.78	0.78
Meadow area	0.89	0.32	0.28	0.37
Distance X Salmon density	-2.86	0.72	0.37	1.09
Stream depth	-11.57	3.45	-0.29	3.83
Neg. binomial dispersion parameter	7.4	0.99	0.43	0.04
Zero-inflation parameter	0.02	0.02	$1X10^{-6}$	$9.6X10^{-9}$
Random Effects:				
Site	Variance	SD	Variance	SD
Intercept	0.39	0.62	0.68	0.82
Year	Variance	SD	Variance	SD
Intercept	0.41	0.64	0.53	0.73
	Total	NZ	Total	NZ
Data points	716	553	716	374
Sites	16		16	
Years	5		5	

Table A.5. Estuary carcass top model. NZ=non-zero data points.

Model:		
Covariates	Estimate	SE
Intercept	-1.72	0.21
Spawning reach length	-0.89	0.26
Salmon spp	0.40	0.41
Salmon density	1.04	0.23
Spawn length X Salmon spp	1.35	0.39
Quasibinomial dispersion parameter	319.66	
Null deviance	22578.4	
Residual Deviance	8752.4	
	Total	NZ
Data points	35	32
Sites	9	
Years	2	

Table A.6. **Summary of live and dead salmon counts by site and year. Live = live spawning salmon, Senescent = dead without signs of predation, Wolf = wolf transferred, Bear = bear transferred.**

Site	Year	Pink Salmon				Chum Salmon			
		Live	Senescent	Wolf	Bear	Live	Senescent	Wolf	Bear
Ada	2009	545	10	1	13	645	118	3	16
Ada	2010	12	0	0	0	688	30	0	10
Ada	2011	415	7	0	3	691	132	0	8
Ada	2012	3	1	0	0	1848	164	0	0
Ada	2013	172	49	0	4	988	627	0	17
Beales Left	2009	2164	799	29	202	85	118	3	28
Beales Left	2010	176	0	0	0	264	0	0	1
Beales Left	2011	80	27	1	10	4	26	0	7
Beales Left	2012	582	59	20	0	39	14	3	2
Beales Left	2013	1212	444	15	38	215	234	7	27
Bullock Main	2012	1301	133	2	22	569	780	2	14
Bullock Main	2013	2015	1092	14	7	366	1653	7	14
Clatse	2009	18271	7368	354	305	1041	5515	58	390
Clatse	2010	2309	198	18	15	3071	1100	62	281
Clatse	2013	9417	461	19	33	2844	94	2	6
Codville	2009	92	0	0	1	0	0	0	0
Codville	2013	82	75	1	15	0	23	0	2
Fancy Head	2009	207	33	0	1	40	93	0	2
Fancy Head	2010	2	0	0	0	118	1	1	10
Fancy Head	2011	32	0	0	0	152	34	15	15
Fancy Head	2012	30	1	0	0	595	13	0	0
Fancy Head	2013	106	12	0	7	288	284	0	11
Fancy Right	2009	529	1	0	1	133	6	0	4
Fancy Right	2011	183	6	1	1	189	58	5	9
Fancy Right	2012	2	0	0	0	389	4	0	0
Fancy Right	2013	167	4	1	8	489	124	1	79
Fannie Left	2009	13420	55	14	19	1151	153	5	0
Fannie Left	2010	519	17	0	3	2749	2251	0	104
Fannie Left	2012	900	66	5	1	2741	3802	0	5
Fannie Left	2013	3719	1205	53	90	289	2435	6	45
Hooknose	2009	4566	154	170	28	1247	65	46	55
Hooknose	2010	156	12	0	1	780	142	1	36
Hooknose	2012	448	5	4	2	757	74	6	30

Site	Year	Pink Salmon				Chum Salmon			
		Live	Senescent	Wolf	Bear	Live	Senescent	Wolf	Bear
Hooknose	2013	1542	2445	5	39	165	2428	2	54
Kill Creek	2011	510	220	5	4	115	1387	12	106
Kill Creek	2012	72	1	0	0	1316	311	1	29
Kill Creek	2013	545	51	1	16	1622	590	1	21
Kunsoot Main	2013	15172	187	378	42	2952	153	19	6
Lee	2010	8	6	0	0	142	183	0	33
Lee	2011	451	161	11	14	62	457	10	14
Lee	2013	586	74	2	1	1832	2117	1	51
Mosquito Bay Right	2012	161	16	0	2	230	172	2	9
Mosquito Bay Right	2013	1661	115	0	19	704	218	0	0
Neekas	2010	852	290	1	27	7225	11152	0	1011
Neekas	2012	4746	1222	4	5	235	4397	7	22
Neekas	2013	5573	2270	7	27	7869	18983	8	126
Rainbow	2009	14	1	0	0	62	25	0	7
Rainbow	2012	1	0	0	0	209	153	0	0
Rainbow	2013	27	2	0	2	325	7	0	4
Sagar	2009	957	522	0	60	339	70	0	12
Sagar	2010	24	1	0	1	762	152	3	24
Sagar	2011	241	245	0	10	583	591	0	21
Sagar	2012	62	4	0	0	541	112	0	4
Sagar	2013	49	34	3	6	45	50	0	10

Table A.7. Authors, sources and license information for open source images.

Image	Author	Source	License
Pink Salmon	Timothy Knepp, US Fish and Wildlife Service	https://commons.wikimedia.org/wiki/File:Pink_salmon_FWS.jpg	http://creativecommons.org/publicdomain/zero/1.0/
Chum Salmon	Timothy Knepp, US Fish and Wildlife Service	https://commons.wikimedia.org/wiki/File:Salmon_chum_fish_oncorhynchus_keta.jpg	http://creativecommons.org/publicdomain/zero/1.0/
Wolf Silhouette	Tracy A. Heath	http://phylopic.org/image/e4e306cd-73b6-4ca3-a08c-753a856f7f12/	http://creativecommons.org/publicdomain/zero/1.0/
Bear Silhouette	Steven Traver	http://phylopic.org/image/05f87521-20d4-4a05-8ac6-aa0bab7f1394/	http://creativecommons.org/publicdomain/zero/1.0/

Appendix B.

Supporting material for Chapter 3

Table B.1. Model weights of salmon linear models predicting $\delta^{15}N$ and $\delta^{13}C$ in soft-shell clam foot muscle tissue.

$\delta^{15}N$ Salmon Model	Weight	$\delta^{13}C$ Salmon Model	Weight
Mean pink 2006-07	0.82	Mean pink 2006-07	0.89
Mean pink 2006-08	0.18	Mean pink 2006-09	0.11
Mean pink 2006-09	6.94E-08	Mean pink 2006-08	3.14E-06
Year prior pink	1.25E-12	Mean salmon 2006-10	1.91E-06
Mean salmon 2006-10	6.00E-13	Mean salmon 2006-09	1.47E-06
Mean salmon 2006-09	1.14E-13	Mean salmon 2006-07	7.79E-09
Mean salmon 2006-08	1.13E-16	Mean salmon 2006-08	6.06E-10
Mean chum 2006-09	2.36E-17	Year prior pink	3.69E-10
Year prior salmon	2.19E-17	Mean chum 2006-09	2.64E-10
Mean salmon 2006-07	1.39E-18	Mean chum 2006-07	1.20E-10
Mean chum 2006-08	1.88E-20	Year prior salmon	1.11E-10
Year prior chum	2.32E-21	Mean chum 2006-08	8.81E-11
Mean chum 2006-07	3.48E-22	Year prior chum	8.19E-11

Table B.2. **Average coefficient estimates from multi-model analysis of candidate model set for soft-shell clam foot muscle tissue $\delta^{15}N$.**

Covariate	Estimate	SE	Lower CI	Upper CI	RVI
Intercept	8.91	0.08	8.75	9.06	
Age	0.07	0.01	0.05	0.09	1.00
Lower	-0.08	0.07	-0.22	0.05	1.00
Salmon*Lower	-1.01	0.36	-1.72	-0.29	1.00
Salmon	2.05	0.75	0.58	3.53	1.00
Mass	0.00	0.00	0.00	0.01	1.00
Depth	0.17	0.07	0.03	0.30	0.96
WS	-0.02	0.05	-0.12	0.09	0.94
WS*Lower	-0.06	0.03	-0.11	-0.01	0.88
Middle	-0.07	0.05	-0.17	0.04	0.74
Salmon*Middle	-0.61	0.38	-1.35	0.14	0.42
WS*Middle	0.04	0.03	-0.02	0.09	0.29
Below Stream	0.00	0.05	-0.10	0.10	0.28
Temperature	-0.02	0.04	-0.09	0.05	0.19
Salmon*Below Stream	-0.52	0.42	-1.34	0.31	0.09
WS*Below Stream	0.02	0.03	-0.04	0.08	0.03

Table B.3. Candidate model set from multi-model inference of soft-shell clam foot muscle tissue $\delta^{15}N$.

$\delta^{15}N$ Models	*k*	logLik	AICc	ΔAICc	Weight
Age+ Depth+ Mass+ Salmon*Middle+ Salmon*Lower+ WS*Lower	14	-168.21	365.52	0.00	0.11
Age+ Depth+ Mass+ Salmon*Lower+ WS*Lower	12	-170.42	365.65	0.13	0.10
Age+ Middle+ Depth+ Mass+ Salmon*Lower+ WS*Lower	13	-169.70	366.34	0.83	0.07
Age+ Depth+ Mass+ Salmon*Middle+ WS*Middle+ Salmon*Lower+ WS*Lower	15	-167.60	366.45	0.94	0.07
Age+ Depth+ Mass+ WS*Middle+ Salmon*Lower+ WS*Lower	14	-168.75	366.59	1.08	0.06
Age+ Depth+ Temperature+ Mass+ Salmon*Middle+ Salmon*Lower+ WS*Lower	15	-168.01	367.29	1.77	0.04
Age+ Depth+ Temperature+ Mass+ Salmon*Lower+ WS*Lower	13	-170.22	367.39	1.88	0.04
Age+ Below Stream+ Depth+ Mass+ Salmon*Middle+ Salmon*Lower+ WS*Lower	15	-168.20	367.66	2.15	0.04
Age+ Below Stream+ Depth+ Mass+ Salmon*Lower+ WS*Lower	13	-170.39	367.72	2.21	0.03
Age+ Depth+ Mass+ Salmon*Below Stream+ Salmon*Lower+ WS*Lower	14	-169.42	367.95	2.43	0.03
Age+ Depth+ Mass+ WS*Middle+ Salmon*Lower	13	-170.50	367.95	2.44	0.03
Age+ Middle+ Depth+ Temperature+ Mass+ Salmon*Lower+ WS*Lower	14	-169.53	368.16	2.64	0.03
Age+ Depth+ Temperature+ Mass+ Salmon*Middle+ WS*Middle+ Salmon*Lower+ WS*Lower	16	-167.41	368.25	2.73	0.03
Age+ Depth+ Mass+ Salmon*Middle+ WS*Middle+ Salmon*Lower	14	-169.60	368.31	2.79	0.03
Age+ Depth+ Temperature+ Mass+ WS*Middle+ Salmon*Lower+ WS*Lower	15	-168.58	368.42	2.91	0.02
Age+ Below Stream+ Middle+ Depth+ Mass+ Salmon*Lower+ WS*Lower	14	-169.69	368.48	2.97	0.02
Age+ Below Stream+ Depth+ Mass+ Salmon*Middle+ WS*Middle+ Salmon*Lower+ WS*Lower	16	-167.60	368.62	3.11	0.02
Age+ Depth+ Mass+ Salmon*Lower	10	-174.06	368.69	3.17	0.02
Age+ Depth+ Mass+ Salmon*Middle+ Salmon*Lower	12	-171.95	368.71	3.19	0.02
Age+ Middle+ Depth+ Mass+ Salmon*Below Stream+ Salmon*Lower+ WS*Lower	15	-168.75	368.75	3.24	0.02
Age+ Below Stream+ Depth+ Mass+ WS*Middle+ Salmon*Lower+ WS*Lower	15	-168.75	368.75	3.24	0.02
Age+ Mass+ Salmon*Middle+ Salmon*Lower+ WS*Lower	13	-170.91	368.78	3.26	0.02
Age+ Depth+ Mass+ Salmon*Below Stream+ Salmon*Middle+ Salmon*Lower+ WS*Lower	16	-167.72	368.88	3.36	0.02
Age+ Depth+ Mass+ Salmon*Below Stream+ WS*Middle+ Salmon*Lower+ WS*Lower	16	-167.95	369.34	3.82	0.02
Age+ Depth+ Mass+ WS*Below Stream+ Salmon*Lower+ WS*Lower	14	-170.13	369.35	3.83	0.02
Age+ Middle+ Depth+ Mass+ Salmon*Lower	11	-173.33	369.35	3.84	0.02
Age+ Below Stream+ Depth+ Temperature+ Mass+ Salmon*Middle+ Salmon*Lower+ WS*Lower	16	-168.01	369.45	3.94	0.01
Age+ Below Stream+ Depth+ Temperature+ Mass+ Salmon*Lower+ WS*Lower	14	-170.18	369.47	3.95	0.01

$\delta^{15}N$ Models	*k*	logLik	AICc	ΔAICc	Weight
Age+ Middle+ Mass+ Salmon*Lower+ WS*Lower	12	-172.34	369.48	3.97	0.01
Age+ Depth+ Mass+ WS*Below Stream+ Salmon*Middle+ Salmon*Lower+ WS*Lower	16	-168.04	369.51	3.99	0.01

Table B.4. Average coefficient estimates from multi-model analysis of candidate model set for soft-shell clam foot muscle tissue $\delta^{13}C$.

Covariate	Estimate	SE	Lower CI	Upper CI	RVI
Intercept	-18.32	0.07	-18.46	-18.19	
Age	0.07	0.01	0.05	0.09	1.00
Below Stream	-0.20	0.05	-0.29	-0.11	1.00
WS*Below Stream	-0.09	0.03	-0.15	-0.03	1.00
Lower	-0.12	0.05	-0.21	-0.03	1.00
Temperature	-0.10	0.03	-0.16	-0.04	1.00
Salmon	1.85	0.68	0.51	3.18	1.00
Mass	0.00	0.00	0.00	0.01	1.00
WS	-0.12	0.05	-0.21	-0.02	1.00
WS*Lower	-0.06	0.02	-0.10	-0.01	0.96
Salmon*Lower	-0.67	0.30	-1.26	-0.07	0.95
Middle	0.03	0.05	-0.06	0.12	0.53
WS*Middle	0.04	0.02	-0.01	0.09	0.30
Depth	-0.04	0.06	-0.16	0.08	0.21
Salmon*Below Stream	0.16	0.38	-0.59	0.90	0.19
Salmon*Middle	-0.36	0.34	-1.04	0.32	0.12

Table B.5. Candidate model set from multi-model inference of soft-shell clam foot muscle tissue $\delta^{13}C$.

$\delta^{13}C$ Models	*k*	logLik	AICc	ΔAICc	Weight
Age+ Temperature+ Mass+ WS*Below Stream+ Salmon*Lower+ WS*Lower	14	-127.74	284.57	0.00	0.21
Age+ Temperature+ Mass+ WS*Below Stream+ WS*Middle+ Salmon*Lower+ WS*Lower	16	-126.21	285.84	1.27	0.11
Age+ Middle+ Temperature+ Mass+ WS*Below Stream+ Salmon*Lower+ WS*Lower	15	-127.47	286.21	1.63	0.09
Age+ Depth+ Temperature+ Mass+ WS*Below Stream+ Salmon*Lower+ WS*Lower	15	-127.48	286.21	1.64	0.09
Age+ Temperature+ Mass+ Salmon*Below Stream+ WS*Below Stream+ Salmon*Lower+ WS*Lower	15	-127.67	286.60	2.03	0.08
Age+ Temperature+ Mass+ WS*Below Stream+ Salmon*Middle+ Salmon*Lower+ WS*Lower	16	-126.77	286.98	2.41	0.06
Age+ Temperature+ Mass+ WS*Below Stream+ Salmon*Middle+ WS*Middle+ Salmon*Lower+ WS*Lower	17	-125.76	287.13	2.55	0.06
Age+ Temperature+ Salmon+ Mass+ WS*Below Stream+ WS*Lower	13	-130.26	287.48	2.90	0.05
Age+ Depth+ Temperature+ Mass+ WS*Below Stream+ WS*Middle+ Salmon*Lower+ WS*Lower	17	-126.06	287.74	3.16	0.04
Age+ Temperature+ Mass+ Salmon*Below Stream+ WS*Below Stream+ WS*Middle+ Salmon*Lower+ WS*Lower	17	-126.11	287.83	3.25	0.04
Age+ Temperature+ Mass+ WS*Below Stream+ WS*Middle+ Salmon*Lower	15	-128.29	287.84	3.27	0.04
Age+ Depth+ Temperature+ Mass+ Salmon*Below Stream+ WS*Below Stream+ Salmon*Lower+ WS*Lower	16	-127.33	288.10	3.52	0.04
Age+ Middle+ Depth+ Temperature+ Mass+ WS*Below Stream+ Salmon*Lower+ WS*Lower	16	-127.35	288.12	3.55	0.04
Age+ Middle+ Temperature+ Mass+ Salmon*Below Stream+ WS*Below Stream+ Salmon*Lower+ WS*Lower	16	-127.39	288.21	3.64	0.03

Table B.6. Average coefficient estimates from multi-model analysis of candidate model set for soft-shell clam mass.

Covariate	Estimate	SE	Lower CI	Upper CI	RVI
Intercept	39.67	3.11	33.59	45.76	
Age	4.74	0.31	4.13	5.35	1.00
Below Stream	-1.73	1.99	-5.63	2.16	1.00
Salmon*Below Stream	65.08	15.55	34.61	95.55	1.00
WS*Below Stream	6.13	1.21	3.76	8.50	1.00
Middle	6.89	2.05	2.87	10.92	1.00
Lower	8.58	2.77	3.16	14.01	1.00
Depth	-10.45	2.97	-16.27	-4.62	1.00
Salmon	-35.15	29.89	-93.75	23.44	1.00
WS	2.27	2.08	-1.80	6.34	1.00
WS*Lower	1.43	1.13	-0.79	3.65	0.43
Salmon*Lower	16.45	14.31	-11.60	44.49	0.40
WS*Middle	0.39	1.04	-1.65	2.42	0.18
Salmon*Middle	-2.20	13.18	-28.03	23.63	0.17
Temperature	0.22	1.44	-2.60	3.04	0.17

Table B.7. Candidate model set from multi-model inference of soft-shell clam mass.

Mass Models	*k*	logLik	AICc	ΔAICc	Weight
Age+ Middle+ Lower+ Depth+ Salmon*Below Stream+ WS*Below Stream	14	-1644.03	3317.16	0.00	0.17
Age+ Middle+ Depth+ Salmon*Below Stream+ WS*Below Stream+ WS*Lower	15	-1643.35	3317.97	0.80	0.12
Age+ Middle+ Depth+ Salmon*Below Stream+ WS*Below Stream+ Salmon*Lower	15	-1643.45	3318.17	1.00	0.11
Age+ Middle+ Depth+ Salmon*Below Stream+ WS*Below Stream+ Salmon*Lower+ WS*Lower	16	-1642.52	3318.46	1.30	0.09
Age+ Lower+ Depth+ Salmon*Below Stream+ WS*Below Stream+ WS*Middle	15	-1644.00	3319.26	2.10	0.06
Age+ Lower+ Depth+ Salmon*Below Stream+ WS*Below Stream+ Salmon*Middle	15	-1644.00	3319.26	2.10	0.06
Age+ Middle+ Lower+ Depth+ Temperature+ Salmon*Below Stream+ WS*Below Stream	15	-1644.02	3319.30	2.13	0.06
Age+ Depth+ Salmon*Below Stream+ WS*Below Stream+ WS*Middle+ WS*Lower	16	-1643.17	3319.76	2.60	0.05
Age+ Depth+ Salmon*Below Stream+ WS*Below Stream+ Salmon*Middle+ WS*Lower	16	-1643.29	3320.02	2.86	0.04
Age+ Middle+ Depth+ Temperature+ Salmon*Below Stream+ WS*Below Stream+ WS*Lower	16	-1643.34	3320.11	2.94	0.04
Age+ Middle+ Depth+ Temperature+ Salmon*Below Stream+ WS*Below Stream+ Salmon*Lower	16	-1643.44	3320.31	3.14	0.04
Age+ Depth+ Salmon*Below Stream+ WS*Below Stream+ WS*Middle+ Salmon*Lower	16	-1643.44	3320.32	3.15	0.04
Age+ Depth+ Salmon*Below Stream+ WS*Below Stream+ Salmon*Middle+ Salmon*Lower	16	-1643.45	3320.34	3.18	0.04
Age+ Depth+ Salmon*Below Stream+ WS*Below Stream+ WS*Middle+ Salmon*Lower+ WS*Lower	17	-1642.37	3320.36	3.20	0.04
Age+ Middle+ Depth+ Temperature+ Salmon*Below Stream+ WS*Below Stream+ Salmon*Lower+ WS*Lower	17	-1642.50	3320.62	3.45	0.03
Age+ Depth+ Salmon*Below Stream+ WS*Below Stream+ Salmon*Middle+ Salmon*Lower+ WS*Lower	17	-1642.52	3320.65	3.48	0.03

Table B.8. **Average coefficient estimates from multi-model analysis of candidate model set for soft-shell clam %N.**

Covariate	Estimate	SE	Lower CI	Upper CI	RVI
Intercept	9.96	0.08	9.79	10.12	
Below Stream	0.48	0.14	0.20	0.76	1.00
Depth	0.49	0.13	0.24	0.74	1.00
WS	0.14	0.06	0.03	0.25	1.00
Lower	0.27	0.11	0.04	0.49	0.99
Middle	0.11	0.09	-0.06	0.29	0.58
Salmon	-0.73	0.73	-2.15	0.69	0.51
WS*Below Stream	0.13	0.09	-0.05	0.30	0.49
WS*Lower	-0.06	0.04	-0.15	0.03	0.46
WS*Middle	-0.05	0.05	-0.14	0.04	0.17
Salmon*Lower	0.77	0.65	-0.51	2.05	0.16
Mass	0.00	0.00	0.00	0.00	0.15
Salmon*Middle	0.95	0.66	-0.34	2.24	0.14
Age	0.00	0.01	-0.02	0.03	0.13
Temperature	0.01	0.04	-0.06	0.07	0.13
Salmon*Below Stream	0.19	1.21	-2.17	2.55	0.05

Table B.9. Candidate model set from multi-model inference of soft-shell clam %N.

%N Models	k	logLik	AICc	ΔAICc	Weight
Below Stream+ Lower+ Depth+ WS	9	-407.80	834.07	0.00	0.029
Lower+ Depth+ WS*Below Stream	10	-406.78	834.13	0.06	0.028
Below Stream+ Depth+ WS+ WS*Lower	10	-406.95	834.46	0.39	0.024
Below Stream+ Middle+ Lower+ Depth+ WS	10	-406.98	834.53	0.45	0.023
Depth+ WS*Below Stream+ WS*Lower	11	-405.97	834.63	0.56	0.022
Middle+ Lower+ Depth+ WS*Below Stream	11	-405.99	834.66	0.59	0.021
Below Stream+ Middle+ Depth+ WS*Lower	11	-406.16	835.02	0.94	0.018
Depth+ WS*Below Stream+ WS*Middle+ WS*Lower	13	-404.04	835.03	0.96	0.018
Below Stream+ Lower+ Depth+ Salmon+ WS	10	-407.28	835.13	1.06	0.017
Lower+ Depth+ Salmon+ WS*Below Stream	11	-406.25	835.19	1.12	0.016
Middle+ Depth+ WS*Below Stream+ WS*Lower	12	-405.22	835.25	1.18	0.016
Below Stream+ Middle+ Lower+ Depth+ Salmon+ WS	11	-406.36	835.41	1.34	0.015
Below Stream+ Depth+ Salmon+ WS*Lower	11	-406.40	835.48	1.41	0.014
Below Stream+ Depth+ WS*Middle+ WS*Lower	12	-405.36	835.53	1.45	0.014
Middle+ Lower+ Depth+ Salmon+ WS*Below Stream	12	-405.37	835.55	1.48	0.014
Depth+ Salmon+ WS*Below Stream+ WS*Lower	12	-405.42	835.65	1.58	0.013
Depth+ WS*Below Stream+ Salmon*Middle+ Salmon*Lower	14	-403.33	835.75	1.68	0.012
Below Stream+ Lower+ Depth+ Mass+ WS	10	-407.63	835.83	1.76	0.012
Below Stream+ Middle+ Depth+ Salmon+ WS*Lower	12	-405.53	835.87	1.80	0.012
Below Stream+ Depth+ WS+ Salmon*Middle+ Salmon*Lower	13	-404.46	835.87	1.80	0.012
Depth+ Salmon+ WS*Below Stream+ WS*Middle+ WS*Lower	14	-403.43	835.95	1.88	0.011
Lower+ Depth+ Mass+ WS*Below Stream	11	-406.68	836.05	1.98	0.011
Age+ Below Stream+ Lower+ Depth+ WS	10	-407.76	836.08	2.01	0.010
Depth+ WS*Below Stream+ WS*Middle	12	-405.64	836.09	2.02	0.010
Middle+ Depth+ Salmon+ WS*Below Stream+ WS*Lower	13	-404.58	836.11	2.03	0.010
Below Stream+ Depth+ Mass+ WS*Lower	11	-406.74	836.16	2.09	0.010
Age+ Lower+ Depth+ WS*Below Stream	11	-406.74	836.17	2.10	0.010
Below Stream+ Lower+ Depth+ Temperature+ WS	10	-407.80	836.17	2.10	0.010
Lower+ Depth+ Temperature+ WS*Below Stream	11	-406.78	836.24	2.17	0.010
Below Stream+ Depth+ WS+ Salmon*Lower	11	-406.80	836.28	2.21	0.010
Below Stream+ Lower+ Depth+ WS*Middle	11	-406.80	836.29	2.22	0.009
Below Stream+ Lower+ Depth+ WS+ Salmon*Middle	12	-405.75	836.31	2.24	0.009
Depth+ WS*Below Stream+ Salmon*Lower	12	-405.76	836.33	2.26	0.009
Lower+ Depth+ WS*Below Stream+ Salmon*Middle	13	-404.69	836.33	2.26	0.009
Below Stream+ Depth+ Salmon+ WS*Middle+ WS*Lower	13	-404.74	836.43	2.36	0.009

%N Models	k	logLik	AICc	ΔAICc	Weight
Age+ Below Stream+ Depth+ WS*Lower	11	-406.89	836.46	2.39	0.009
Below Stream+ Middle+ Lower+ Depth+ Mass+ WS	11	-406.89	836.48	2.40	0.009
Depth+ Mass+ WS*Below Stream+ WS*Lower	12	-405.84	836.50	2.43	0.009
Below Stream+ Depth+ Salmon*Middle+ WS*Lower	13	-404.79	836.54	2.47	0.008
Below Stream+ Depth+ Temperature+ WS*Lower	11	-406.94	836.57	2.50	0.008
Age+ Below Stream+ Middle+ Lower+ Depth+ WS	11	-406.95	836.59	2.52	0.008
Below Stream+ Middle+ Lower+ Depth+ Temperature+ WS	11	-406.98	836.64	2.57	0.008
Age+ Depth+ WS*Below Stream+ WS*Lower	12	-405.92	836.65	2.58	0.008
Depth+ WS*Below Stream+ Salmon*Middle+ WS*Lower	14	-403.78	836.66	2.59	0.008
Below Stream+ Middle+ Depth+ WS+ Salmon*Lower	12	-405.93	836.68	2.61	0.008
Middle+ Lower+ Depth+ Mass+ WS*Below Stream	12	-405.95	836.71	2.64	0.008
Age+ Middle+ Lower+ Depth+ WS*Below Stream	12	-405.96	836.74	2.67	0.008
Depth+ Temperature+ WS*Below Stream+ WS*Lower	12	-405.97	836.75	2.68	0.008
Middle+ Lower+ Depth+ Temperature+ WS*Below Stream	12	-405.99	836.79	2.72	0.007
Depth+ WS*Below Stream+ Salmon*Middle+ Salmon*Lower+ WS*Lower	15	-402.76	836.79	2.72	0.007
Middle+ Depth+ WS*Below Stream+ Salmon*Lower	13	-404.92	836.80	2.73	0.007
Depth+ WS*Below Stream	9	-409.17	836.80	2.73	0.007
Below Stream+ Depth+ Salmon*Middle+ Salmon*Lower+ WS*Lower	14	-403.85	836.80	2.73	0.007
Below Stream+ Depth+ WS	8	-410.26	836.90	2.83	0.007
Below Stream+ Lower+ Depth+ Salmon+ Mass+ WS	11	-407.12	836.92	2.85	0.007
Below Stream+ Middle+ Depth+ Mass+ WS*Lower	12	-406.06	836.92	2.85	0.007
Depth+ Mass+ WS*Below Stream+ WS*Middle+ WS*Lower	14	-403.94	836.99	2.91	0.007
Depth+ WS*Below Stream+ Salmon*Middle+ WS*Middle+ WS*Lower	15	-402.87	837.00	2.93	0.007
Age+ Depth+ WS*Below Stream+ WS*Middle+ WS*Lower	14	-403.96	837.02	2.95	0.007
Lower+ Depth+ Salmon+ WS*Below Stream+ WS*Middle	13	-405.04	837.02	2.95	0.007
Age+ Below Stream+ Middle+ Depth+ WS*Lower	12	-406.13	837.07	3.00	0.006
Below Stream+ Depth+ Salmon*Lower+ WS*Lower	12	-406.13	837.07	3.00	0.006
Age+ Below Stream+ Lower+ Depth+ Salmon+ WS	11	-407.20	837.10	3.02	0.006
Below Stream+ Lower+ Depth+ Temperature+ Salmon+ WS	11	-407.22	837.13	3.06	0.006
Lower+ Depth+ Salmon+ Mass+ WS*Below Stream	12	-406.16	837.13	3.06	0.006
Below Stream+ Middle+ Depth+ Temperature+ WS*Lower	12	-406.16	837.14	3.07	0.006
Lower+ Depth+ Salmon*Below Stream+ WS*Below Stream	12	-406.17	837.15	3.08	0.006
Age+ Lower+ Depth+ Salmon+ WS*Below Stream	12	-406.18	837.18	3.11	0.006
Depth+ Temperature+ WS*Below Stream+ WS*Middle+ WS*Lower	14	-404.04	837.18	3.11	0.006
Lower+ Depth+ Temperature+ Salmon+ WS*Below Stream	12	-406.20	837.21	3.14	0.006

%N Models	k	logLik	AICc	ΔAICc	Weight
Below Stream+ Lower+ Depth+ Salmon+ WS*Middle	12	-406.20	837.22	3.15	0.006
Below Stream+ Depth+ Salmon+ Mass+ WS*Lower	12	-406.20	837.22	3.15	0.006
Depth+ WS*Below Stream+ Salmon*Lower+ WS*Lower	13	-405.14	837.23	3.15	0.006
Lower+ Depth+ WS+ Salmon*Below Stream	11	-407.28	837.25	3.17	0.006
Middle+ Depth+ Mass+ WS*Below Stream+ WS*Lower	13	-405.16	837.28	3.21	0.006
Age+ Middle+ Depth+ WS*Below Stream+ WS*Lower	13	-405.19	837.33	3.26	0.006
Below Stream+ Depth+ Mass+ WS*Middle+ WS*Lower	13	-405.19	837.33	3.26	0.006
Middle+ Depth+ Temperature+ WS*Below Stream+ WS*Lower	13	-405.22	837.39	3.32	0.005
Below Stream+ Middle+ Lower+ Depth+ Salmon+ Mass+ WS	12	-406.29	837.40	3.33	0.005
Depth+ WS*Below Stream+ Salmon*Middle+ WS*Middle+ Salmon*Lower+ WS*Lower	16	-402.00	837.42	3.35	0.005
Age+ Below Stream+ Depth+ Salmon+ WS*Lower	12	-406.30	837.42	3.35	0.005
Age+ Below Stream+ Middle+ Lower+ Depth+ Salmon+ WS	12	-406.31	837.44	3.37	0.005
Below Stream+ Middle+ Lower+ Depth+ Temperature+ Salmon+ WS	12	-406.32	837.45	3.38	0.005
Below Stream+ Depth+ Temperature+ Salmon+ WS*Lower	12	-406.34	837.49	3.42	0.005
Depth+ WS*Below Stream+ Salmon*Middle+ WS*Middle+ Salmon*Lower	15	-403.12	837.49	3.42	0.005
Age+ Below Stream+ Depth+ WS*Middle+ WS*Lower	13	-405.28	837.50	3.43	0.005
Below Stream+ Depth+ Salmon*Middle+ WS*Middle+ WS*Lower	14	-404.20	837.50	3.43	0.005
Below Stream+ Middle+ Depth+ Salmon*Lower+ WS*Lower	13	-405.29	837.54	3.47	0.005
Middle+ Lower+ Depth+ WS+ Salmon*Below Stream	12	-406.36	837.54	3.47	0.005
Middle+ Lower+ Depth+ Salmon*Below Stream+ WS*Below Stream	13	-405.30	837.55	3.48	0.005
Depth+ Salmon+ Mass+ WS*Below Stream+ WS*Lower	13	-405.30	837.55	3.48	0.005
Age+ Depth+ WS*Below Stream+ Salmon*Middle+ Salmon*Lower	15	-403.15	837.57	3.50	0.005
Age+ Middle+ Lower+ Depth+ Salmon+ WS*Below Stream	13	-405.32	837.60	3.52	0.005
Depth+ Salmon*Below Stream+ WS*Lower	12	-406.40	837.61	3.54	0.005
Middle+ Lower+ Depth+ Temperature+ Salmon+ WS*Below Stream	13	-405.33	837.61	3.54	0.005
Age+ Depth+ Salmon+ WS*Below Stream+ WS*Lower	13	-405.34	837.62	3.55	0.005
Depth+ WS*Below Stream+ WS*Middle+ Salmon*Lower+ WS*Lower	15	-403.18	837.63	3.55	0.005
Middle+ Lower+ Depth+ Salmon+ Mass+ WS*Below Stream	13	-405.34	837.63	3.56	0.005
Depth+ Salmon*Below Stream+ WS*Below Stream+ WS*Lower	13	-405.35	837.65	3.58	0.005
Age+ Below Stream+ Depth+ WS+ Salmon*Middle+ Salmon*Lower	14	-404.28	837.66	3.59	0.005

%N Models	k	logLik	AICc	ΔAICc	Weight
Below Stream+ Depth+ Temperature+ WS*Middle+ WS*Lower	13	-405.36	837.66	3.59	0.005
Depth+ Temperature+ Salmon+ WS*Below Stream+ WS*Lower	13	-405.36	837.68	3.61	0.005
Depth+ Temperature+ WS*Below Stream+ Salmon*Middle+ Salmon*Lower	15	-403.24	837.74	3.67	0.005
Middle+ Depth+ WS*Below Stream+ Salmon*Lower+ WS*Lower	14	-404.33	837.76	3.69	0.005
Below Stream+ Depth+ Mass+ WS+ Salmon*Middle+ Salmon*Lower	14	-404.35	837.80	3.73	0.004
Depth+ Mass+ WS*Below Stream+ Salmon*Middle+ Salmon*Lower	15	-403.28	837.81	3.74	0.004
Below Stream+ Middle+ Depth+ Salmon+ Mass+ WS*Lower	13	-405.43	837.81	3.74	0.004
Below Stream+ Depth+ Temperature+ WS+ Salmon*Middle+ Salmon*Lower	14	-404.37	837.84	3.77	0.004
Below Stream+ Depth+ Salmon*Middle+ WS*Middle+ Salmon*Lower	14	-404.38	837.86	3.79	0.004
Age+ Depth+ Salmon+ WS*Below Stream+ WS*Middle+ WS*Lower	15	-403.30	837.87	3.79	0.004
Age+ Below Stream+ Middle+ Depth+ Salmon+ WS*Lower	13	-405.46	837.87	3.80	0.004
Depth+ Salmon*Below Stream+ WS*Below Stream+ Salmon*Middle+ Salmon*Lower	15	-403.31	837.88	3.81	0.004
Below Stream+ Middle+ Depth+ Temperature+ Salmon+ WS*Lower	13	-405.48	837.91	3.84	0.004
Depth+ Salmon+ Mass+ WS*Below Stream+ WS*Middle+ WS*Lower	15	-403.34	837.94	3.87	0.004
Age+ Below Stream+ Lower+ Depth+ Mass+ WS	11	-407.63	837.94	3.87	0.004
Below Stream+ Lower+ Depth+ Temperature+ Mass+ WS	11	-407.63	837.94	3.87	0.004
Depth+ WS+ Salmon*Below Stream+ Salmon*Middle+ Salmon*Lower	14	-404.44	837.98	3.91	0.004
Middle+ Depth+ Salmon*Below Stream+ WS*Lower	13	-405.53	838.00	3.93	0.004
Depth+ Salmon*Below Stream+ WS*Below Stream+ WS*Middle+ WS*Lower	15	-403.37	838.00	3.93	0.004
Below Stream+ Depth+ Salmon*Middle+ WS*Middle+ Salmon*Lower+ WS*Lower	15	-403.37	838.01	3.94	0.004
Depth+ Temperature+ Salmon+ WS*Below Stream+ WS*Middle+ WS*Lower	15	-403.38	838.03	3.96	0.004
Below Stream+ Depth+ Mass+ WS+ Salmon*Lower	12	-406.63	838.07	4.00	0.004

Appendix C.

Supporting material for Chapter 4

Table C.1. Description of Dungeness crab shell age categories. Adapted from crab survey methodology of Department of Fisheries and Oceans, Canada (Dunham et al., 2011).

Code	Description	Shell Age	Description
1	Moulting	0 days	Shell is splitting and in the process of moulting. Suture (joint line between upper and lower halves of the shell) must be opening at time of observation.
2	Plastic soft	1-2 days	Shell has a yellow-pink colour and every part of the shell can be easily deformed with light pressure.
3	Crackly soft	2 days- 1 month	Usually has bright orange downy hair on underside of carapace. Carapace is easily deformed with moderate pressure of thumb and makes a crackly sound.
4	Springy hard new	1-4 months	Slight carapace deflection with heavy pressure on underside. Little fouling or abrasion present. Barnacles may be present but will be small. Claws will be sharp lack detectable wear. Underside of carapace may still have dense orange or yellowish hair.
5	Hard new	Less than 1 year	No carapace deflection on underside of carapace with heavy pressure from thumb. Few if any signs of wear or abrasion on carapace. Barnacles may be present but small. Very little claw wear with tips of claws sharp and hooked.
6	Old worn	1-2 years	No deflection on underside of carapace. Claw wear present- i.e. worn cusps, ivory coloured, frequently broken claw tips. Barnacle growth or other encrustation present but otherwise a healthy crab. Males crabs frequently show mating marks on claws. Carapace spines and tips of walking legs may also be blunted.
7	Very old	Over 2 years	Barnacle encrusted shell with extreme shell and claw wear. Males typically show old mating marks that have often worn through claw. May shows signs of shell disease and tips of walking legs may be black or rotting. Crabs appear lethargic and moribund.
8	Not sure	NA	Cannot identify shell as old or new. Shell shows signs of wear, especially on cusps and tips of claws, but crab is still relatively clean and active.

Table C.2. AICc summary for univariate linear models of recent salmon metrics describing a historical mean salmon index between 1996-2005 for a subset of five sites with extensive salmon count data.

Model	*k*	AICc	ΔAICc	Weight	ER
Salmon index 2006-09	3	-69.61	0	0.999	1
Salmon index 2008	3	-39.49	30.12	<<0.001	> 1 million
Salmon index 2009	3	-2.52	67.09	<<0.001	> 1 million
Salmon index 2006-08	3	9.12	78.73	<<0.001	> 1 million
Salmon index 2006-07	3	20.09	89.71	<<0.001	> 1 million
Salmon index 2006	3	20.92	90.54	<<0.001	> 1 million
Salmon index year prior	3	27.52	97.14	<<0.001	> 1 million
Salmon index 2007	3	28.02	97.63	<<0.001	> 1 million

Note: *k* = number of model parameters, ΔAICc = change in AICc score from top model, weight = AICc model weight, ER = top model weight divided by model *i* weight.

Table C.3. Candidate model set (those from the global model set with a ΔAICc less than 4.0) from multi-model inference of Dungeness crab muscle tissue δ15N.

δ^{15}N Models	k	logLik	AICc	ΔAICc	Weight
salmon density + watershed size + percent alder + shell age	9	-152.55	324.72	0.00	0.23
salmon density + watershed size + percent alder + shell age + shell width	10	-151.63	325.27	0.55	0.17
salmon density + watershed size + percent alder	8	-154.13	325.54	0.82	0.15
salmon density + watershed size + percent alder + shell width	9	-153.07	325.75	1.03	0.14
salmon density + watershed size + percent alder + shell age + estuary area	10	-152.54	327.08	2.36	0.07
salmon density + watershed size + percent alder + shell age + shell width + estuary area	11	-151.63	327.68	2.96	0.05
salmon density + watershed size + shell age	8	-155.24	327.76	3.04	0.05
salmon density + watershed size + percent alder + estuary area	9	-154.13	327.88	3.16	0.05
salmon density + watershed size + shell age + shell width	9	-154.21	328.03	3.32	0.04
salmon density + watershed size + percent alder + shell width + estuary area	10	-153.07	328.13	3.41	0.04

Note: logLik = model log likelihood, other table headings are as described in Table C.1.

Table C.4. **Candidate model set (those from the global model set with a ΔAICc less than 4.0) from multi-model inference of Dungeness crab muscle tissue $\delta^{13}C$.**

$\delta^{13}C$ Models	*k*	logLik	AICc	ΔAICc	Weight
shell age + watershed size	7	-150.92	316.86	0.00	0.24
shell age + watershed size + estuary area	8	-150.40	318.11	1.26	0.13
shell age + watershed size + shell width	8	-150.65	318.62	1.76	0.10
shell age + watershed size + salmon density	8	-150.77	318.86	2.01	0.09
shell age + watershed size + salmon density + estuary area	9	-149.60	318.87	2.01	0.09
shell age + percent alder	7	-152.28	319.57	2.71	0.06
shell age + watershed size + shell width + estuary area	9	-150.10	319.86	3.00	0.05
shell age + percent alder + estuary area	8	-151.44	320.20	3.34	0.05
shell age + watershed size + estuary area + salmon density + percent alder	10	-149.17	320.40	3.54	0.04
watershed size	6	-153.85	320.45	3.59	0.04
shell age + watershed size + salmon density + shell width	9	-150.51	320.69	3.84	0.04
shell age + watershed size + estuary area + salmon density + shell width	10	-149.32	320.70	3.85	0.04
shell age + salmon density + estuary area + percent alder	9	-150.54	320.74	3.88	0.03

Note: Table headings are as described in Table C.3.

Table C.5. Candidate model set (those from the global model set with a ΔAICc less than 4.0) from multi-model inference of mean Dungeness crab catch per unit effort (CPUE †).

CPUE Models	*k*	logLik	AICc	ΔAICc	Weight
estuary area	4	-40.17	90.01	0.00	0.33
estuary area + watershed size	5	-39.39	91.38	1.37	0.16
estuary area + fishing intensity	5	-39.47	91.55	1.54	0.15
estuary area + percent alder	5	-39.75	92.12	2.11	0.11
estuary area + trap depth	5	-40.06	92.73	2.72	0.08
estuary area + salmon density	5	-40.16	92.94	2.93	0.08
estuary area + watershed size + fishing intensity	6	-39.09	94.00	3.99	0.04
estuary area + watershed size + trap depth	6	-39.09	94.01	4.00	0.04

Note: Note: Table headings are as described in Table S3.

† The number of crabs caught per trap day of fishing.

Table C. 6. **Candidate model set (those from the global model set with a ΔAICc less than 4.0) from multi-model inference of mean Dungeness crab mass (kg).**

Mass Models	*k*	logLik	AICc	ΔAICc	Weight
watershed size	4	20.57	-31.48	0.00	0.36
watershed size + salmon density	5	21.04	-29.46	2.01	0.13
null	3	18.09	-29.22	2.26	0.12
watershed size + mean crab CPUE	5	20.87	-29.13	2.35	0.11
watershed size + percent alder	5	20.84	-29.07	2.41	0.11
watershed size + estuary area	5	20.58	-28.56	2.92	0.08
watershed size + fishing intensity	5	20.57	-28.54	2.94	0.08

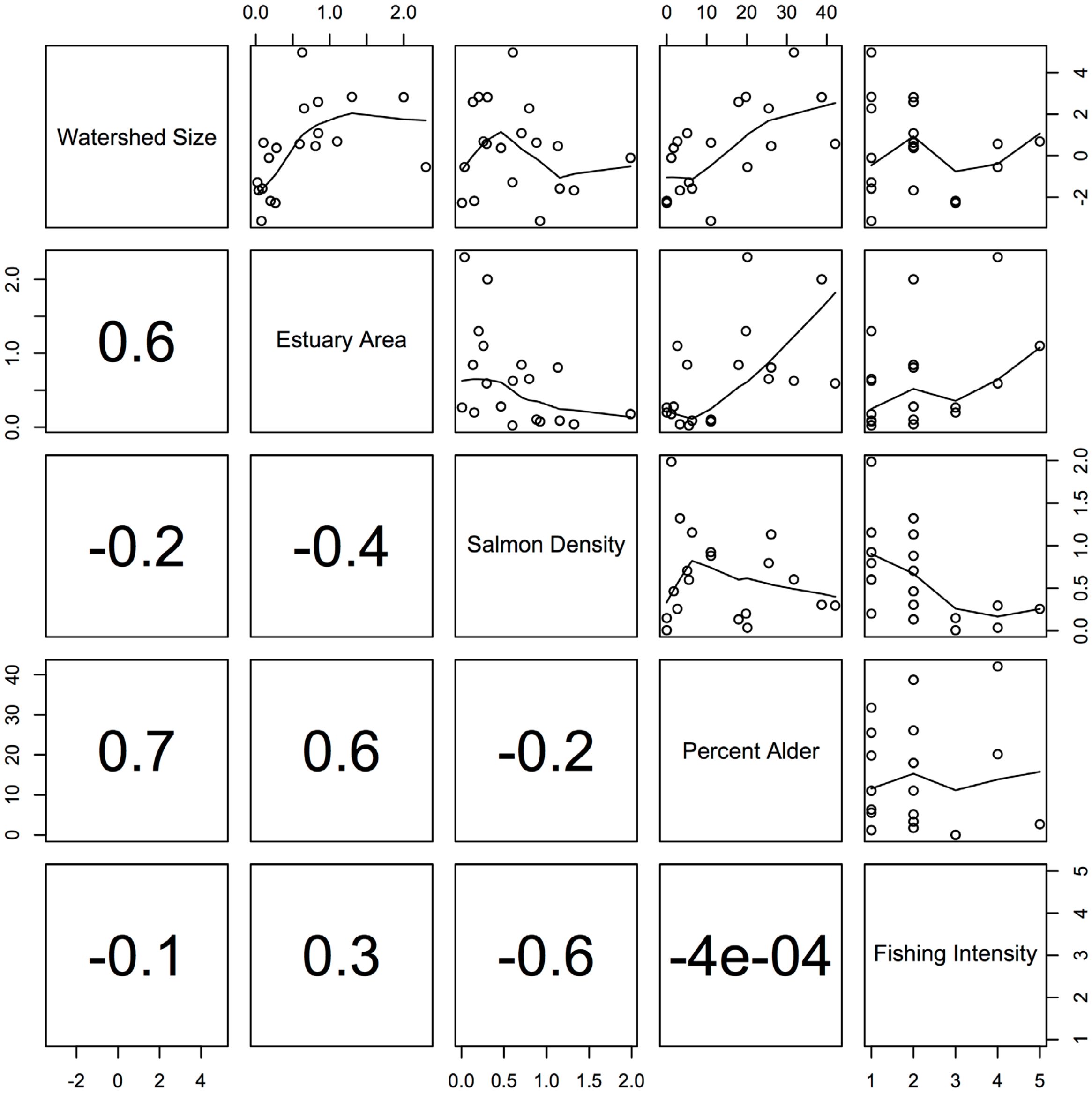

Figure C.7. **Multi-panel scatterplots of site-level covariates as used in Zuur et al. (2010). Upper-right panels show pair-wise plots of covariates with a LOESS smoother. Lower-left panels indicate Pearson correlation coefficients of each covariate pair. Not all covariates were used in every analysis (refer to methods and results).**

Appendix D.

Supporting material for Chapter 5

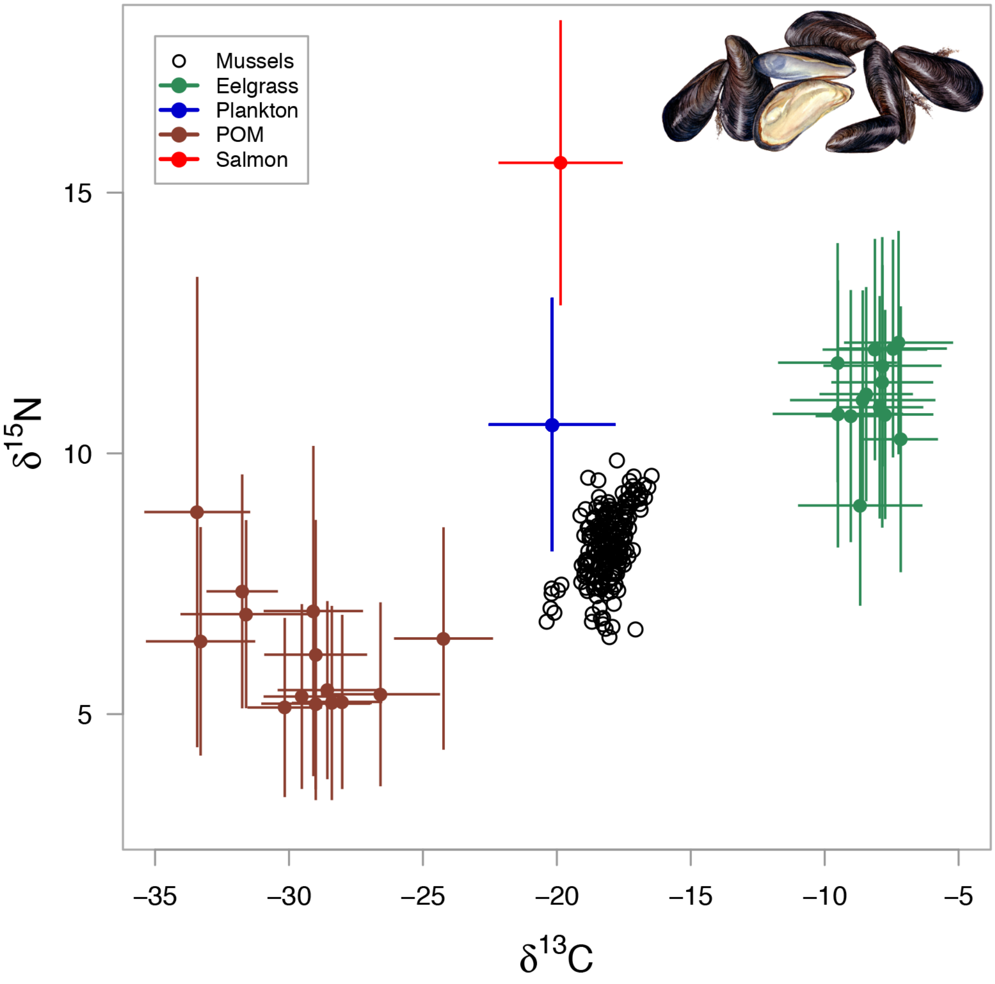

Figure D.1. **Iso-space plot of mussels collected in the summer with inferred dietary sources considered. Error bars indicate combined SD from sampling and fractionation.**

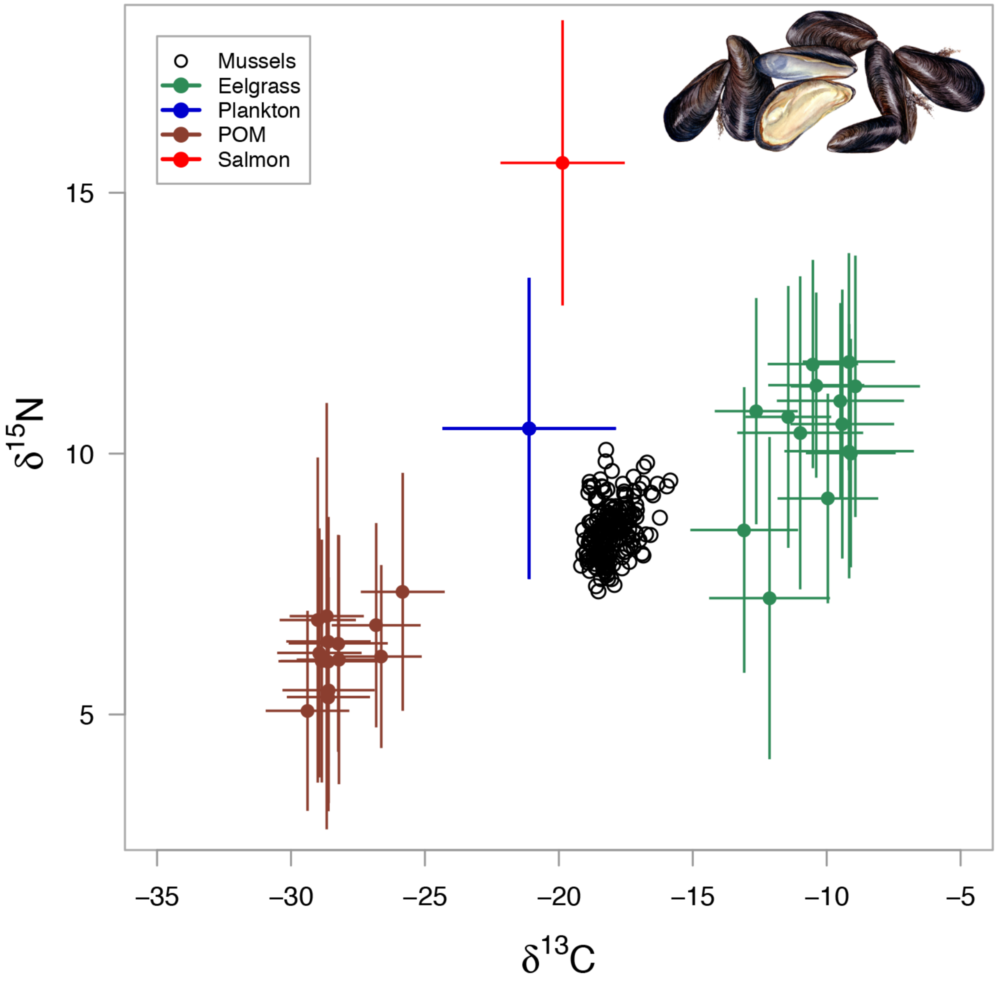

Figure D.2. **Iso-space plot of mussels collected in the fall with inferred dietary sources considered. Error bars indicate combined SD from sampling and fractionation.**

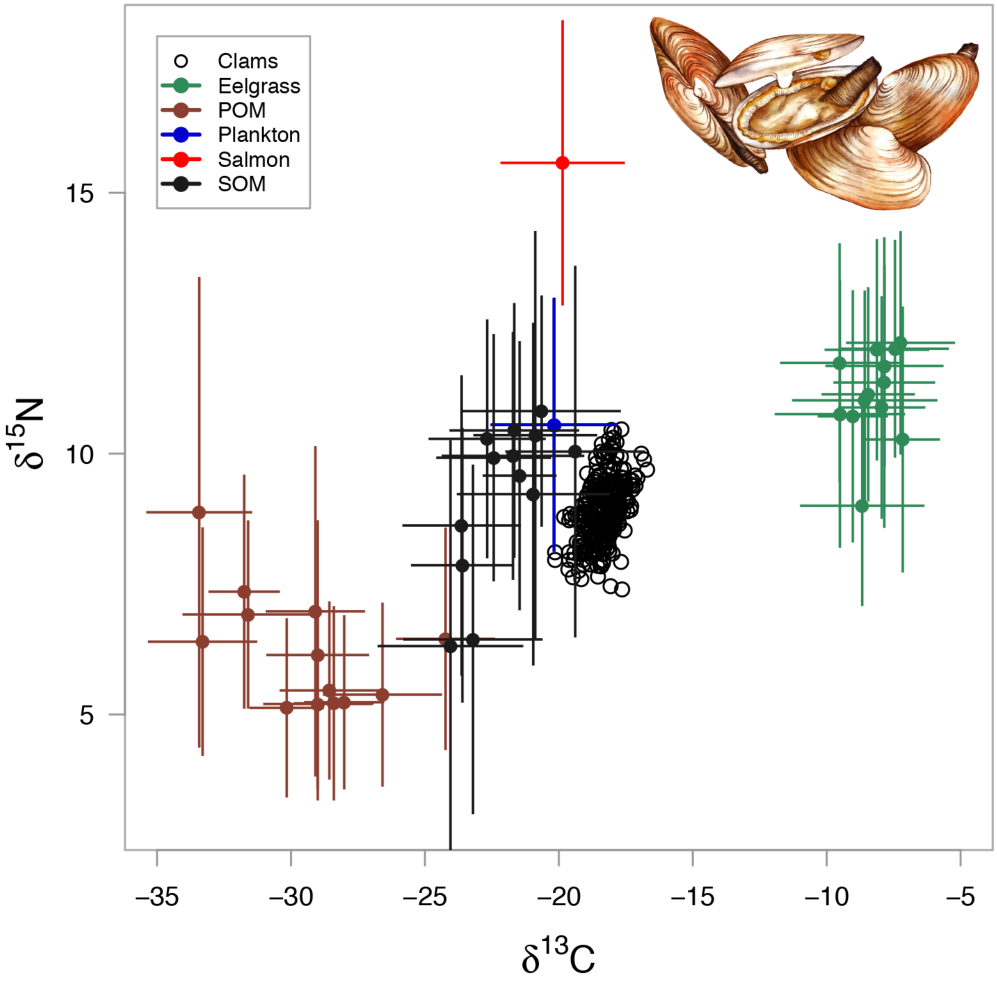

Figure D.3. **Iso-space plot of soft-shell clams with inferred dietary sources considered. Error bars indicate combined SD from sampling and fractionation.**

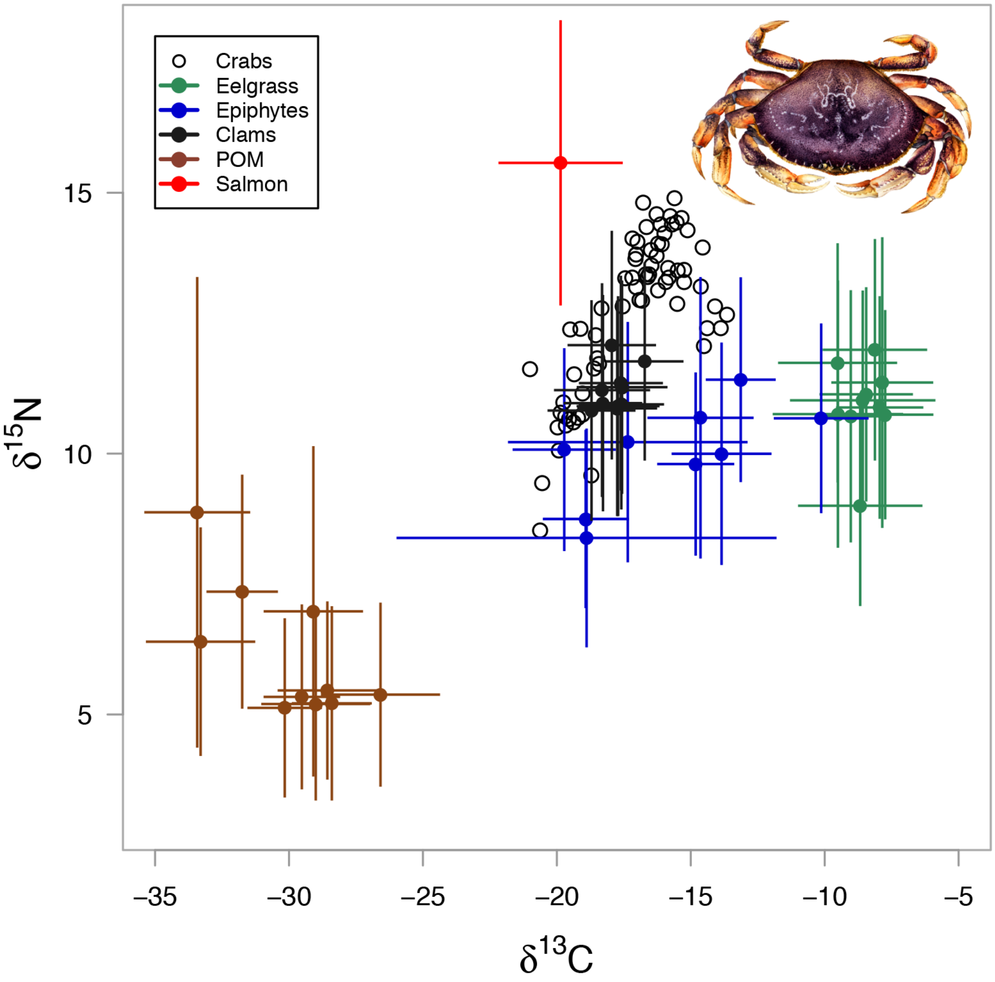

Figure D.4. **Iso-space plot of Dungeness crabs with inferred dietary sources considered. Error bars indicate combined SD from sampling and fractionation.**

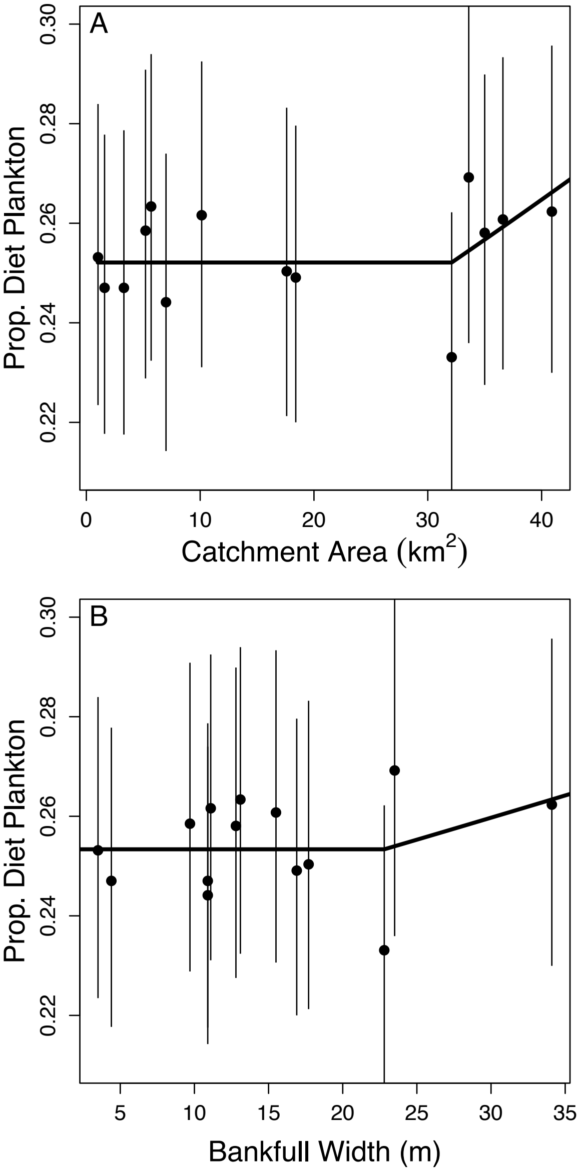

Figure D.5. Broken-stick beta regressions of A) catchment area and b) stream bankfull width describing proportional contributions of plankton to the diet of mussels collected during the summer season. Data points indicate median posterior estimates from isotope mixing models with 25-75% credible intervals.

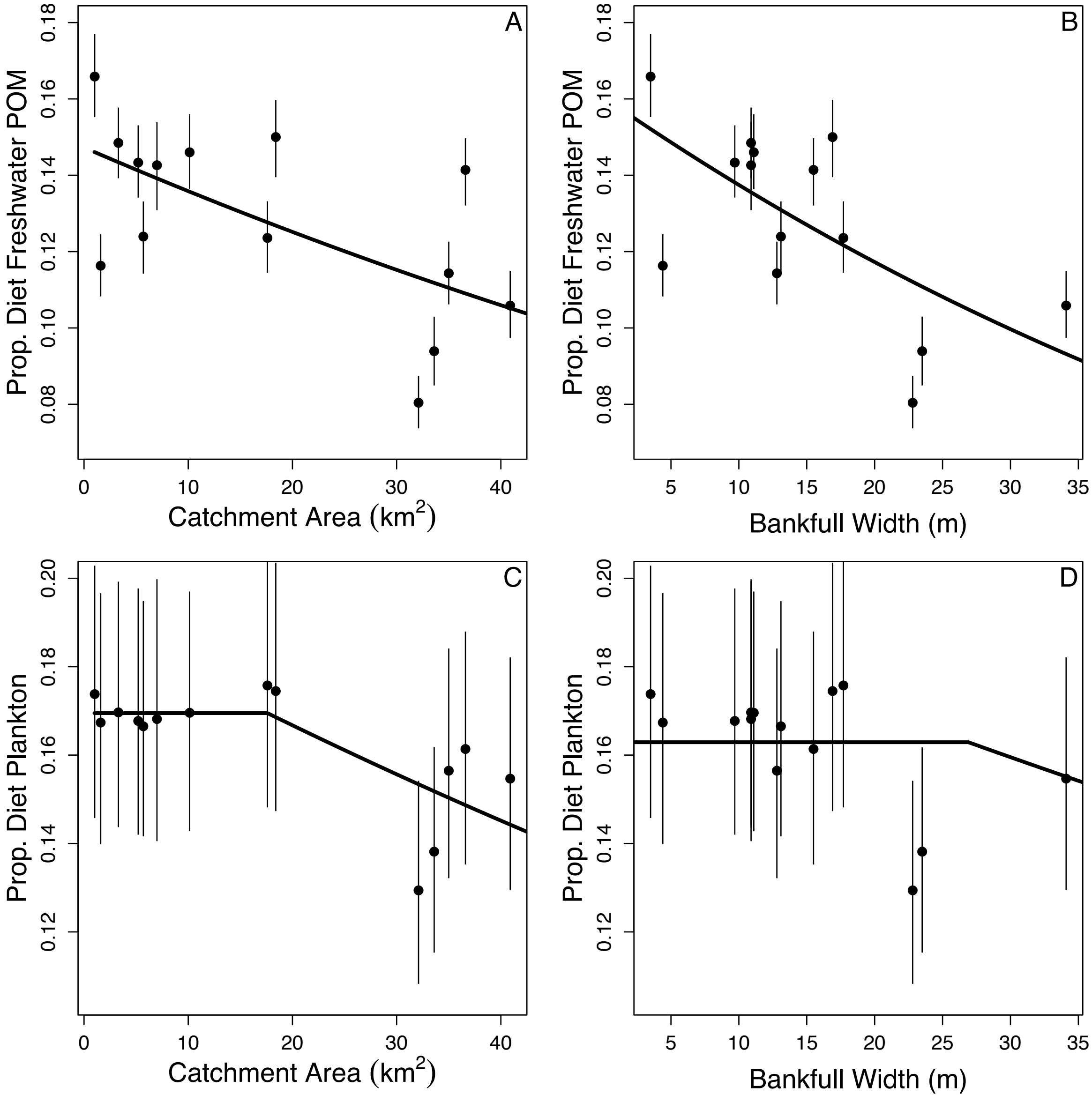

Figure D.6. **Linear regressions of POM dietary contributions vs. A) catchment area and B) stream bankfull width; and broken-stick regressions of plankton dietary contributions vs. C) catchment area and D) stream bankfull width for mussels collected during the fall season. Data points indicate median posterior estimates from isotope mixing models with 25-75% credible intervals.**

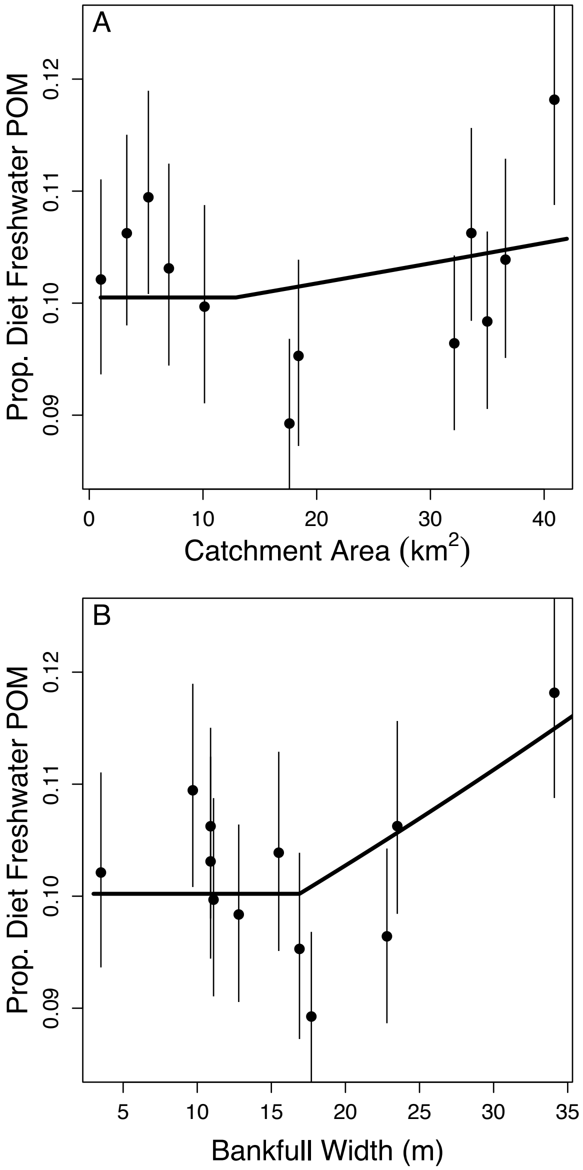

Figure D.7. **Broken-stick beta regressions of A) catchment area and b) stream bankfull width describing proportional contributions of freshwater particulate organic matter (POM) to the diet of soft-shell clams. Data points indicate median posterior estimates from isotope mixing models with 25-75% credible intervals.**

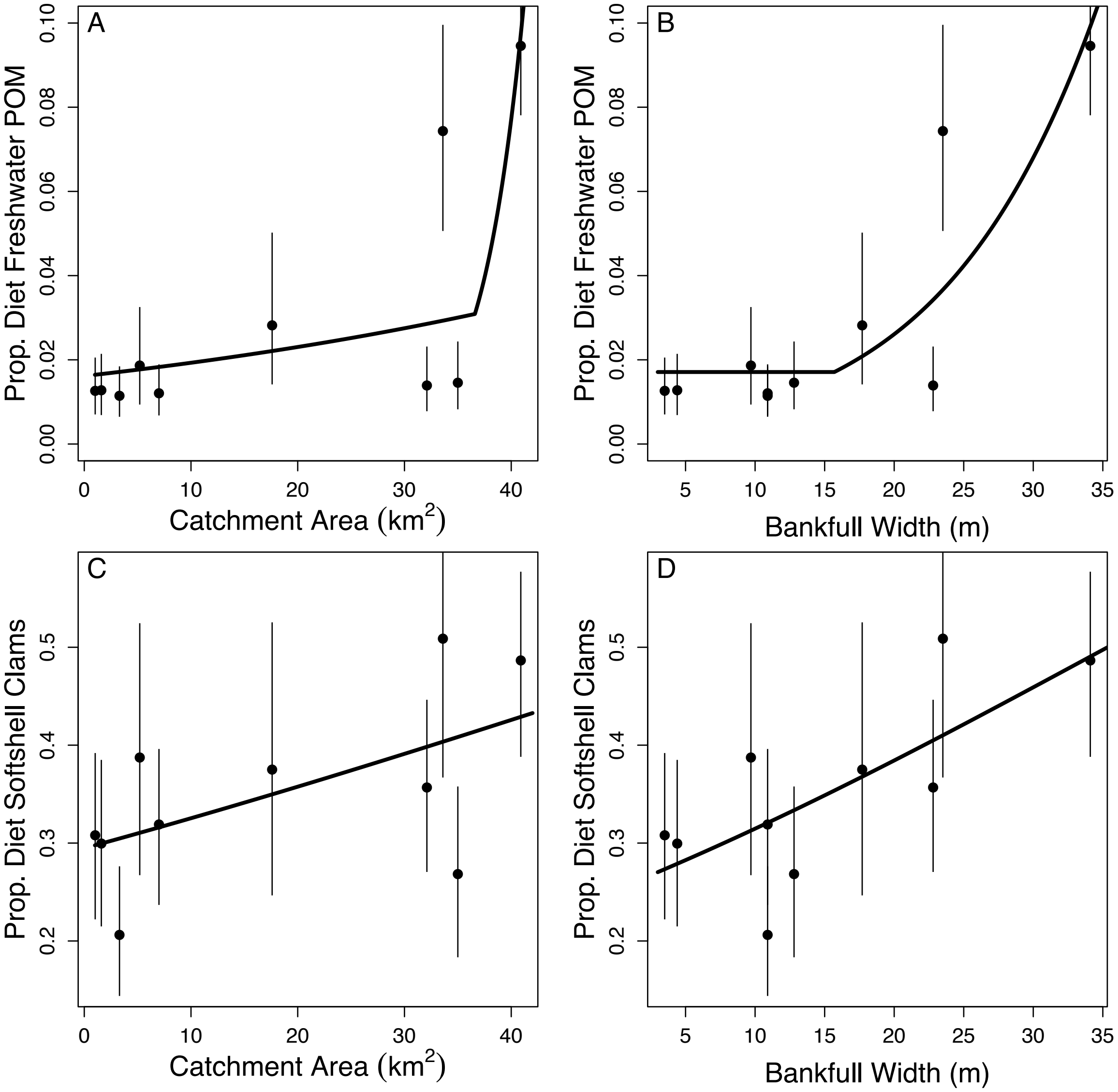

Figure D.8. Broken-stick regressions of POM dietary contributions vs. A) catchment area and B) stream bankfull width; and linear regressions of soft-shell clam dietary contributions vs. C) catchment area and D) stream bankfull width for Dungeness crabs. Data points indicate median posterior estimates from isotope mixing models with 25-75% credible intervals.