From earth and ocean:
investigating the importance of cross-ecosystem resource linkages to a mobile estuarine consumer

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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 two 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 can constitute 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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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 subsides 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. 2004, 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 northeastern 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 (J. M. S. 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 molting) 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 which 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
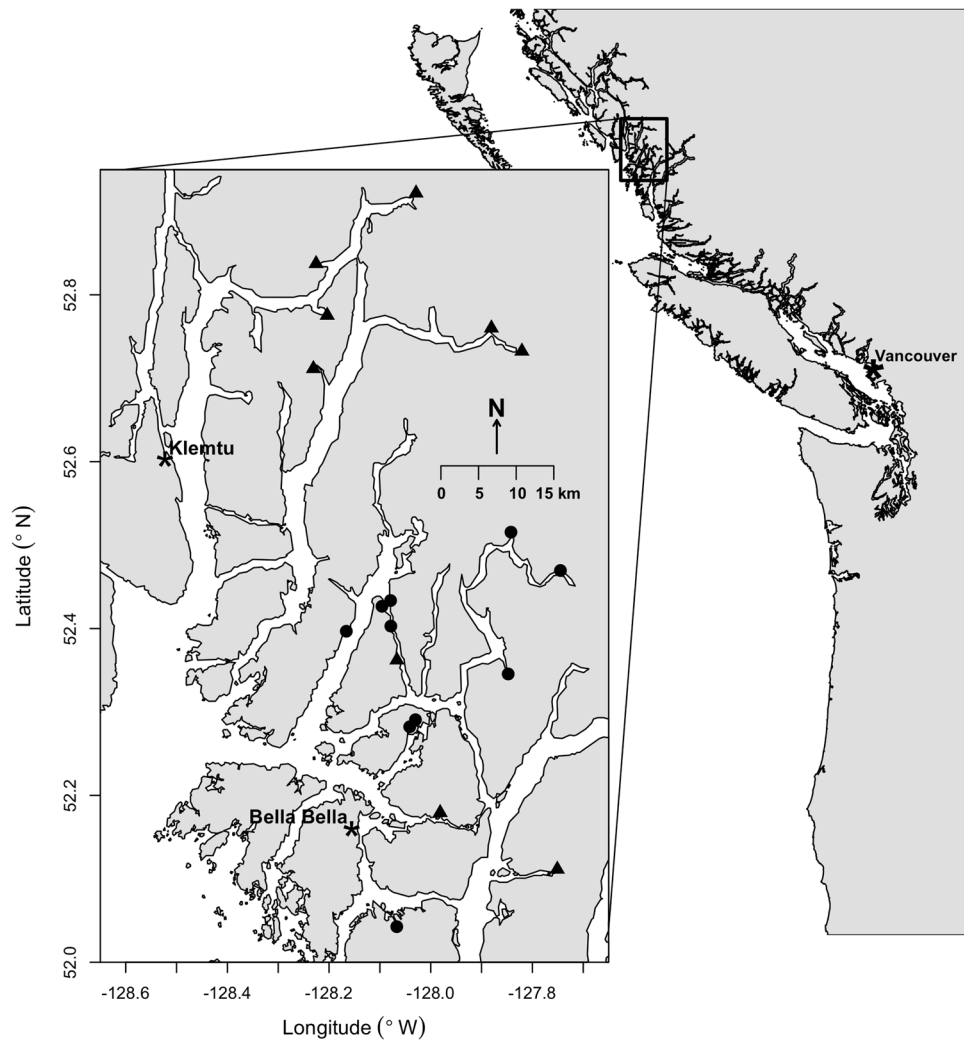
Fig. 1. Study site locations. Circles indicate sites sampled in both 2007 and 2008 and triangles indicate sites sampled only in 2007. Asterisks show locations of the Coastal First Nations communities of Bella Bella and Klemtu, British Columbia, Canada.

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.

STUDY AREA

Research was conducted on the central coast of British Columbia, Canada, within the Great Bear Rainforest (Fig. 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.

Table 1. Summary of site-level covariates used in models to describe δ^{15}N and δ^{13}C of Dungeness crab muscle tissue, mass and catch per unit effort (CPUE).

Site code	Catchment area (km^2)	Mean bankfull width (m)	Mean depth (m)	Mean bank height (m)	Estuary area (km^2)	Mean salmon biomass density (kg/m^2)	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 2).

We sampled 19 estuaries that varied in upstream catchment area, stream channel size, estuary area, upstream salmon spawning density, and red alder dominance (Table 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*).

METHODS

Crab surveys

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 × 61 × 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 (molting) to 7 (very old). 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.

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:

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

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 iMapBC (Government of British Columbia

Table 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 per year) + Rare commercial fishing
4	Frequent commercial fishing (commercial sets observed more than once per year) + Rare to occasional local or recreational fishing
5	Frequent local or recreational fishing + Frequent commercial fishing

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 2).

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/Xaixais 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:

$$\text{salmon density} = \frac{\sum (N_i \times W_i)}{A}$$

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 to 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 and 2009 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 10 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 five sites. The 2006–2009 index had the highest likelihood with a model weight approaching 1. We log transformed the 2006–2009 salmon density index for analysis of δ^{15}N to better describe the asymptote observed in the raw data.

Stable isotope analysis

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). A set amount of sample (0.8–1.2 µg) was packaged in standard pressed tin capsules (3.5 × 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, Cheshire, UK). Stable isotopes are expressed as the difference between the sample and a known standard, or δ, in parts per thousand (‰):

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

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.

Statistical analyses

The open source statistical software R was used for all analyses (R Development 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 δ^{15}N and δ^{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 $\delta^{13}C$ and $\delta^{15}N$ 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 $\delta^{13}C$ and $\delta^{15}N$ values of dorsal muscle tissue from spawning chum and pink salmon at 8 watersheds in our study region (five samples of each species per site). For estuarine sources we used mean $\delta^{13}C$ and $\delta^{15}N$ values of eelgrass (Zostera marina) collected from 20 estuaries within our study region (five random samples from each site over two seasons). Terrestrial POM isotope samples were attained by vacuum filtering 500 ml of stream water through pre-combusted glass fiber filters (Whatman GF/F, 47 mm, 0.7 µm). 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. Eelgrass samples were thoroughly cleaned and rinsed with de-ionized 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 0.4 per trophic level (TL) for $\delta^{13}C$ from Post (2002) and 2.54 per TL for $\delta^{15}N$ from Vanderklift and Ponsard (2003). 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:

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

$$p_B = \frac{(\delta^{15}\bar{N}_D - \delta^{15}\bar{N}_C) - (\delta^{15}\bar{N}_A - \delta^{15}\bar{N}_C)p_A}{\delta^{15}\bar{N}_B - \delta^{15}\bar{N}_C}$$

$$p_C = 1 - p_A - p_B$$

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. and represent the overall mean isotopic ratios for sources A, B, and C or the site-level mean isotopic ratios for D.

Table 3. Summary of Dungeness crab surveys in 2007 and 2008 on the central coast of British Columbia.

Site code	Year	No. 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
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

† CPUE, catch per unit effort, is the number of crabs caught per trap day of fishing.

RESULTS

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 3).

Crab isotopes

$\delta^{15}N$.—Watershed size, salmon density and percent alder all correlated strongly with $\delta^{15}N$ of crab muscle tissue. As predicted, crab $\delta^{15}N$ was depleted in estuaries below larger watersheds and with higher percentages of alder (Fig. 2A, C). Also as predicted, crab $\delta^{15}N$ enriched with increasing salmon density (Fig. 2B). Both watershed size and salmon density had the highest relative importance (Fig. 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 (Fig. 2D). Crabs that were large or had older

shells had slightly enriched $\delta^{15}N$, as predicted, but these effects were uncertain with CI crossing zero. Contrary to our prediction, estuary size had no effect on $\delta^{15}N$ 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 A3–A6.

$\delta^{13}C$.—Watershed size had the strongest effect on $\delta^{13}C$ of crab muscle tissue (Fig. 3C). As predicted, crabs with older shells had more enriched $\delta^{13}C$ and those below larger watersheds had more depleted $\delta^{13}C$ (Fig. 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 (Fig. 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.
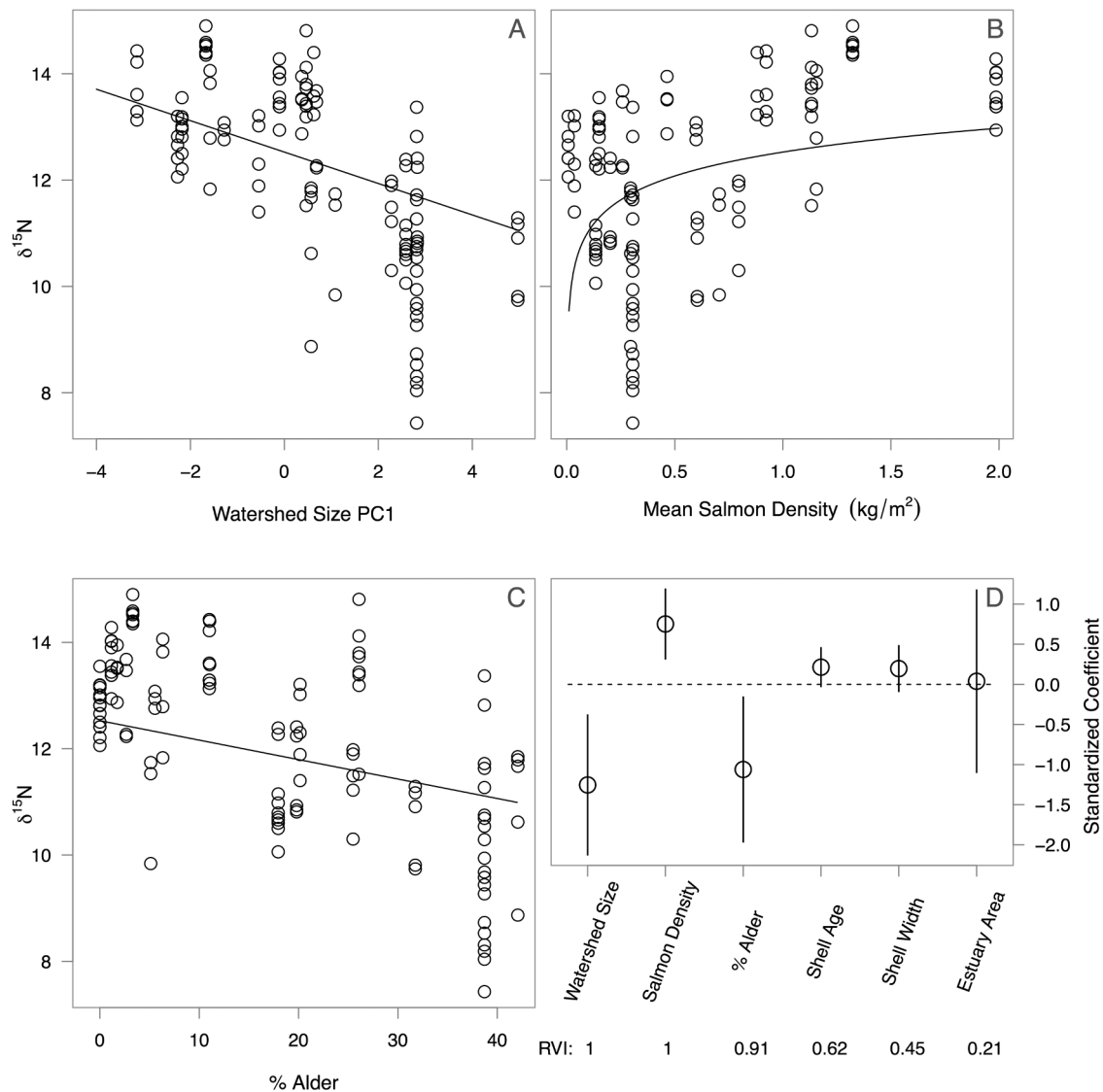
Fig. 2. (A) Dungeness crab muscle tissue $\delta^{15}N$ vs. watershed size principal component 1. (B) $\delta^{15}N$ vs. mean salmon density with trend line based on log-transformed salmon density. (C) $\delta^{15}N$ vs. percent alder basal area upstream relative to total basal area of all tree species. 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.

Catch per unit effort

As predicted, catch per unit effort (CPUE) of Dungeness crabs was highest in the largest estuaries (Fig. 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.
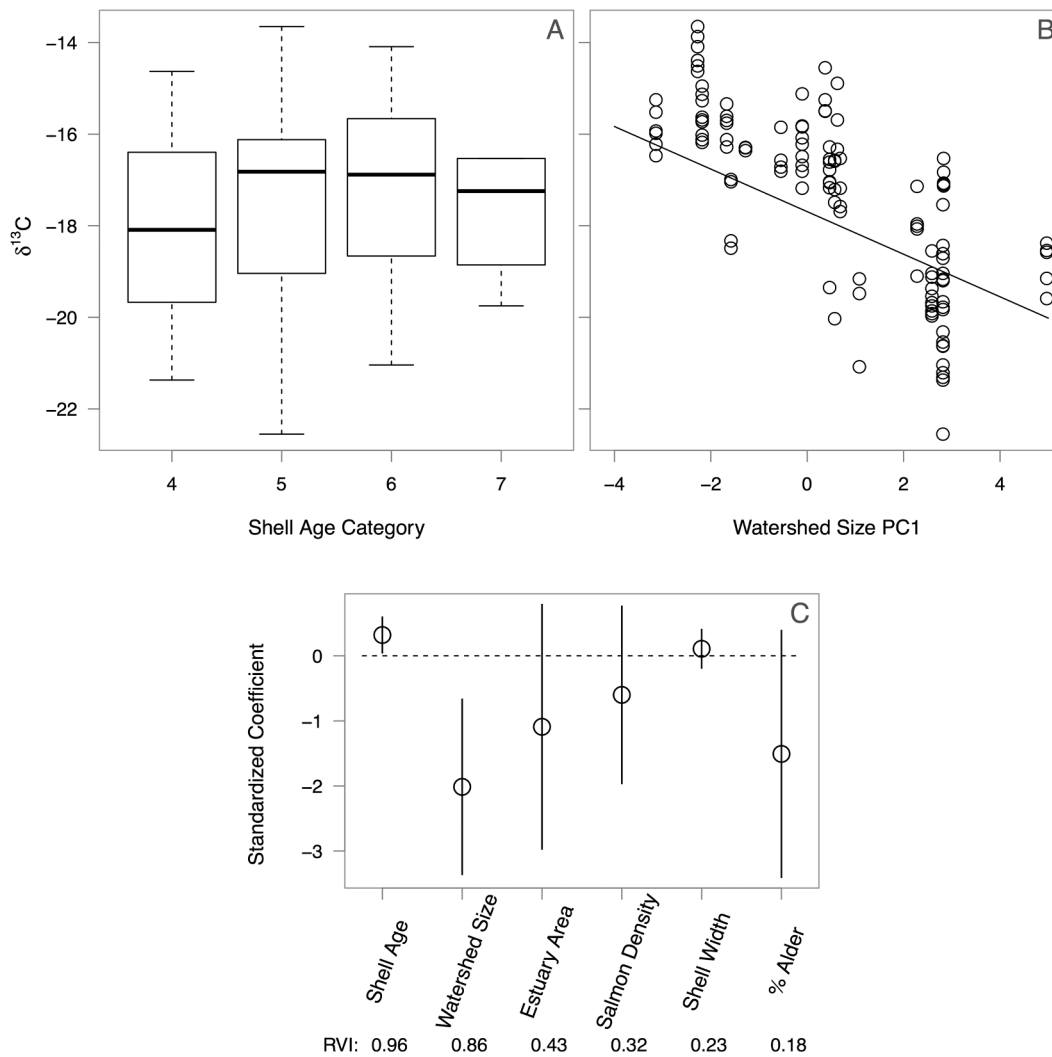
Fig. 3. (A) Dungeness crab muscle tissue $\delta^{13}C$ vs. shell age category, from younger to older (see Appendix: Table A2). (B) $\delta^{13}C$ vs. watershed size principal component 1. Trend line for panel B represents univariate model using intercept and coefficient from multi-model output (see explanation of data fitting in caption of Fig. 2). (C) Standardized coefficients (mean = 0, standard deviation = 2) with 95% confidence intervals for all covariates considered in the $\delta^{13}C$ 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.

Fishing intensity correlated negatively but, as with trap depth and percent alder, it had very weak support (Fig. 4B). Salmon density had a negligible relationship with CPUE, with a cumulative weight of only 0.08 from the candidate set.

Crab size

Crabs were heavier in estuaries located below larger watersheds. This was not one of our predictions but was strongly supported (Fig.

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 (Fig. 5B).

Isotope mixing model

Source isotope ratios fully encompassed the range of individual Dungeness crab isotope ratios (Fig. 6). Source dietary contributions
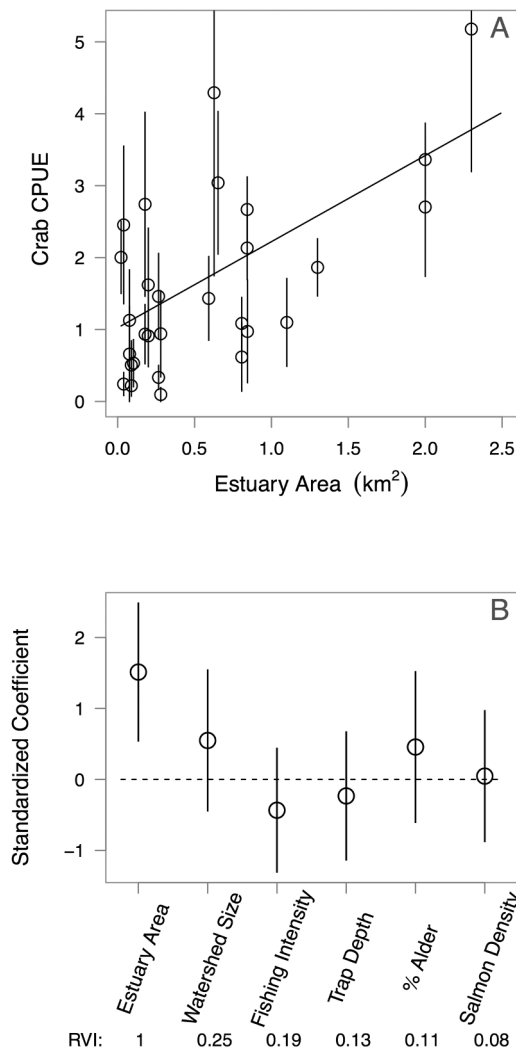
Fig. 4. (A) Mean Dungeness crab catch per unit effort (CPUE) vs. estuary area, with standard error bars. CPUE was calculated as the number of crabs caught per individual trap day fished. The trend line represents univariate model using intercept and coefficient from multi-model output (see explanation of data fitting in caption of Fig. 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.
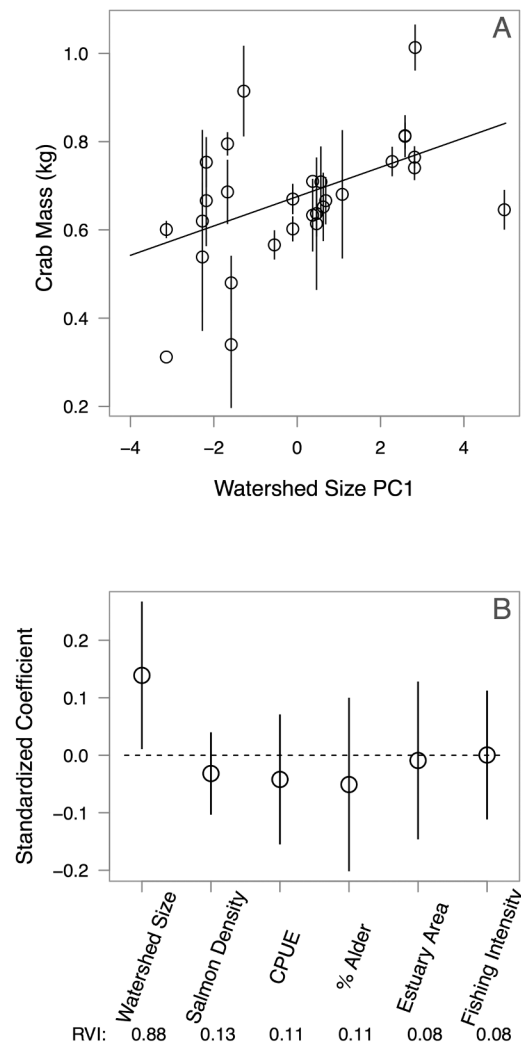

Fig. 5. (A) Mean Dungeness crab mass vs. watershed size principal component 1. The trend line was constructed from a univariate model using the intercept and coefficient from multi-model output (see explanation of data fitting in caption of Fig. 2). (B) Standardized coefficients (mean = 0, standard deviation = 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.

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 (Fig. 7).
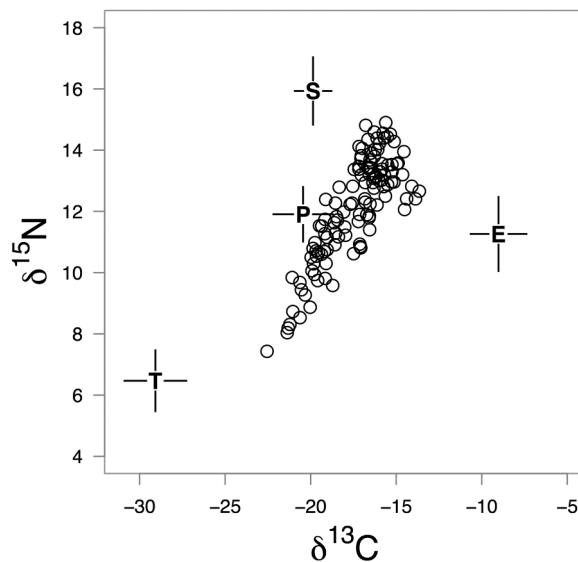
Fig. 6. Isotope bi-plot of individual crabs and three sources used in isotope-mixing model analysis: 'S', 'T', and 'E' which indicate salmon, terrestrial, and estuarine sources, respectively. Terrestrial sources are stream particulate organic matter and estuarine sources are *Zostera marina*. Error bars 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 two trophic levels of fractionation except for a 1.5 trophic level correction for salmon.

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 nutri-
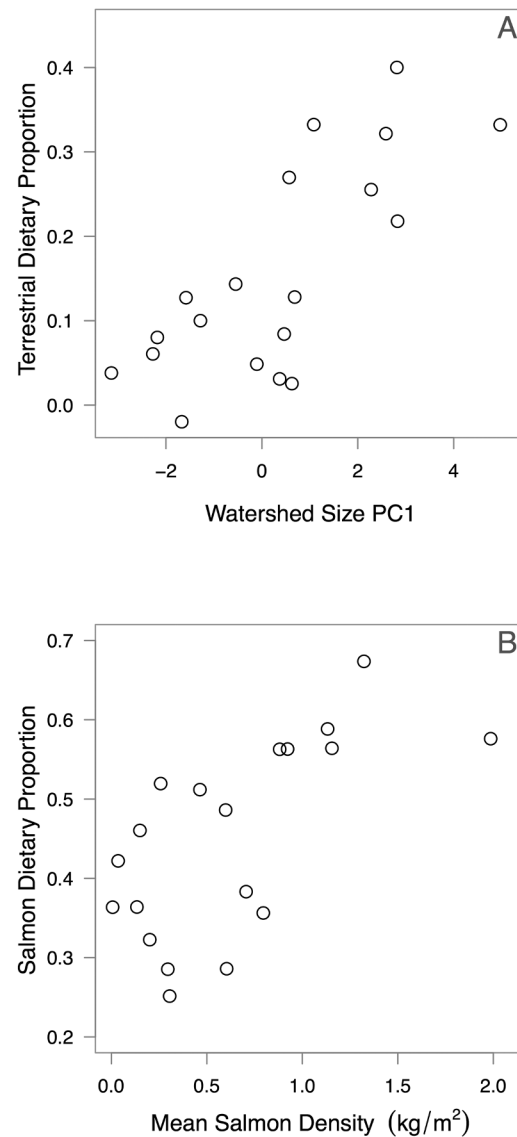

Fig. 7. (A) Proportional contribution of terrestrial resource subsidies to the diet of Dungeness crabs vs. watershed size principal component 1. (B) Proportional contribution of salmon resource subsidies to the diet of Dungeness crabs vs. mean upstream salmon density. Proportional dietary contributions 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.

ents, 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 $\delta^{15}N$ and $\delta^{13}C$ 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 $\delta^{15}N$. Alders fix nitrogen directly from the atmosphere as a result of symbiotic bacterial associations and can saturate forest soils with nitrogen, which can leach $\delta^{15}N$-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 $\delta^{13}C$ but this was not observed for $\delta^{15}N$. 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 molting.

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 (Fig. 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 (Fig. 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 (Fig. 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.

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Supplemental Material

Appendix

Table A1. 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 2006–2009	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 2006–2008	3	9.12	78.73	<<0.001	>1 million
Salmon index 2006–2007	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 A2. 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	Molting	0 days	Shell is splitting and in the process of molting. 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 color 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 colored, 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 A3. 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 δ^{15}N.

δ^{15}N model	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 A1.

Table A4. 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 $\delta^{13}C$.

$\delta^{13}C$ model	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 A3.

Table A5. Candidate model set (those from the global model set with a ΔAICc less than 4.0) from multi-model inference of mean Dungeness crab CPUE.†

CPUE model	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: Table headings are as described in Table A3.
† CPUE, catch per unit effort, is the number of crabs caught per trap day of fishing.

Table A6. 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 model	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

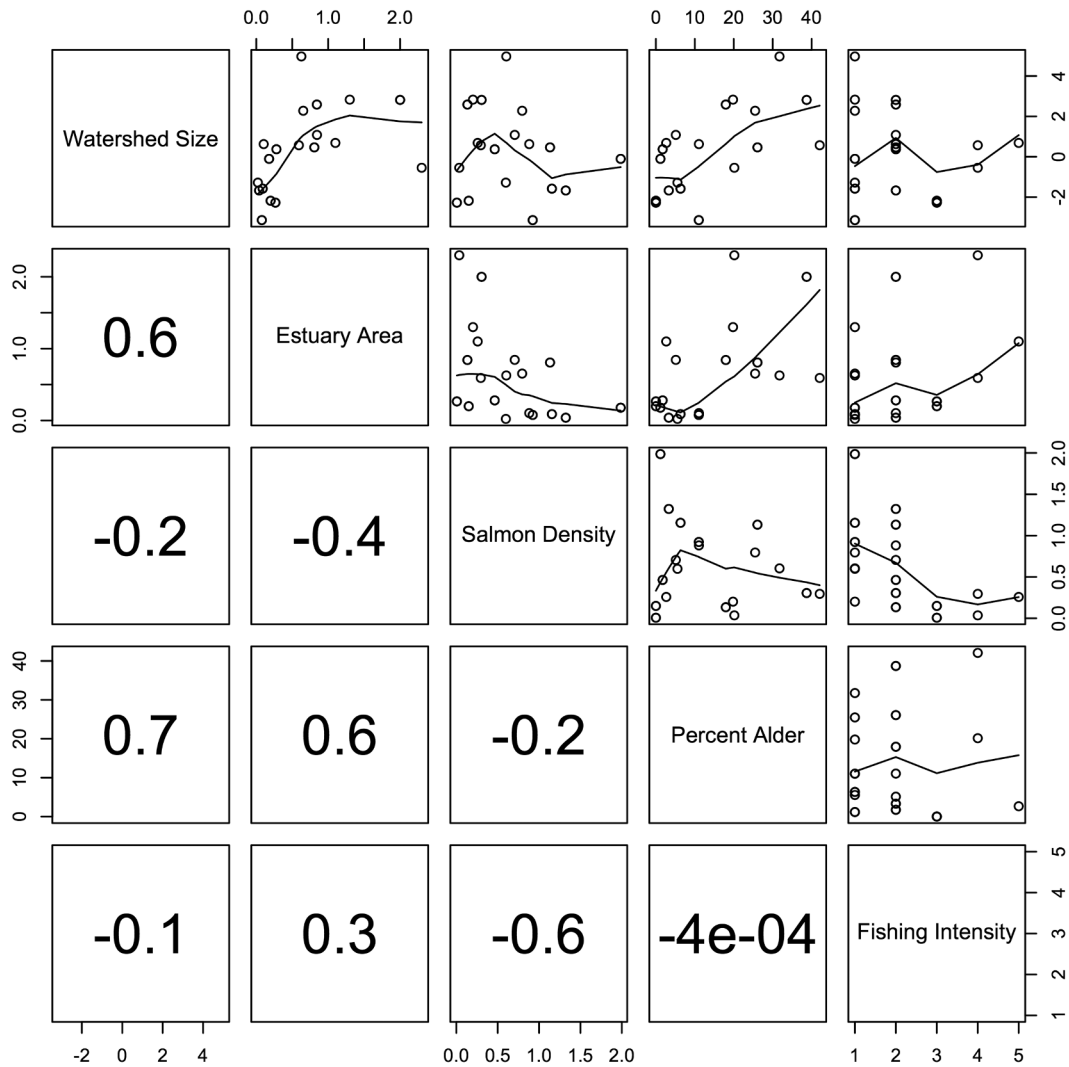*Note:* Table headings are as described in Table A3.

Fig. A1. 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 (see *Methods* and *Results*).