TERRESTRIAL-AQUATIC FOOD WEB LINKAGES ACROSS FLOODPLAINS OF DIFFERENT AGES, GLACIER BAY, ALASKA

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Abstract

The linkages between the stream and its riparian zone have been well studied in many diverse systems on short (generally annual) timescales. No research has yet considered this in the context of longer (multi-decadal to centennial) timescales at which landscape and successional processes operate. Glacier Bay National Park and Preserve, in southeast Alaska, has a well-documented history of glacial retreat, which allows for the study of ecosystem development using a space-for-time chronosequence approach. This research was unique in analysing terrestrial invertebrates on floodplains of different ages in Glacier Bay, and was the first to utilise two complementary methods of dietary analysis to study the movement of resources between terrestrial and aquatic habitats at sites of different ages. A combination of gut contents dietary analysis and stable isotope analysis was used to determine the food sources of aquatic and terrestrial consumers. Physical habitat complexity, rather than substrate age alone, was an important factor in structuring reciprocal subsidies. This has clear implications for river managers seeking to restore streams to their natural state, particularly where juvenile salmonids are present, as well as underlining the importance of considering a stream in the wider context of its riparian zone.

Acknowledgements

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1

GLACIER BAY NATIONAL PARK AND PRESERVE

1.1 Introduction

Worldwide, glaciers are receding, new streams are forming and others are lengthening (Robinson et al., 2014). Macroinvertebrate communities of glacial and post-glacial streams have been well documented worldwide (e.g. Europe: Brown et al., 2007, Finn et al., 2013, Khamis et al., 2014, North America: Milner, 1994, Flory and Milner, 2000, Milner et al., 2000, Milner et al., 2008, Milner et al., 2011, South America: Cauvy-Fraunié et al., 2015, and New Zealand: Cadbury et al., 2011), but the longer term influence of glacial recession on food webs and reciprocal subsidies between the aquatic and terrestrial communities are less well known.

Glacier Bay National Park and Preserve, in southeast Alaska, provides a unique opportunity to investigate the development of stream communities over time owing to its well documented glacial retreat. Glacier retreat creates floodplains of different ages (Figure 1.1), which can be used to study the effects of primary succession on community interactions over 200 years. In order to study this ecologically long timescale, a chronosequence ('space-for-time-substitution') approach was utilised, whereby spatially separated sites of different ages were assumed to represent the study of a single site over time (Walker and Del Moral, 2003). This approach has been used in numerous studies to examine aquatic macroinvertebrate community development over time (e.g. Milner et al., 2000, 2007, Milner and Robertson, 2010), but has not been applied to studies of linkages between the stream and the riparian zone. The space-for-time substitution approach has been criticised, and evidence from studies testing published chronosequences through comparative, empirical methods (e.g. palynology and long-term plots) has invalidated earlier conclusions regarding successional sequences (Johnson and Miyanishi, 2008). However, for this research, long-term plots are not feasible for 200 year time-scales, and the use of techniques such as palynology, soil cores, or even the analysis of samples collected in earlier studies is not appropriate to the research questions asked (for example, preservatives can affect isotope signatures (Arrington and Winemiller, 2002, Bicknell et al., 2011), and so analysing samples of invertebrates collected in the earliest studies of streams in Glacier Bay to reconstruct past food webs would not be a reliable methodology).

Table 1.1: Stream floodplains sampled in Glacier Bay, age indicates the length of time the stream mouths have been ice-free

Stream	**Code**	**Age (years)**	**Longitude**	**Latitude**	**Dominant riparian vegetation**	**Large woody debris present in stream channel**
Upper Muir 1	UM*	<20	59°04’43.1”	136°19’10.8”	*Dryas* sp.	No
Upper Muir 2	UM*	<20	59°04’02.5”	136°17’09.9”	*Dryas* sp.	No
Wolf Point Creek	WPC	55	58°59’48.3”	136°10’18.1”	Alder, some cottonwood	No
Nunatak Creek	NUN	70	58°58’40.5”	136°5’41.2”	Alder, cottonwood	No
Ice Valley Stream	IVS	130	58°49’10.9”	136°9’49.6”	Alder, spruce	Yes
Berg Bay South Stream**	BB	170	58°30’17.5”	136°14’0.62”	Alder, spruce, cottonwood	Yes
Rush Point Creek	RPC	200	58°28’11.2”	136°06’08.5”	Spruce	Yes

*Samples from Upper Muir 1 and 2 were combined as one site for the analysis due to low sample number
**Berg Bay South Stream hereafter referred to as Berg Bay

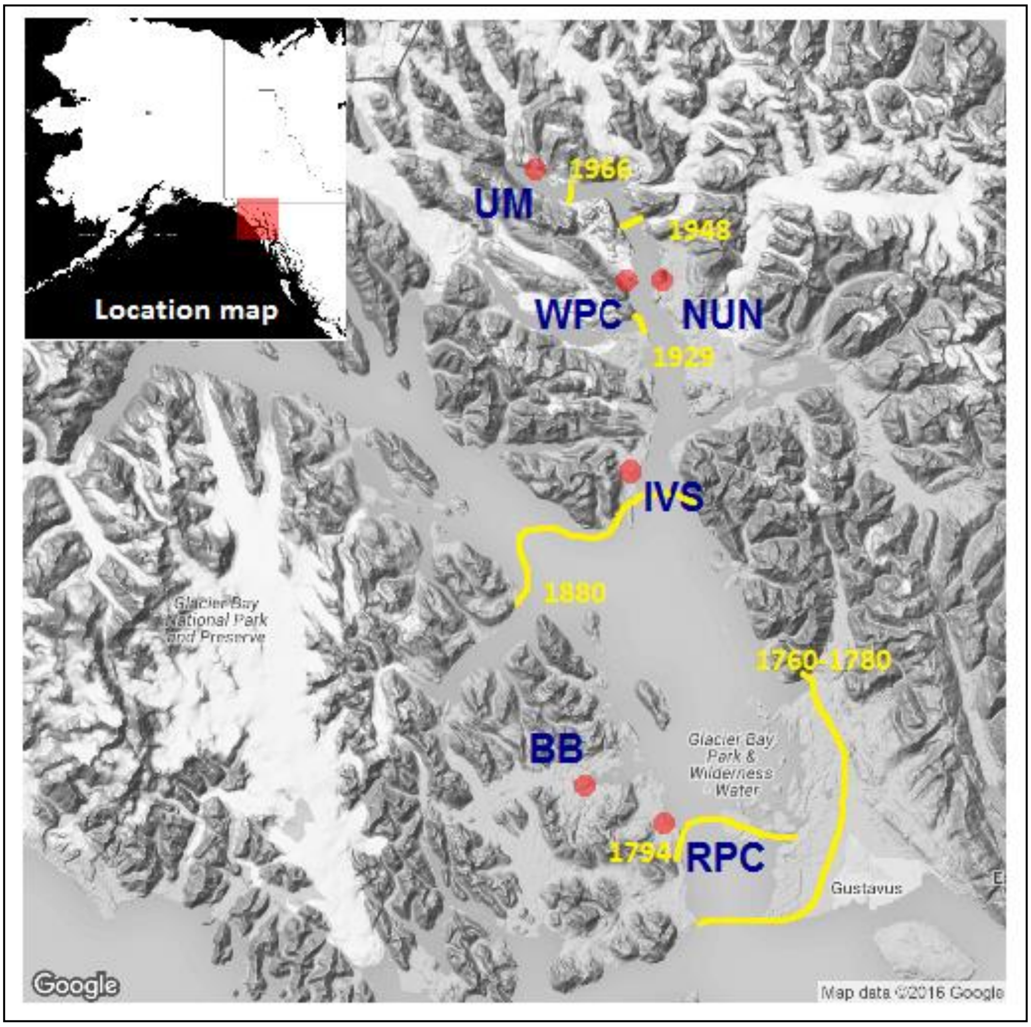

Figure 1.1 Location of field sites in Glacier Bay National Park and Preserve. Sites codes correspond to names in Table 1.1. Approximate position of glacier termini indicated with dates

1.2 Glacier Bay: previous stream research

There has been a long history of research regarding primary successional processes in Glacier Bay. Early work concentrated on terrestrial habitat development: Cooper (1923, 1939) and Chapin et al. (1994) documented the vegetational changes over time, and Crocker and Major (1955) described the soil development in Glacier Bay. Very young sites (<50 years old) are characterised by nitrogen limitation and vegetation dominated by black crust communities comprised of lichens, cyanobacteria, and bryophytes, as well as mats of *Dryas* sp., and low growing shrubs. Carbon and nitrogen pools build up over time, and vegetation becomes dominated by alder and cottonwoods between 50 and 100 years since deglaciation (Milner et al., 2007). The oldest substrates are covered by dense forests of maturing spruce and hemlock trees.

Streams, and the aquatic communities within them, have also been extensively studied in Glacier Bay since the 1970s (e.g. Milner, 1994, 1997, Milner et al., 2000, 2007, 2008). Young streams typically originate from pro-glacial lakes, which can buffer flows and provide stream channel stability. Overtime, these lakes become disconnected from the stream, leading to a decrease in channel stability, thereby facilitating recolonization by certain taxa, which are poor competitors. Increases in riparian vegetation, meanwhile, act to stabilise stream banks and reduce channel migration. Over time, channel stability increases, which facilitates colonisation by competitively dominant species, and early successional taxa are extirpated. After 130-150 years since ice retreat, coarse woody debris deposits become significant stabilisers of stream features, such as gravel bars (Milner et al., 2007). Stream stabilisation over time, along with accumulations of coarse woody debris, leads to an increase in instream habitat heterogeneity, thereby potentially enhancing biodiversity (Tews et al., 2004, Milner et al., 2008). This heterogeneity reaches a maximum at mid-successional sites (c. 140-160 years since deglaciation; Klaar et al., 2009), but differs between young streams which are typically dominated by faster flowing habitats, and older streams which are typified by the presence of slower flowing areas, including pools (Klaar et al., 2009).

Despite this extensive literature relating specifically to primary successional processes in Glacier Bay, no published research has yet investigated the linkages between the aquatic and riparian fauna across floodplains of different ages, nor has this question been addressed, to my knowledge, anywhere else in the world on the scale of multiple decades. The stream, and the organisms inhabiting it, should not be viewed in isolation from the riparian zone and a large body of literature exists describing the role of allochthonous subsidies to streams, particularly in terms of fish diets (e.g. Jellyman, 1979, Domermuth and Reed, 1980, Hubert and Rhodes, 1989, Garman, 1991, Edwards and Huryn, 1995, McDowall et al., 1996, Nakano et al., 1999, Baxter et al., 2005). The reciprocal nature of nutrient movement has also been studied, although again not in the context of community development over time: aquatic invertebrates, emerging as adults from the stream, provide a major food source for riparian consumers (e.g. Nakano et al., 1999, Kawaguchi and Nakano, 2001, Murakami and Nakano, 2002, Kawaguchi et al., 2003, Baxter et al., 2004). A conceptual diagram of these reciprocal subsidy flows between the stream and riparian zone is outlined in Figure 1.2. This research investigated the movement of subsidies between the stream and the riparian zone in Glacier Bay across a range of floodplains of different ages covering 200 years of glacial recession.

1.3 Aims and objectives of the research

The aim of this research was to explore the role of terrestrial invertebrates as subsidies to the stream environment across a chronosequence of increasing floodplain age. The reciprocal nature of subsidy movement between the stream and its riparian zone was also explored, along with aquatic food webs within each stream in order to provide a detailed understanding of the food sources of consumers in these environments. Two main methods were combined to explore the utilisation of resources in these systems: stomach contents analysis and stable isotope analysis. The merits of using both methods are discussed in the relevant chapters and synthesised into an assessment of the suitability of these methods, as well as demonstrating the importance of incorporating both in order to achieve a more detailed understanding of the system. The main objectives were:

- To characterise the terrestrial invertebrate assemblage on gravel bars on floodplains of different ages. Gravel bars were selected as similar sampling sites have been well studied in other areas outside of Glacier Bay, thereby allowing comparison;
- To explore the utilisation of resources linking the stream and riparian zone by terrestrial and aquatic consumers respectively, using two complementary methods (stomach contents analysis and stable isotopes);
- To examine how the aquatic food web structure changed over time, both in terms of the diets of juvenile salmonids (and thus the utilisation of terrestrial subsidies), and the diets of aquatic macroinvertebrates.

1.4 Thesis structure

This thesis was written as a series of extended papers, and therefore will contain some repeated information in the field methodologies. Figure 1.2 summarises how each chapter corresponds to the reciprocal movement of subsidies between the stream and the riparian zone.

The riparian terrestrial communities present in the selected study sites in Glacier Bay were examined in **Chapter 2**. Carabid beetles were identified to species and their morphology examined across the chronosequence in an effort to understand if successional processes have a role in structuring these communities.

Chapter 3 examined the role of the terrestrial communities as a food source for fish in the study streams. Stomach contents analysis was utilised to elucidate the diets of juvenile salmonids, and to determine what proportion was derived from terrestrial sources.

The aquatic component of the food web was explored in more detail in **Chapter 4**, expanding on the stomach contents analysis of juvenile salmonids in Chapter 3 by including the diets of the aquatic invertebrates. Food web structure was examined across a range of stream ages and was compared to studies in other regions.

Chapter 5 utilised stable isotope analyses to assess the reciprocal movement of resources across the stream and riparian interface. The importance of terrestrial subsidies to the stream was determined through calculation of the proportion of juvenile salmonid diets derived from allochthonous resources. Similarly, the diets of the dominant riparian consumers were examined to assess the input of aquatic sources to their diets.

The stable isotope data was further explored for the stream and riparian consumers in the context of the trophic niche in **Chapter 6**. Dietary breadths of consumers were compared between sites of different ages.

Chapter 7 summarised the research and highlighted future directions for both the utilisation of the methods outlined above, as well as research in Glacier Bay itself.

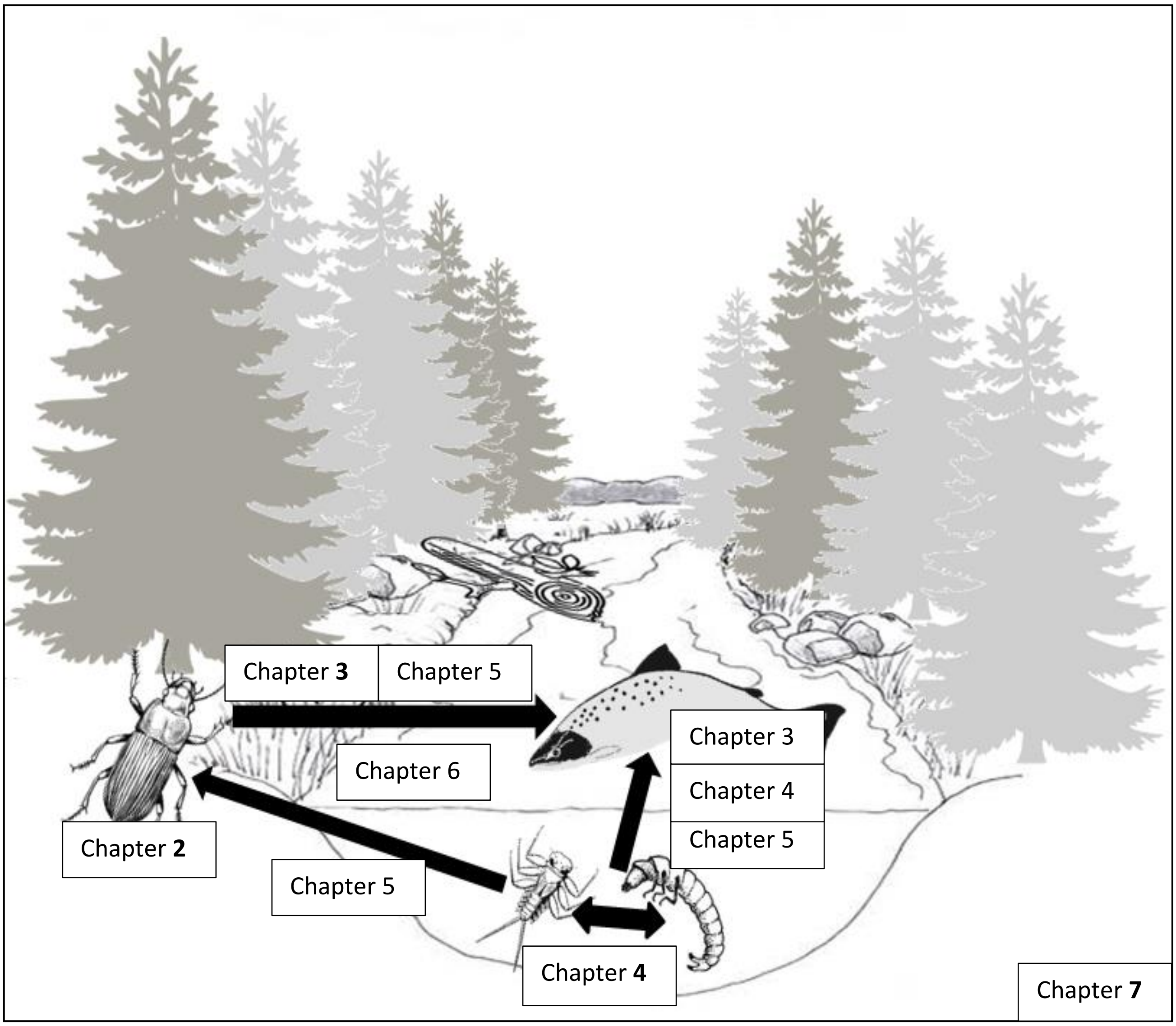

Figure 1.2: Conceptual diagram of the movement of reciprocal subsidies between the stream and the riparian zone. The relevant chapters associated with each part of the diagram are highlighted

1.5 Site photographs

Figure 1.3: Upper Muir Stream (<20 years old)

Figure 1.4: Wolf Point Creek (55 years old)

Figure 1.5: Nunatak Creek (70 years old)

Figure 1.6: Ice Valley Stream (130 years old)

Figure 1.7: Berg Bay South Stream (170 years old)

Figure 1.8: Rush Point Creek (200 years old)

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2

BEETLE COMMUNITIES ON FLOODPLAINS OF DIFFERENT AGES AND COMPLEXITY IN GLACIER BAY, ALASKA

Abstract

Carabid beetles were collected along the stream margins on floodplains of different ages between 20 and 200 years since deglaciation in Glacier Bay National Park and Preserve, southeast Alaska. This was the first attempt to sample carabid beetles on floodplains in this area, and one of only two studies to document the terrestrial invertebrate fauna of Glacier Bay. The carabid species collected were frequently characterised by high mobility (e.g. Nebria mannerheimi, N. metallica, N. sahlbergi, *and* Bembidion quadrifoveolatum), *but the assemblages also contained flightless taxa (e.g.* Trechus chalybeus). *Large flightless species with specialised modes of feeding* (Scaphinotus *sp.) were found only in the forest habitats at the oldest sites, suggesting that some species only colonize later in the chronosequence. A tolerance model of succession of carabid beetles in this habitat was supported, with many taxa persisting across the chronosequence.*

2.1 Introduction

Glacier Bay, in southeast Alaska, has been well studied in terms of successional processes following glacial retreat since the Little Ice Age. Glaciers reached their Little Ice Age maxima in the 18th century, and rapid glacial recession began between 1735 and 1785 (Miller, 1964), and still continues to the present day for a few glaciers. Pioneering early research in the area documented the primary succession of terrestrial vegetation (e.g. Cooper, 1923, Chapin et al., 1994), soil development (Crocker and Major, 1955), and more recently extensive research investigating the successional processes of freshwater communities has been undertaken (e.g. Milner, 1994, Milner et al., 2007, Milner et al., 2008). An early study of the colonisation of substrates in Muir Inlet by terrestrial invertebrates was carried out by Goldthwaite et al. (1966, see Part 5 by D.M. DeLong), which covered 0-90 years since glacier recession. However, no research from Glacier Bay has documented colonisation by terrestrial invertebrate taxa across a longer temporal gradient of 200 years following retreat of the Little Ice Age maxima. The focus of this study was the carabid (ground beetle) fauna of Glacier Bay in relation to changing floodplain characteristics as a function of site age since deglaciation.

The ground beetles (Coleoptera: Carabidae) are a large and diverse family (Lovei and Sunderland, 1996) which has been well studied on stream margins, particularly in Europe (e.g. Bates et al., 2005, 2007, Sadler and Bates, 2008, O'Callaghan et al., 2013) and in a successional context on glacier forelands (e.g. Kaufmann, 2001, Gobbi et al., 2007, 2011, Brambilla and Gobbi, 2014, Gobbi, 2014, Pizzolotto et al., 2014, Tampucci et al., 2015). However, outside of Europe, studies of terrestrial invertebrate succession on deglaciated areas are uncommon (Hodkinson et al., 2004). Although ground beetles occupy a variety of habitats, the focus of this study was on the communities associated with the riparian zone of streams, particularly gravel bars, on floodplains of different ages (time since deglaciation), where these beetles operate as highly mobile key predators. This was in order to support complementary studies regarding food web linkages between the stream and the riparian zone across floodplains of different ages and complexity.

The carabid taxa common on the recently exposed post-glacial sediments of alpine forelands are typically habitat generalists with good dispersal abilities, and wingless, poor dispersers are rare (Brambilla and Gobbi, 2014). In contrast, older substrates are typically more stable than younger substrates, and are characterised by taxa that are weak dispersers (i.e. have short wings) with narrow ecological ranges (i.e. more likely to be specialists; Pizzolotto, 2009). In a study including multiple families of terrestrial invertebrates, taxonomic richness increased with substrate age (Vater, 2012). Vater (2012) also reported an additive process of community change as site age increased, with few species lost as new species were added, reminiscent of the tolerance model of succession proposed by Connell and Slatyer (1977). This contrasts to the findings of Kaufmann (2001) and Gobbi et al. (2006) where taxonomic turnover occurred and species became extinct as new taxa colonised. In another study, Tampucci et al. (2015) found terrestrial invertebrate succession on glacier floodplains was characterised by two distinct assemblages: an early, pioneer community on recently deglaciated substrates and a later successional community, both of which overlap on substrates c.100-150 years since deglaciation. In addition to taxonomic turnover, it has been found that the size (recorded as mean individual biomass) of beetles increases with time since deglaciation (Gobbi, 2014): carabid beetles found on younger substrates tend to be smaller, and have good dispersal ability as compared to those on older substrates (Schwerk and Szyszko, 2007).

2.2 Study aim and research questions

The aim of this study was to characterise the assemblage of carabid beetles in riparian zones of floodplains of different ages in Glacier Bay National Park and Preserve, Alaska. Due to constraints on sampling effort (time and weather predominantly) the data set presented was limited and analysis was thus restricted to descriptive measures. Spiders were also collected using the same methods and were taken to the University of Wyoming for identification by a student there, however the results of the identification were never returned and therefore the spider fauna of the sites sampled could not be reported. The specific research questions addressed were:

- Does species turnover occur between floodplains of different ages in Glacier Bay?
- Does the highest species richness occur at mid-aged sites? It was anticipated that if taxonomic turnover occurred, mid-aged sites would contain a mixture of early and later colonising species;
- Are flightless, less mobile taxa only present at older, more stable sites? It was anticipated that beetles without wings would have a low dispersal capacity and therefore be absent at the youngest sites;
- Does beetle body size (at the level of individual and community) increase with site age as has been found on other glacial substrates?

Table 2.1: Stream floodplains sampled in Glacier Bay, age indicates the length of time the stream mouths have been ice-free

Stream	Code	Age (years)	Longitude	Latitude	Dominant riparian vegetation
Upper Muir 1*	UM*	<20	59°04’43.1”	136°19’10.8”	*Dryas* sp.
Upper Muir 2*	UM*	<20	59°04’02.5”	136°17’09.9”	*Dryas* sp.
Wolf Point Creek	WPC	55	58°59’48.3”	136°10’18.1”	Alder, some cottonwoods
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Ice Valley Stream	IVS	130	58°49’10.9”	136°9’49.6”	Alder, spruce
Berg Bay South Stream**	BB	170	58°30’17.5”	136°14’0.62”	Alder, spruce, cottonwood
Rush Point Creek	RPC	200	58°28’11.2”	136°06’08.5”	Spruce

*Samples from Upper Muir 1 and 2 were combined as one site for the analysis due to low sample number
**Berg Bay South Stream hereafter referred to as Berg Bay

2.3 Methodology

Glacier Bay National Park and Preserve is situated in southeast Alaska (Figure 2.1). The area is a unique site for studying ecosystem development following well documented and rapid glacial retreat (Miller, 1964, Milner et al., 2007, Milner and Robertson, 2010). Spanning an area of 11,000km^2, it is a deglaciated landscape over 220 years old (Milner and Robertson, 2010), surrounded by mountains rising to 5000m above sea level and including many kilometres of shoreline, exposed bedrock, unconsolidated glacial sediments and temperate rainforest (Milner et al., 2007). The climate of Glacier Bay is temperate maritime, with mean monthly temperatures ranging from -3°C to 13°C and a mean annual precipitation of 1400mm (Milner and Robertson, 2010).

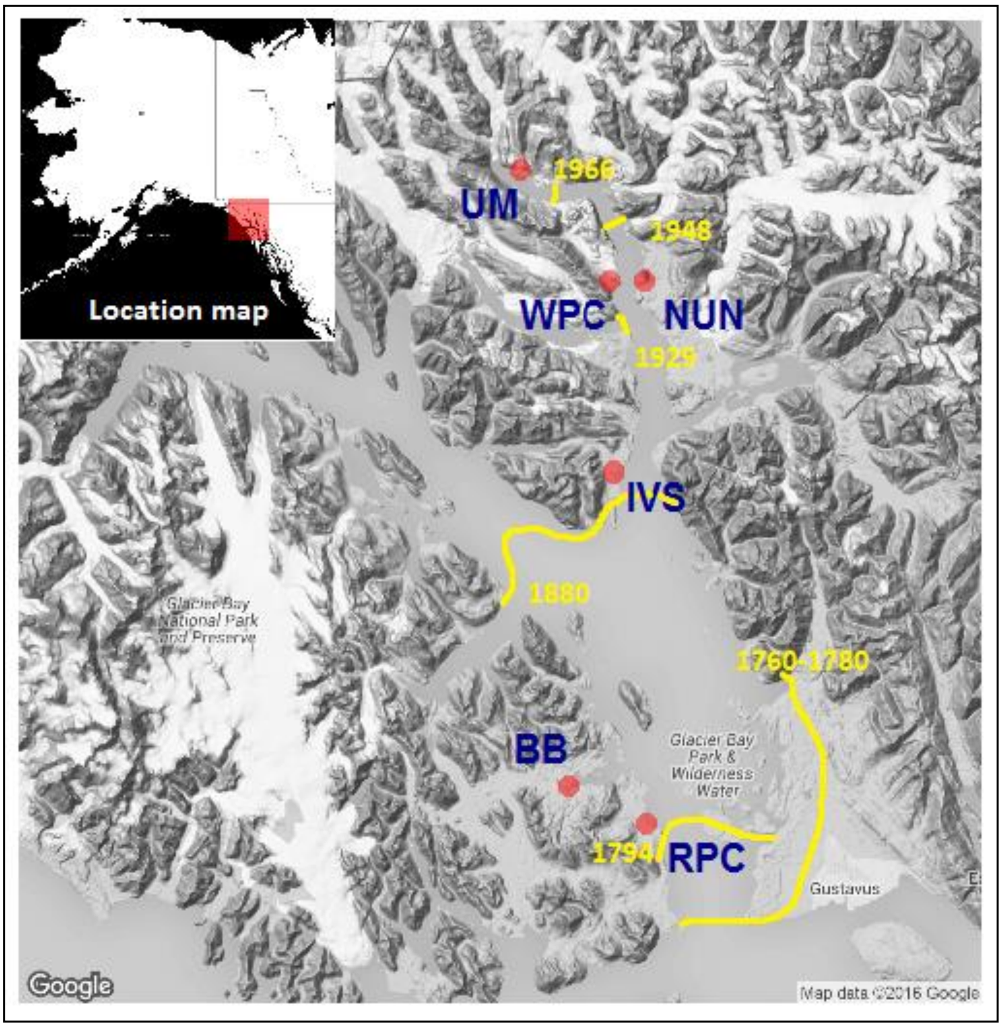

Figure 2.1: Location of field sites in Glacier Bay National Park and Preserve. Sites codes correspond to names in Table 2.1. Approximate position of glacier termini indicated with dates

Table 2.2: Catch per unit effort (CPUE) and number of sampling events (n) for each habitat at each site. Traps at the edge of the forest were frequently empty. A total of 280 individual beetles were collected by pitfall trapping

Site	Habitat	Mean CPUE	n	Mean Taxon Richness
WPC	Forest	1.35	4	2.25
WPC	Riparian	2.67	3	4.00
WPC	Edge of forest	0.00	1	0
NUN	Forest	0.87	3	2.33
NUN	Riparian	2.95	4	3.25
NUN	Edge of forest	0.20	1	1.00
IVS	Forest	0.93	3	1.67
IVS	Riparian	1.40	3	3.00
IVS	Edge of forest	1.20	1	2.00
BB	Forest	0.40	2	1.00
BB	Riparian	2.27	3	4.67
BB	Edge of forest	0.00	1	0
RPC	Forest	0.60	3	1.67
RPC	Riparian	3.20	3	3.67
RPC	Edge of forest	0.00	1	0

2.3.1 Sampling design

Five streams were sampled during each of the summers of 2013 and 2014 (Figure 2.1; Table 2.1). In 2013, streams were sampled up to 3 times, but inclement weather conditions in 2014 restricted pitfall sampling to just one overnight sampling at each site. Streams were selected to represent a range of floodplain ages. For each stream, one reach (c.10m long) was selected, approximately 0.75km from the stream mouth (*sensu* Milner et al., 2008). Each reach consisted of an unvegetated gravel bank, with riparian forest behind. Two streams, in addition to the principal five streams, were sampled in Upper Muir Inlet once in 2014. Access to this part of Glacier Bay by motorized boat was restricted for part of the field season, thereby resulting in the single field visit. These data from the two new sites were limited, but included for comparison.

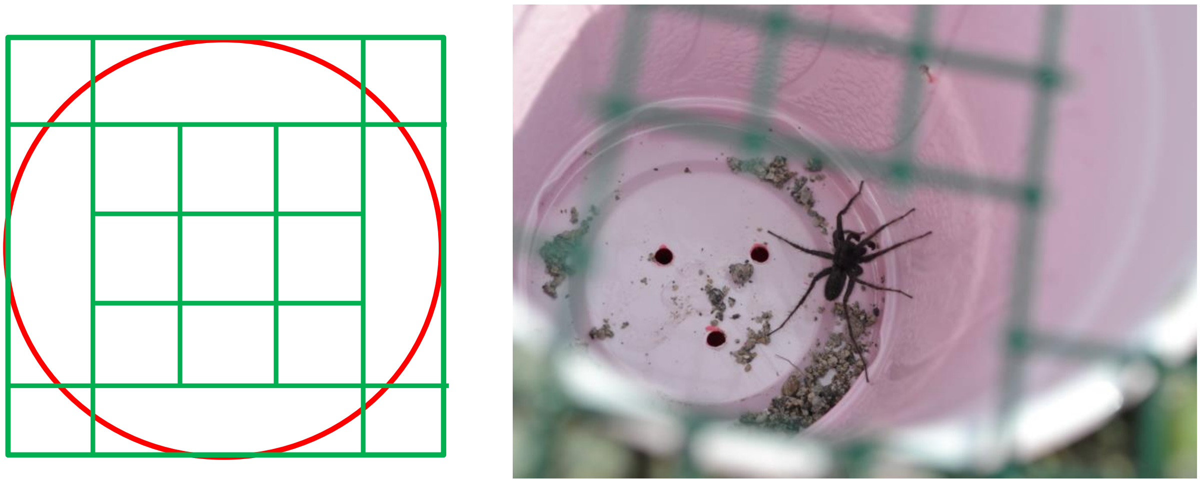

Figure 2.2: Schematic of pitfall trap mesh design (left) and photograph of pitfall trap with mesh (right)

Terrestrial invertebrates were collected at each site using pitfall traps: 500ml plastic cups with a 9cm diameter (*sensu* Woodcock, 2008, Hancock and Legg, 2012). Traps were covered by 2cm wire mesh to prevent entry by small mammals, particularly shrews. Holes at the edge of the traps were enlarged to rectangles 3x2cm to increase access to the traps for the beetles (Figure 2.2). Traps were placed on the edge of the stream channel (<50cm from the stream edge) and in the riparian forest, approximately 20m from the stream edge, depending on the size of the gravel bars. In 2014 traps were also placed on the edge of the gravel bar, close to where the riparian forest began. Traps were filled to a depth of 2cm with ethylene glycol and left for 24 hours. Five traps were placed in a line at each distance, separated by 50cm and parallel to the stream channel. Contents at each distance from the stream were pooled to reduce pseudoreplication (*sensu* Fuller et al., 2008). Heavy rainfall, particularly in 2014, led to flooding and subsequent loss of traps at some sites, and animal disturbance meant some other traps were destroyed; therefore successful trapping events were fewer than the number of site visits. Catch per unit effort (CPUE), and number of successful trapping events (n) are shown in Table 2.2. Ethylene glycol was replaced with industrial methylated spirit (IMS) on return to the laboratory to preserve samples until identification. The very youngest sites in Upper Muir could only be visited on one occasion in 2014 and beetles were therefore collected by hand searching.

2.3.2 Data analysis

Carabid beetles were identified to species using a binocular dissecting microscope with reference to Lindroth (1969). Sites where <3 individuals were collected were excluded from further analysis, which included all samples from the Upper Muir streams. Carabid morphology was investigated for the most common species to evaluate the relationships between site age and body, wing, and leg length. Beetle total body length (tip of the labrum to the apex of the elytra; Gobbi, 2014), wing, and hind leg length were measured using an eyepiece graticule. Beetle morphometric measurements were normally distributed and were therefore tested for significant differences using ANOVA and Tukey Honest Significant Difference post-hoc tests in the open source statistical software package R (build v3.1.1; R Core Team, 2014).

In order to calculate mean individual biomass for beetle assemblages, previously calculated length-biomass relationships were used by Schwerk and Szyszko (2007) and Gobbi (2014). However, these have not been applied to beetles in North America, and therefore were not applied to these data. Instead, mean individual length was calculated for the assemblage, and it was assumed that as the calculations by Schwerk and Szyszko (2007) and Gobbi (2014) were based on a linear relationship, the same trends would be evident using mean individual length rather than biomass.

2.4 Results

Seventeen ground beetle species from eight genera were identified from Glacier Bay. Only three species were found at all sites (Table 2.3), namely *Nebria mannerheimi, N. sahlbergi,* and *Bembidion quadrifoveolatum*. *Nebria* sp. and *Diplous aterrimus* were almost exclusively gravel bar specialists, whereas *Scaphinotus* sp. and *Calathus advena* were forest specialists. Taxonomic richness was similar at all sites >55 years in age (Table 2.3). The most species poor sites were the young Upper Muir streams, with only three taxa, but this could be an artefact of limited sampling at these sites.

The carabid beetles collected could be separated into three size class groupings (based on size distributions in Figure S1 in the Appendix): small (≤5.5mm), medium (>5.5 mm and <13 mm) and large (≥13mm). The largest size class of beetles were only collected at the oldest sites across the three habitats sampled. Rush Point Creek was characterised by a high relative abundance of small beetles, as compared to the other size classes present, whereas at all other sites medium size was the most abundant. Considering the different habitats, the largest beetles were present in the riparian forest at the oldest sites, and the relative abundance of large individuals (≥13mm in length) increased with site age, whereas the relative abundance of small and medium individuals was variable (<13mm; Figure 2.3). The gravel bar assemblage was dominated by the medium size-class at the younger sites, but at the oldest site, the relative abundance of small carabids (≤5.5mm) exceeded that of the medium sized individuals for both gravel bar and forest habitats.

Table 2.3: Summary of ground beetle taxa collected at sites of different ages in Glacier Bay, presence of a species at a site is indicated by shading. 'G' indicates species found only on the gravel bars, 'EF' indicates species found only at the edge of the riparian forest, and 'F' indicates species found only in the riparian forest. No riparian forest was present at the Upper Muir sites. * Indicates rare taxa (<3 individuals collected)

Floodplain Age (years)	**Genus**	*Nebria*				*Bembidion*					*Pterostichus*		*Platidiolus*	*Trechus*	*Diplous*	*Calathus*	*Scaphinotus*		
	species	*mannerheimi*	*sahlbergi*	*metallica*	*acuta*	*planiusculum*	*quadrifoveolatum*	*platynoides*	*viator**	*rufinum**	*riparius*	*pinguedineus*	*vandykei**	*chalybeus*	*aterrimus*	*advena*	*marginatus*	*angusticollis*	**Richness**
20	**UM**	G	G			G	G												**4**
55	**WPC**	G	G	▨			▨				▨			▨	G	F			**8**
70	**NUN**	▨	G	G	G		G				▨			▨		F			**8**
130	**IVS**	G	G	G			F	G	EF		F	▨					F		**9**
170	**BB**	G	G				▨						G	F	G			F	**7**
200	**RPC**	G	G			▨	▨			F				F	G			F	**8**

The mean individual body length of the whole beetle assemblage decreased with site age for the gravel bar taxa, but increased for those collected from the forest (Figure 2.4), although the variability was high. The most common species were collected from the gravel bars and body lengths of these were analysed separately (Figure 2.5, Table 2.4). The smallest individuals of *N. mannerheimi* were collected from the three mid-aged sites. *N. sahlbergi* did not significantly differ in body length (*p*>0.05) between sites, although body length at Wolf Point Creek was generally larger that at the older sites. *B. quadrifoveolatum* were variable in body length, but were significantly larger at Wolf Point Creek than at the two oldest sites (*p*<0.05). With the exception of *N. mannerheimi* at Rush Point Creek, there was a general (although non-significant) trend of decreasing carabid body length with site age (Figure 2.5, Table 2.4). Although sample size was small (n<3), body length of *B. quadrifoveolatum*, *N. mannerheimi*, and *N. sahlbergi* at the Upper Muir sites were 3.54, 8.93, and 8.16-8.93mm respectively, which was smaller than almost all individuals at the older sites.

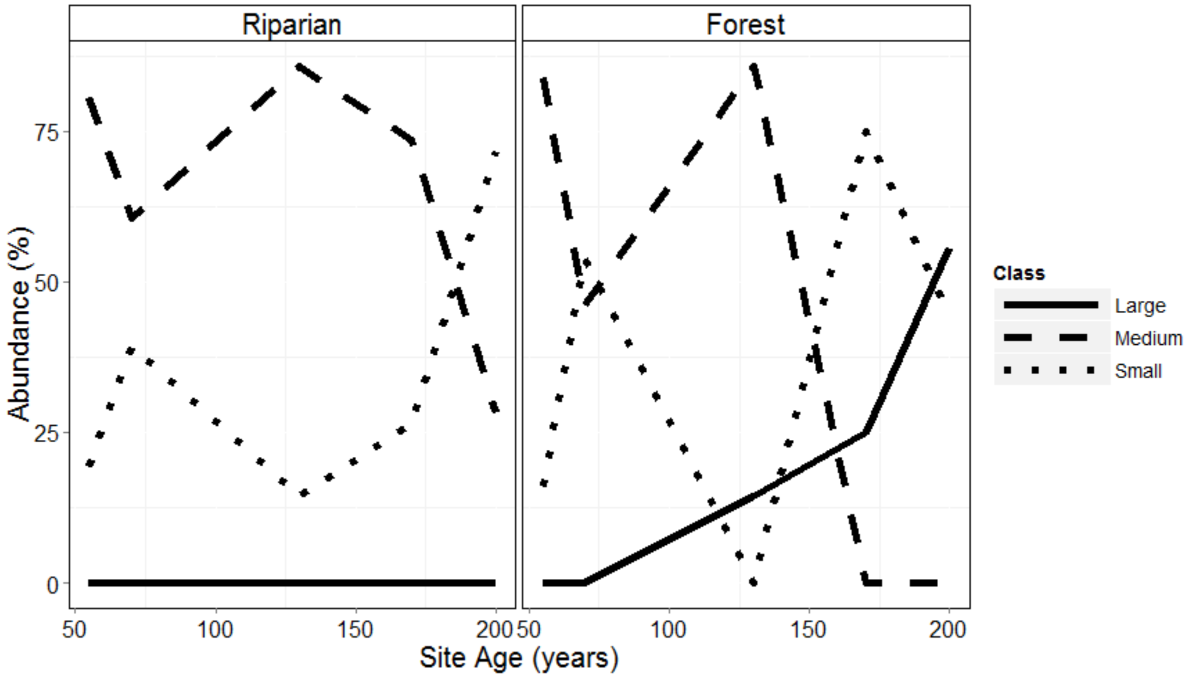

Figure 2.3: Relative abundance (%) of carabid assemblage of each size class across sites of different ages for two habitat types

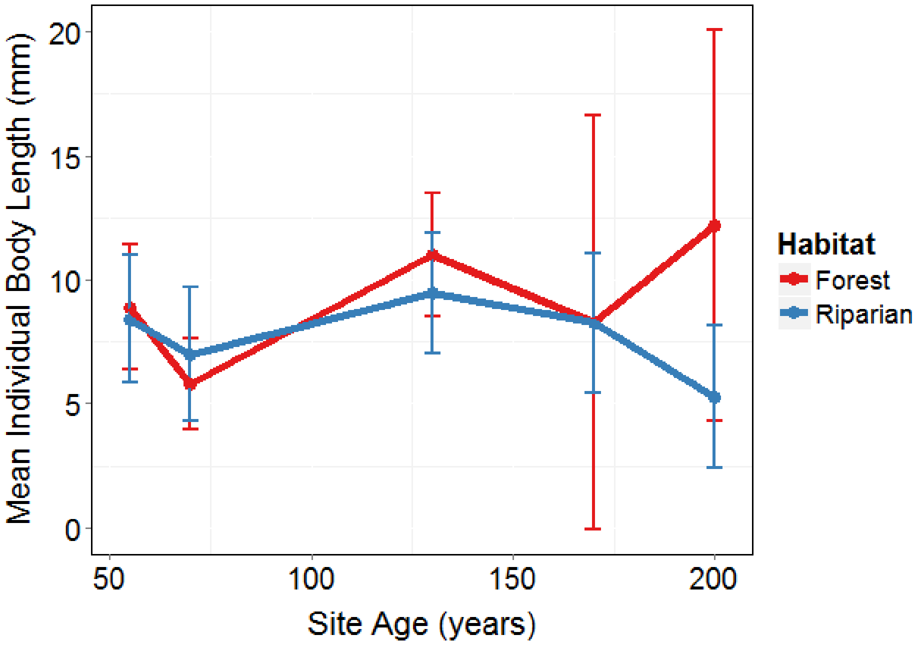

Figure 2.4: Mean individual body length of carabid beetles at each site. Error bars indicate one standard deviation about the mean

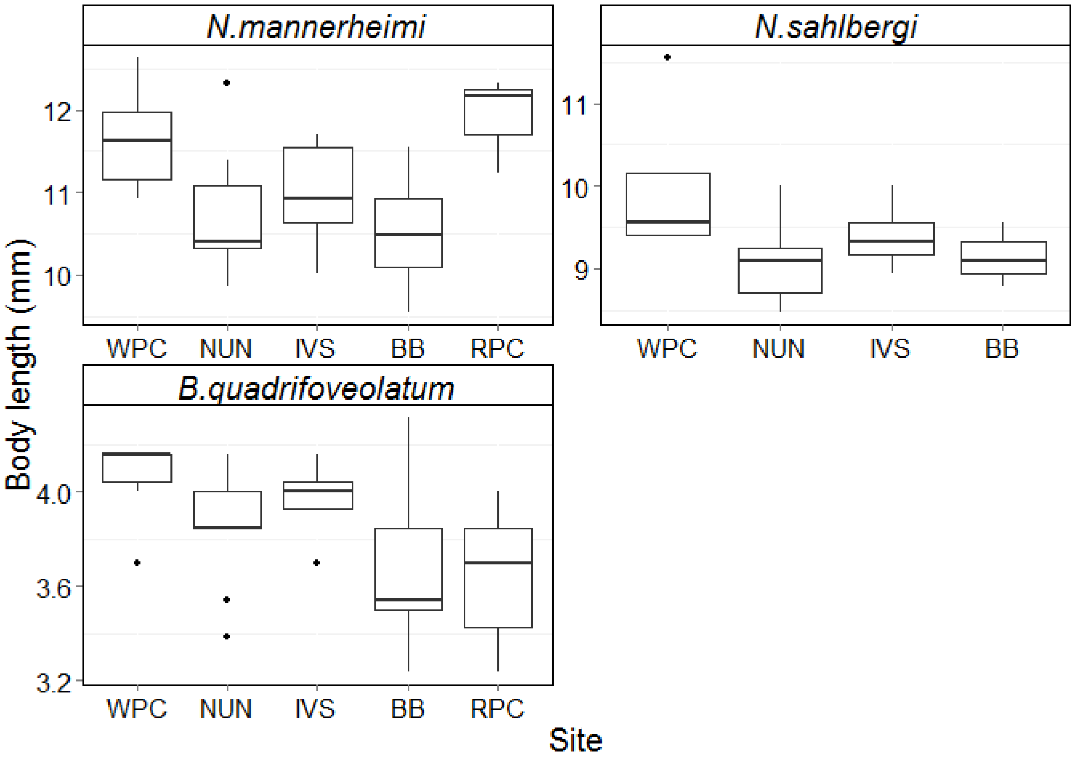

Figure 2.5: Body length of the most common carabid species (significant differences are indicated in Table 2.4)

Table 2.4: Significant differences (p<0.05, indicated by *) in body lengths of common carabid beetles at sites of different ages, as shown in Figure 2.5. Top half of the table corresponds to *N. mannerheimi*, bottom half to *B. quadrifoveolatum*. There were no significant differences (p>0.05) for *N. sahlbergi*

		N. mannerheimi				
	Site	**WPC**	**NUN**	**IVS**	**BB**	**RPC**
B. quadrifoveolatum	**WPC**		*		*	
	NUN					*
	IVS					
	BB	*				*
	RPC	*				

Most beetles collected had wing to body length ratios of around 1 (Figure 2.6), suggesting these individuals have the ability to fly, although none were observed to do so in the field. A few beetles had very short wings (wing to body length ratio <0.5), while brachypterous (flightless) beetles with no wings (wing to body length ratio 0) were collected at all sites except Upper Muir. Individuals of the large, flightless genus *Scaphinotus* were only collected in forested sites at the three oldest streams, whereas the other brachypterous taxa were not confined to the forest and were found on the gravel bars. Only *Trechus chalybeus* was found to be dimorphic, with both winged and non-winged individuals collected at Nunatak Creek, although it was brachypterous at all other sites. *T. chalybeus* differed from the other brachypterous species collected in that individuals had wings present, but they were typically far shorter than the body length, and even when fully extended, they did not exceed the length of one elytrum.

The ratio of wing length to body size did not differ significantly between sites for any common beetle species, apart from *B. quadrifoveolatum* at Ice Valley and Rush Point Creek (*p*<0.05, Figure 2.7). Similarly, the ratio of hind leg length to body length did not differ significantly between sites for all common carabid species (*p*>0.05, Figure 2.8).

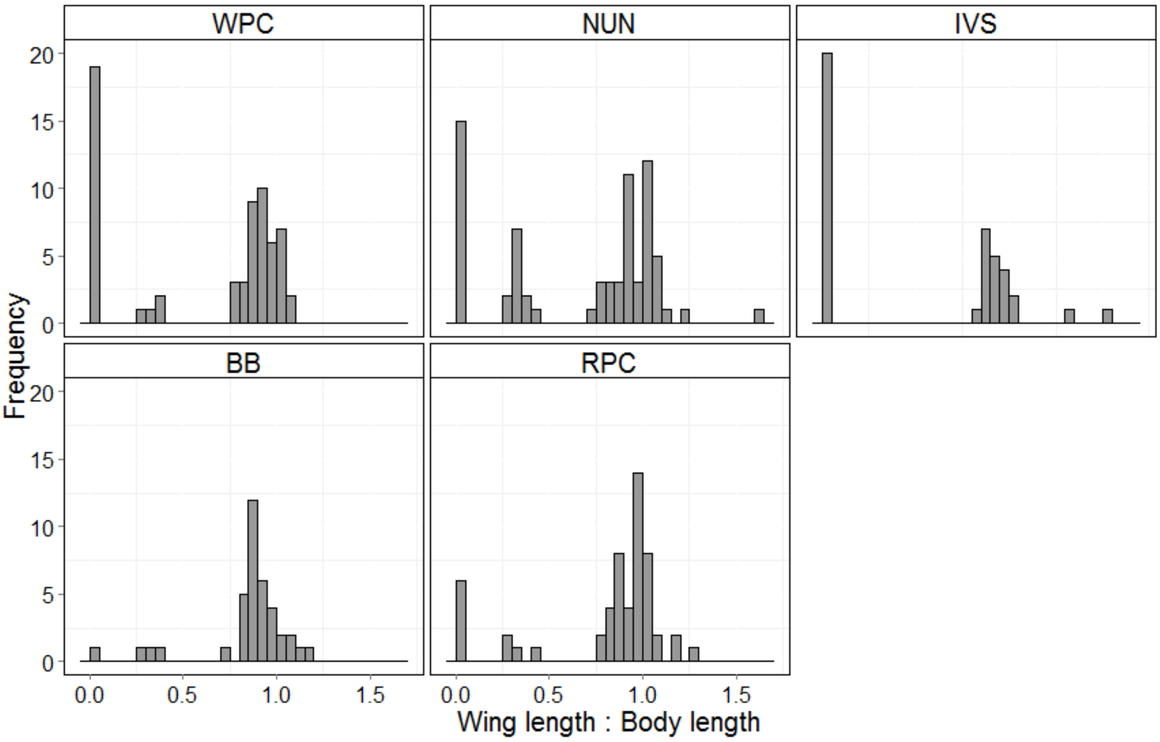

Figure 2.6: Ratio of wing length to body length in carabid beetles at sites of different ages. Few beetles were collected from the Upper Muir streams and therefore these were not included here

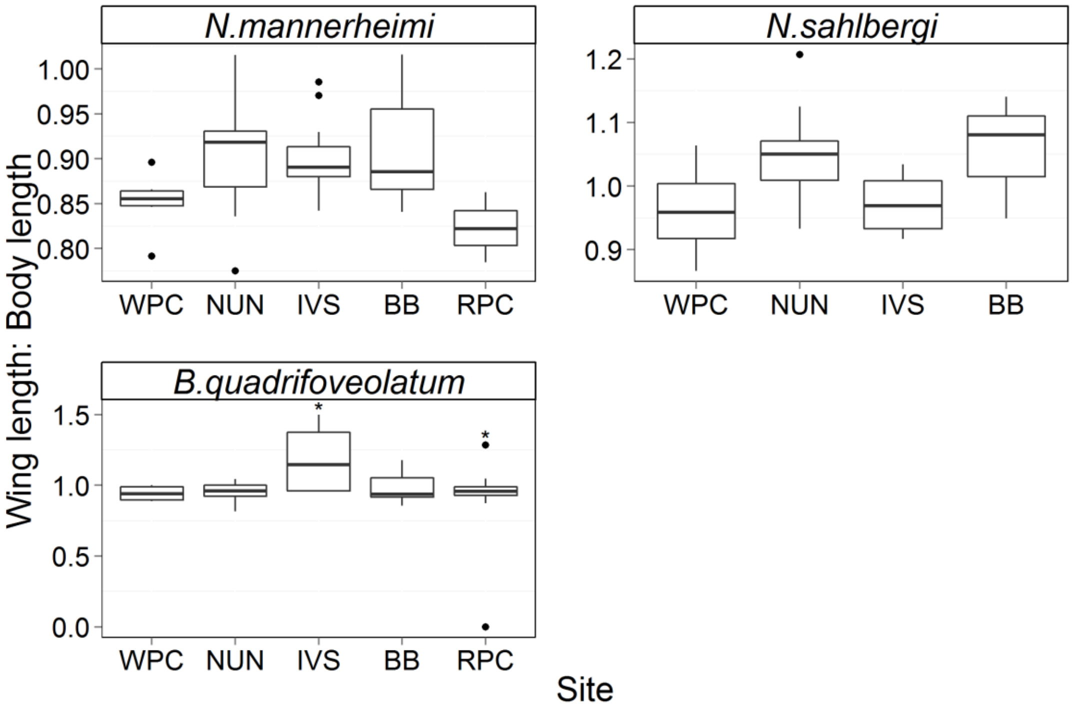

Figure 2.7: ratio of wing length to body length for the most common carabid species. Significant differences (*P*<0.05) occurred only for *B. quadrifoveolatum* and are indicated by *

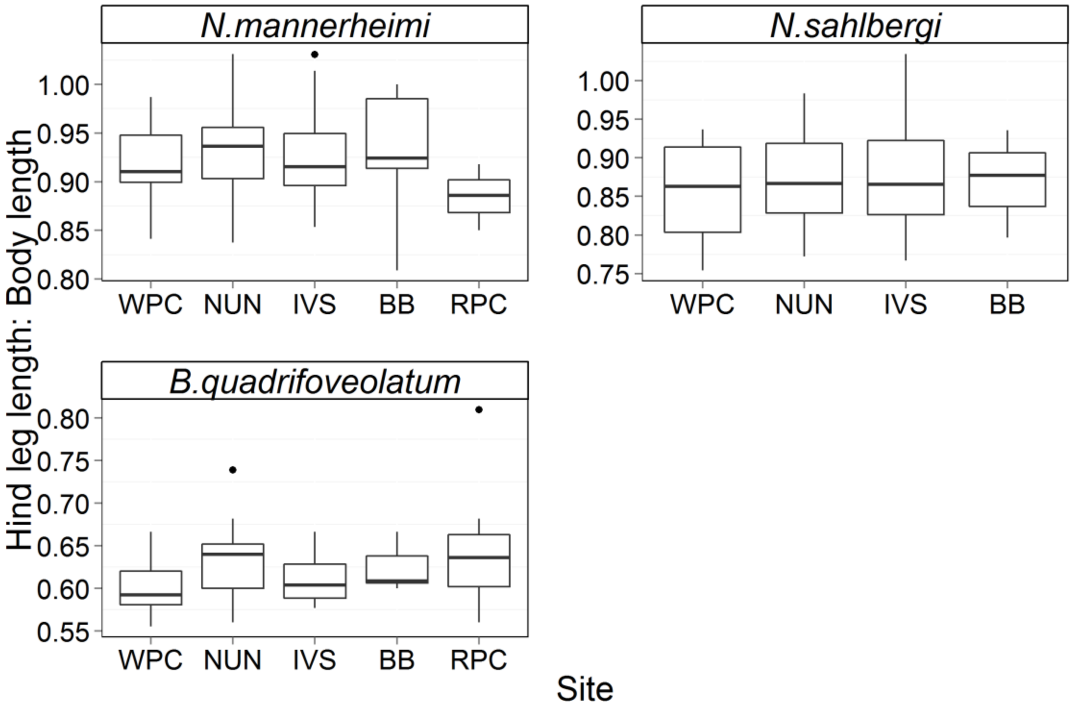

Figure 2.8: ratio of hind leg length to body length for the most common carabid species

2.5 Discussion

This study has provided a first assessment of the carabid beetle fauna across floodplains of different ages in Glacier Bay National Park and Preserve. Floodplain age had some clear effects on the carabid beetle fauna and their characteristics along the margins of streams in Glacier Bay, although its influence was limited. Large, flightless, specialist beetles (*Scaphinotus* spp., specialised to feed on snails; Lindroth, 1969) were only found in forests of the oldest floodplains, whereas the generalist, medium-sized, and highly mobile *Nebria* spp. were found at all sites across the chronosequence. *Nebria* are typical of early successional stages on deglaciated floodplains, and are adapted to unstable conditions (Kaufmann, 2001). The relative instability of the gravel bars allows such generalist taxa to persist across the chronosequence. *Bembidion* spp. were also present at all the sites sampled in Glacier Bay, and have been found to be rapid colonisers in other studies: e.g. on the volcanic plains of Mount St. Helens, various species of *Bembidion* colonised bare substrates within 5 years of the eruption (Sugg and Edwards, 1998).

The only other published study of terrestrial invertebrates in Glacier Bay (Goldthwaite et al., 1966) documented carabid beetles at sites of different ages. The sites selected by Goldthwaite et al. (1966) were not described in detail, but appeared not to be gravel bar habitats on stream margins, and photographs of some of the sampling sites indicate forests were not sampled. Despite the probable differences in habitat choice between the two studies, some species were similar, namely: *Nebria metallica*, *N. sahlbergi*, *Trechus chalybeus*, and *Calathus advena* (listed in Goldthwaite et al. (1966) as *Pristodactyla*, although this name is now classed as invalid and the species is part of *Calathus* (Bousquet, 2012)).

Goldthwaite et al. (1966) also found some similar taxa within the same genera as those collected in this study, namely: *Bembidion complanulum* (which is in the same group (*incertum*) as *B. quadrifoveolatum,* and *B. viator*), and *Pterostichus adstrictus* (listed in Goldthwaite et al. (1966) as *Bothriopterus*, which is in fact a subgroup of *Pterostichus* (Lindroth, 1969)). All of the species listed in Goldthwaite et al. (1966) as occurring on substrates 75-90 years old were found at Nunatak Creek (c. 70 years old) in this study, with the exception of *Elaphrus ruscarius*. Goldthwaite et al. (1966) found fewer taxa on substrates 45-55 years old as compared to Wolf Point Creek (c. 55 years old), which could be as a consequence of sampling different habitat types. The youngest sites studied by Goldthwaite et al. (1966) are analogous to the Upper Muir sites, but unlike this study, no carabid beetles were found. The lack of *Nebria* spp. at sites <45 years old and *N. metallica* at sites <75 years old in the study by Goldthwaite et al. (1966) was surprising as these were observed to be abundant at young sites in this study. This difference may be linked to the different habitats surveyed by Goldthwaite et al. (1966), as *Nebria* are generalist taxa adapted to unstable conditions (Kaufmann, 2001), such as stream margins.

Beetle morphology was investigated to determine whether body size increased with site age, and also whether beetles exhibited the characteristics of high mobility, as might be expected from individuals inhabiting unstable habitats (such as gravel bars) on relatively young floodplains. Body length of the three most common carabid species generally decreased with site age, contrary to findings by other researchers (Schwerk and Szyszko, 2007, Gobbi, 2014) who found larger beetles on older substrates. Body size can be highly variable (Booij et al., 1994) and sample size was small in this study. Most carabid taxa possessed wings which extended beyond the tip of the elytra, suggesting flight. Flight capability is advantageous for individuals on gravel bars to avoid flooding, and it would also allow species to colonise substrates recently exposed: no brachypterous taxa were collected at the very youngest sites. However, flightless taxa were present at all sites over 55 years old, suggesting past a certain floodplain age flightlessness is not a limit to colonisation, or that the energetically costly development of wings is quickly lost once a site is reached by the founding population.

2.6 Conclusion

This study shows that carabid beetle colonisation on floodplains of different ages follows a tolerance model of succession whereby new species colonise, but most persist throughout the chronosequence. The taxa present are similar to other studies of early succession, but differ in their morphology from other glacier forelands in that body size tends to decrease with site age and flightlessness is present across much of the chronosequence. Despite a large volume of work in the region on the successional processes of plants and river systems, further work on the carabid fauna in Glacier Bay is clearly necessary. The following chapters outline the important role that these terrestrial organisms have as nutrient subsidies to stream systems, as well as consumers of emerging adult aquatic insects, which emphasises the need to better quantify these communities. Further work should also incorporate the other orders of terrestrial invertebrates: pitfall traps collected spiders, rove beetles, and click beetles as well as the carabid beetles.

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3

THE ROLE OF TERRESTRIAL INVERTEBRATES IN THE DIETS OF JUVENILE COHO SALMON AND DOLLY VARDEN WITHIN CATCHMENTS OF DIFFERENT AGES

Abstract

Riparian inputs to streams, and their utilisation by fish as a nutrient subsidy, has been well documented in studies around the world. However, no study has yet addressed whether this dietary subsidy differs between streams of different ages and catchment vegetation. This study examined the stomach contents of juvenile coho and Dolly Varden in five streams ranging from 55 to 200 years old in Glacier Bay, Alaska. Results indicated that habitat complexity plays a greater role in determining the diet of juvenile salmonids than site age alone. Mid-aged streams, with a complex physical habitat and the presence of coarse woody debris, support juvenile salmonids with diverse diets, including a higher proportion of terrestrial invertebrates, as compared to younger and older streams.

3.1 Introduction

Riparian influxes of organic material are important to stream systems as an additional energy source for in-stream production. Streams typically lie at low points in the landscape (Leroux and Loreau, 2008), therefore, as nutrients flow downwards, these open systems (Fisher and Likens, 1973) become recipients of allochthonous resources. The movement of terrestrial nutrients into freshwater systems and their utilisation by fish has been well documented (e.g. Jellyman, 1979, Domermuth and Reed, 1980, Hubert and Rhodes, 1989, Garman, 1991, Edwards and Huryn, 1995, McDowall et al., 1996, Nakano et al., 1999, Baxter et al., 2005, O'Gorman et al., 2012). However, despite several studies measuring seasonal fluxes of resources (e.g. Cloe III and Garman, 1996, Dineen et al., 2007a), no studies have yet addressed this at longer, multi-decadal timescales. Glacier Bay in southeast Alaska provides a unique opportunity for such a study due to its well-documented history of glacial recession allowing for the study of primary successional processes across a timescale of c.200 years using space-for-time substitution.

A significant proportion of terrestrial nutrients entering streams originate from the riparian zone. This allochthonous energy flux can include plant material as well as terrestrial invertebrates. Terrestrial invertebrates are an important food source for many juvenile fish due to their relatively large size and high visibility on the water surface when silhouetted against incoming light (Nakano et al., 2001), and their high calorific value compared to aquatic invertebrates (Cummins and Wuycheck, 1971). A wide range of terrestrial invertebrates may enter the stream and be utilised by fish, such as beetles, spiders, true bugs, wasps, and various flies (Jellyman, 1979, Hubert and Rhodes, 1989, Garman, 1991, McDowall et al., 1996).

The input of these terrestrial invertebrates may be influenced by the vegetation and successional stage of the riparian zone. Riparian forests contribute more terrestrial prey to streams than open grassland (Dineen et al., 2007b), and Wipfli (1997) found that young, alder dominated streams supplied a higher input of terrestrial invertebrates than older, spruce dominated streams. Similarly, Syrjänen et al. (2011) found that deciduous and mixed forests both contributed more terrestrial invertebrates to the diets of salmonids than coniferous forests, and Allan et al. (2003) found that alder stems support more invertebrates than spruce and hemlock in southeast Alaskan streams.

In Glacier Bay, riparian vegetation develops as time since deglaciation increases, with a change from a black crust comprised of lichens, cyanobacteria, and bryophytes, alongside small shrubs, to thickets of alder (*Alnus* sp.) and eventually, at around 150+ years post-retreat, a mixed forest of western hemlock (*Tsuga* sp.) and Sitka spruce (*Picea sitchensis*) exists along the streams (Milner et al., 2007). It may, therefore, be anticipated that younger, alder dominated streams would supply greater inputs of terrestrial resources than older streams (Wipfli, 1997). However, as a consequence of the forest development, older streams are characterised by larger and more complex instream woody debris accumulations than younger streams (Klaar et al., 2011), which could provide a source of obligate terrestrial invertebrates associated with wood. Mid-aged sites in Glacier Bay have also been found to have greater habitat complexity than both younger and older streams (Klaar et al., 2009) and as more complex (heterogeneous) habitats often support more diverse and abundant invertebrate fauna, these mid-aged streams may provide juvenile fish with a more varied diet.

In streams where more than one fish species are present, resources can be partitioned between the species to prevent interspecific competition (Nakano and Kaeriyama, 1995). Two juvenile salmonids were present in the study streams in Glacier Bay: coho salmon (*Onchorrhynchus kisutch*) and Dolly Varden char (*Salvelinus malma*). Dolly Varden are bottom dwellers feeding on benthic organisms (Eberle and Stanford, 2010) whereas juvenile coho salmon are typically distributed at mid-depths and feed on surface invertebrates (Nakano and Kaeriyama, 1995), such as terrestrial invertebrates which have entered the stream. This allows for the comparison of different feeding modes (preference for terrestrial or aquatic prey) between these two species. The utilisation of terrestrial resources would be expected to differ between the two salmonid species, with coho consuming more terrestrial invertebrates than Dolly Varden.

Table 3.1: Stream floodplains sampled in Glacier Bay, age indicates the length of time the stream mouths have been ice-free

Stream	**Code**	**Age (years)**	**Longitude**	**Latitude**	**Dominant riparian vegetation**
Wolf Point Creek	WPC	55	58°59’48.3”	136°10’18.1”	Alder, some cottonwoods
Nunatak Creek	NUN	70	58°58’40.5”	136°5’41.2”	Alder, cottonwood
Ice Valley Stream	IVS	130	58°49’10.9”	136°9’49.6”	Alder, spruce
Berg Bay South Stream*	BB	170	58°30’17.5”	136°14’0.62”	Alder, spruce, cottonwood
Rush Point Creek	RPC	200	58°28’11.2”	136°06’08.5”	Spruce

*Berg Bay South Stream hereafter referred to as Berg Bay

3.2 Study aim and research questions

The aim of this study was to determine whether the proportion of allochthonous resources (terrestrial invertebrates) to fish diets changed along a successional gradient of c.200 years. Space-for-time substitution across a glacial recession chronosequence enabled the comparison of streams on a multi-decadal time-scale not previously undertaken for subsidy studies. The specific research questions addressed were:

- Would terrestrial resource utilisation by juvenile coho and Dolly Varden be greatest at mid- to late- successional streams where riparian habitats are most complex?
- Would juvenile coho salmon source a larger proportion of their diet from terrestrial sources compared to benthic-feeding juvenile Dolly Varden? The diets of juvenile coho and Dolly Varden were hypothesised to be dissimilar due to their different feeding modes.

3.3 Methodology

Glacier Bay National Park and Preserve is situated in southeast Alaska. The area is a unique site for studying ecosystem development following well documented and rapid glacial retreat (Miller, 1964, Milner et al., 2007, Milner and Robertson, 2010). Spanning an area of 11,000km^2, it is a deglaciated landscape over 220 years old (Milner and Robertson, 2010), surrounded by mountains rising to 5000m above sea level and including many kilometres of shoreline, exposed bedrock, unconsolidated glacial sediments, and temperate rainforest (Milner et al., 2007). The last glacial maximum occurred around 1700 and glacial recession began (with some regional re-advances) between 1735 and 1785 (Miller, 1964; Figure 3.1).

The climate of Glacier Bay is temperate maritime, with mean monthly temperatures ranging from -3°C to 13°C and a mean annual precipitation of 1400mm (Milner and Robertson, 2010).

3.3.1 Sampling design

Five streams were sampled up to four times from June-August in 2013 and 2014 (Figure 3.1; Table 3. 1) to represent a range of floodplain ages. For each stream, one reach (c.10m long) was selected, approximately 0.75km from the stream mouth (*sensu* Milner et al., 2008). Each reach consisted of a non-meandering stretch of the stream, and an unvegetated gravel bank, with riparian forest behind.

3.3.2 Sample collection

Juvenile salmonids were collected at each stream using minnow traps, baited with salmon eggs (pre-soaked in Betadyne iodine solution) held in a perforated plastic ‘Kinder egg’ capsule. Sites were fished for 90 minutes (Bryant, 2000). Three traps were placed in pools and backwaters of the main stream channel in 2013 and in 2014 ten traps were placed in the stream. Permit restrictions limited the sample to a maximum of five individuals of each species per stream in 2013 and up to twenty in 2014. These fish were taken for isotopic diet analysis, and their stomachs were removed for gut contents analysis. Additional stomach content samples were collected in 2014 by gut flushing: a blunt ended syringe filled with stream water was carefully inserted into the mouth of an individual fish and the stomach contents were flushed into a sample bag (Meehan and Miller, 1978). Fish were allowed to recover in a tray of stream water before being released into the areas where they were captured. No mortalities occurred during stomach flushing.

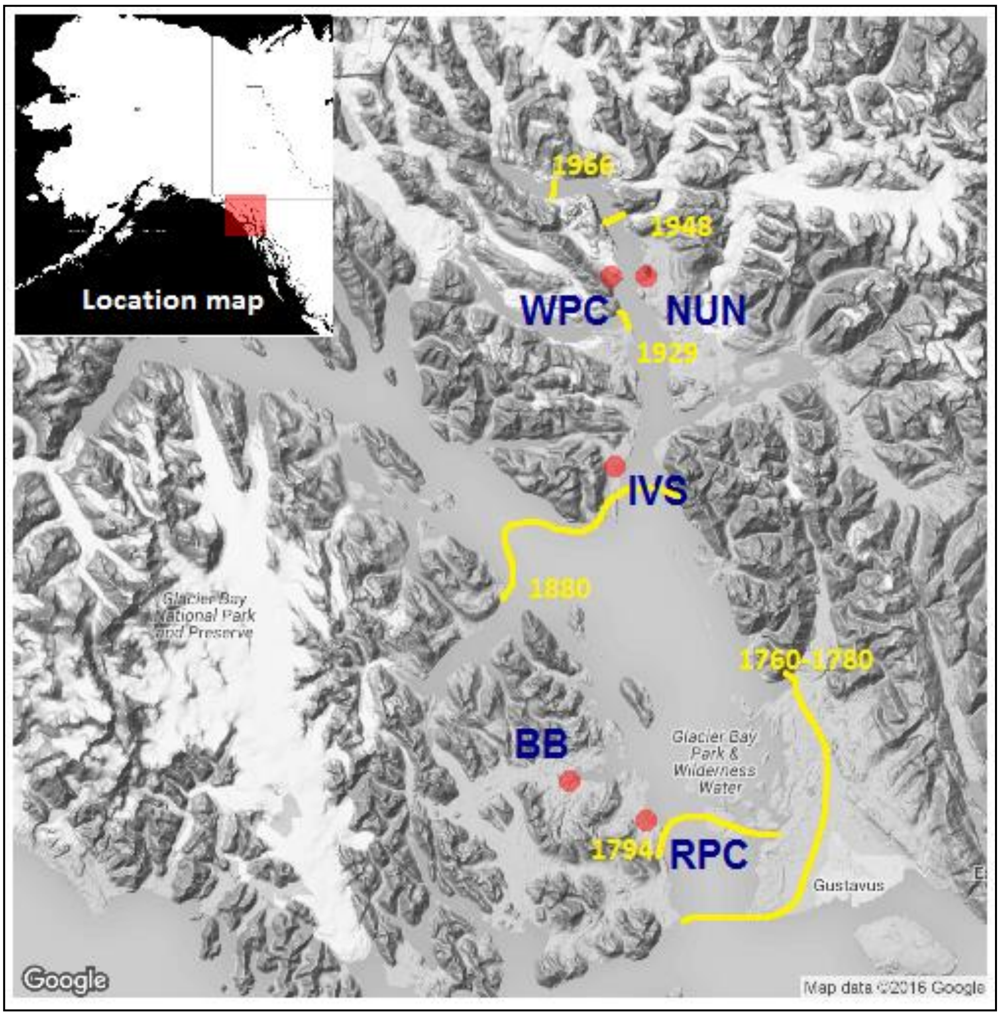

Figure 3.1: Location of field sites in Glacier Bay National Park and Preserve. Sites codes correspond to names in Table 3.1. Approximate position of glacier termini indicated with dates

Fish stomach contents were identified under a dissecting microscope to the lowest practicable level using available taxonomic keys (Lindroth, 1969, White, 1983, Eaton and Kaufman, 2007, Merritt et al., 2008). All analysis was carried out to a minimum of genus level where digestion of the stomach contents permitted. As the main aim of the investigation was to compare between streams in Glacier Bay, standardisation at a lower taxonomic resolution for each site allowed comparisons to be made within the present study (*sensu*

Parker and Huryn, 2013). Individuals were classified as aquatic if they inhabited the water column at the time of consumption by the fish, such as aquatic life stages of invertebrates, and terrestrial if they inhabited the terrestrial environment and therefore were presumably consumed by the fish after unintentionally entering the water. For this reason, adults of aquatic taxa were classed as terrestrial, whereas immature stages are aquatic. This differs from other studies (e.g. Wipfli, 1997, Romero et al., 2005, Webster and Hartman, 2005), but the aim of the investigation was to compare feeding modes of the two juvenile salmonid species and it was therefore deemed appropriate to classify invertebrates by the habitat in which they were present before entering the water column. Very few (18 in total) non-Dipteran adult aquatic invertebrates were found in the stomach contents of individual juvenile coho and Dolly Varden (5 individuals).

3.3.3 Data analysis

Data analysis was carried out using the open source statistical software package R (build v3.1.1; R Core Team, 2014). The number of individual items in the stomach contents of each fish was variable, which may be as a result of an individual's success foraging at a particular point in time, the incomplete flushing of stomachs in the field or because some items were too well digested to allow for reliable identification. Invertebrates were counted by head capsule, therefore if an invertebrate was split in half, both parts would not be counted as single individuals. Simpson's Index of Diversity was used to calculate the diversity of the items in the diets of the fish (Equation 3.1), where n is the total number of items i in the diet and N is the total number of all food items. Dietary overlap was calculated using a proportional similarity index (Equation 3.2; Feinsinger et al., 1981, Dineen et al., 2007a), where P_i and Q_i are the proportion of prey category i consumed by species P or Q. 1 indicates identical (overlapping) diets, 0 indicates entirely different diets.

$$D = 1 - \left(\frac{\sum n_i(n_i - 1)}{N(N-1)}\right) \qquad \text{Equation 3.1}$$

$$I_{PS} = 1 - 0.5 \sum |P_i - Q_i| \qquad \text{Equation 3.2}$$

3.4 Results

Stomach contents of 210 juvenile coho and Dolly Varden were analysed. Juvenile coho and Dolly Varden stomach contents included the aquatic life stages of various macroinvertebrates, such as Dipterans and EPT taxa (Ephemeroptera, Plecoptera, and Trichoptera) as well as adult life stages of these aquatic taxa, various genera of carabid beetles, parasitic wasps (Hymenoptera), spiders, true bugs (Hemiptera) and Collembola. Taxonomic richness of terrestrial invertebrates in the stomach contents of both juvenile coho and Dolly Varden peaked at the second oldest site (Berg Bay), whereas aquatic invertebrate richness reached a maximum at the third oldest site (Ice Valley), then declined for juvenile coho salmon, but remained similar for Dolly Varden at the oldest sites (Figure 3.2).

Table 3.2: Simpson's Index of Diversity and Proportional Similarity Index (I_{PS}) of juvenile coho and Dolly Varden diets at each site

		Simpson's Diversity		
Site	**Age**	**Coho**	**Dolly Varden**	I_{PS}
WPC	55	0.326	0.516	0.912
NUN	70	0.283	0.219	0.927
IVS	130	0.542	0.772	0.919
BB	170	0.604	0.674	0.882
RPC	200	0.219	0.152	0.933

The proportional similarity index indicated that juvenile coho salmon and Dolly Varden diets were relatively similar at each site (Table 3.2), with the least similar diets being at Berg Bay. Simpson's Index of Diversity indicated that the diets of juvenile coho and Dolly Varden were most diverse at mid-aged sites (Ice Valley and Berg Bay; Table 3.2). Aquatic invertebrates comprised the greatest proportion of the diet of juvenile salmonids at all sites (Figure 3.3). There was an increase in the contribution of terrestrial invertebrates with site age up to Berg Bay, but this declined at the oldest site, Rush Point Creek (Figure 3.3).

Of the aquatic invertebrates, chironomids contributed the largest number of individuals to the diets of both fish, and this was particularly evident at Rush Point Creek for Dolly Varden where the mean number of chironomids ingested was more than double that at any other site for both fish species (Figure 3.4). The highest number of terrestrial items in the diets of both juvenile coho and Dolly Varden was at Berg Bay (Figure 3.5). Wood specialist beetles were present in the diets of both fish at Berg Bay, but not at any other site (apart from a single Cerambycidae beetle at Rush Point Creek). Coho diets were comprised of a higher mean number of terrestrial invertebrates than Dolly Varden (Figure 3.5).

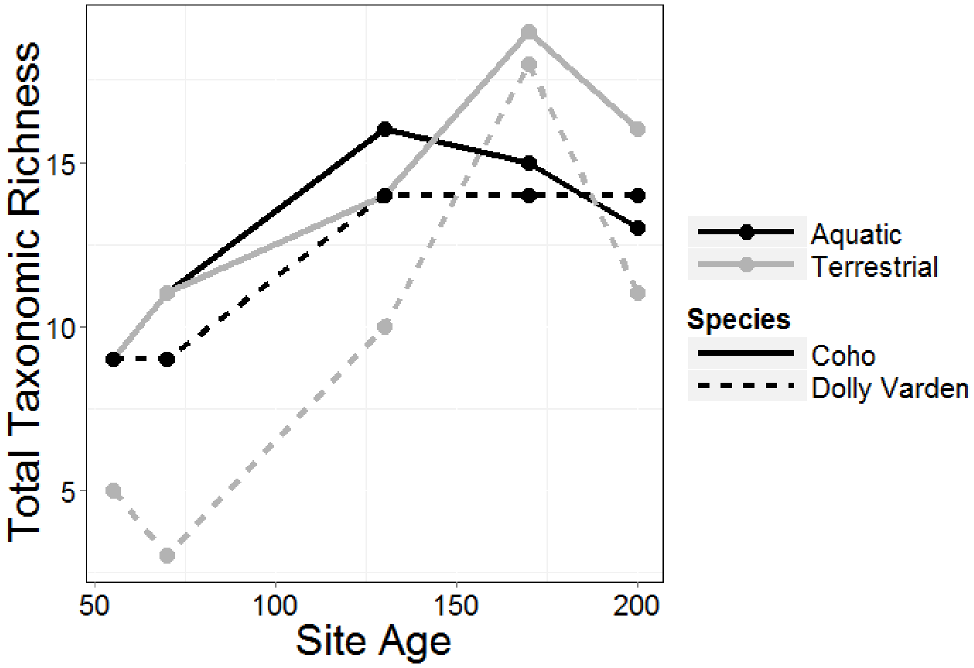

Figure 3.2: Total taxonomic richness of aquatic and terrestrial dietary components in the stomach contents of juvenile coho and Dolly Varden in streams of different ages

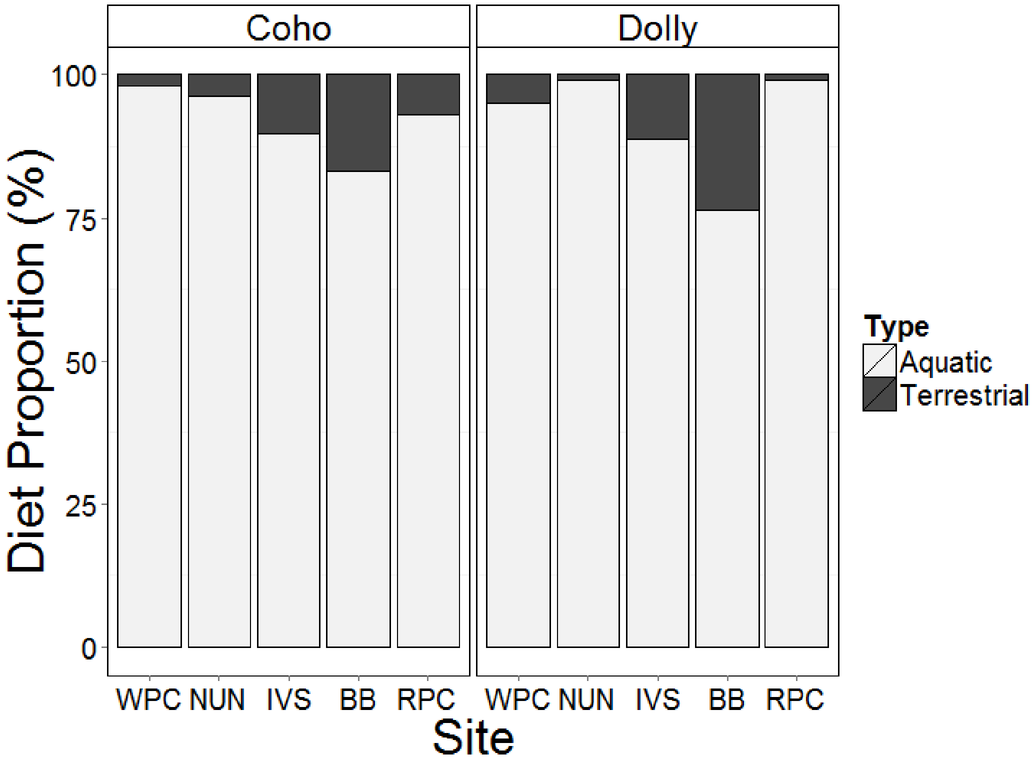

Figure 3.3: Mean proportion of diet of juvenile coho and Dolly Varden sourced from aquatic and terrestrial sources

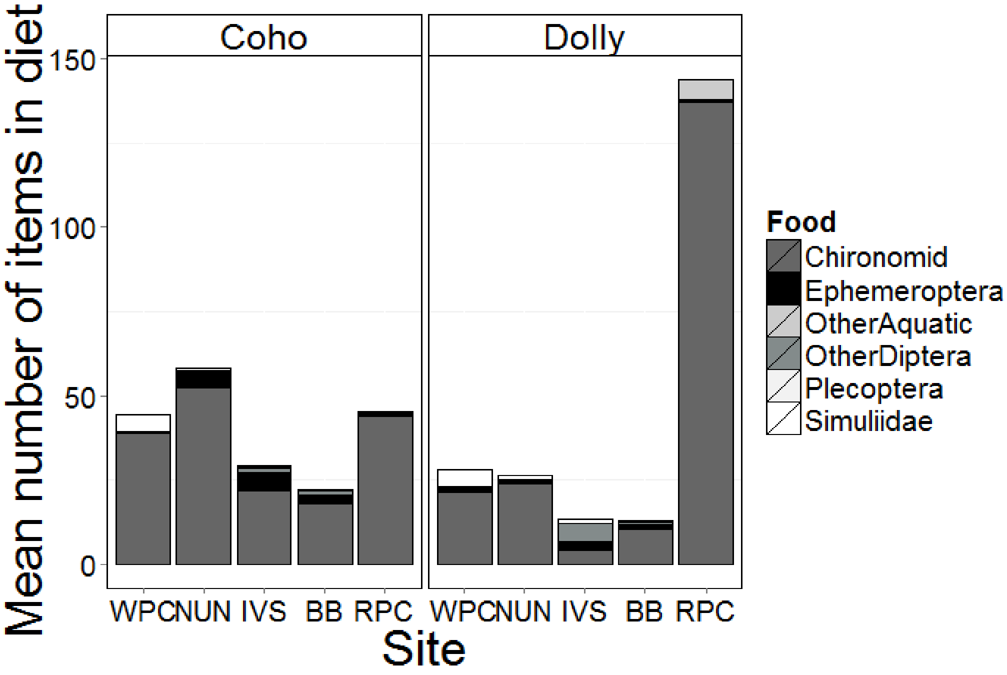

Figure 3.4: Mean number of aquatic items in the diets of juvenile coho and Dolly Varden. Other aquatic includes mites, shrimps, worms and unidentified items; other Diptera includes Ceratopogonidae, Tipulidae and Dicranota. See Appendix for a full list of invertebrates found in the fish diets

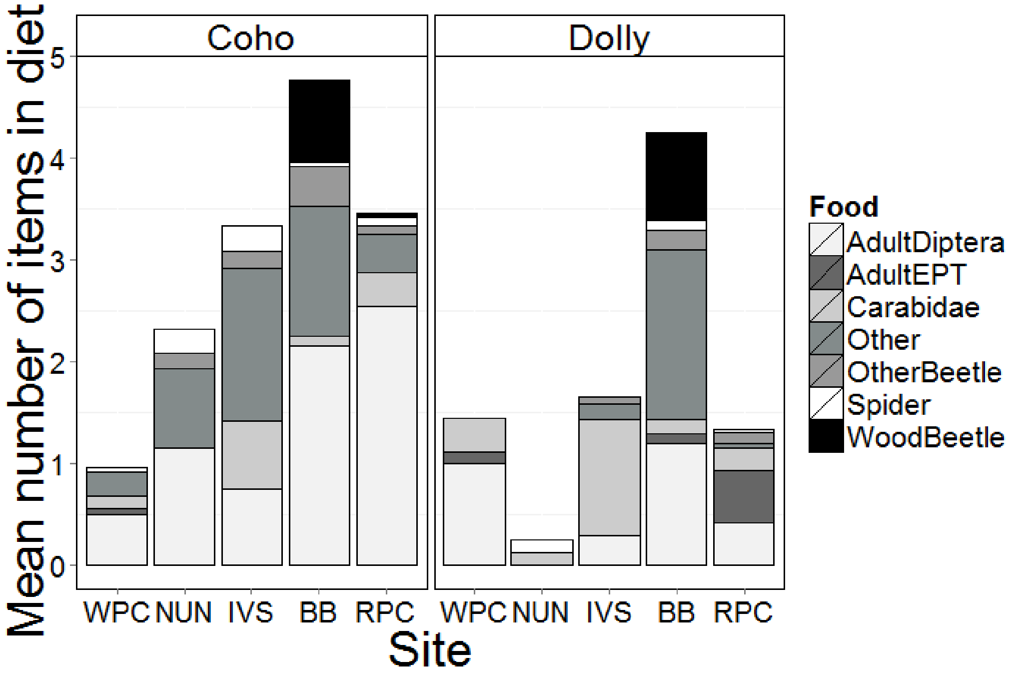

Figure 3.5: Mean number of terrestrial items in the diets of juvenile coho and Dolly Varden. Other includes Lepidopteran larvae, Hymenoptera, and Collembola; other Beetle includes Staphyliniidae, Elateridae and unidentified beetles. See Appendix for a full list of invertebrates found in the fish diets

3.5 Discussion

Juvenile coho salmon and Dolly Varden consumed a variety of aquatic and terrestrial invertebrates. Aquatic invertebrates dominated numerically, comprising >75% of diets at all sites, with dipterans the most important aquatic invertebrate group, dominated by Chironomidae, as has been found by other studies (Nakano and Kaeriyama, 1995, Dineen et al., 2007a, but see Syrjänen et al., 2011). The terrestrial component of the diet increased with site age, reaching a maximum at the second oldest site. Both fish species consumed very similar food resources at all sites, as indicated by their high diet similarity. This was not originally hypothesised, and suggests that there was no resource partitioning occurring at any of the sites. Despite this finding, juvenile coho salmon did consume a slightly higher mean number of terrestrial invertebrates than Dolly Varden.

The number of different food items within the fish stomachs increased with stream age, particularly the terrestrial component. This increased richness of terrestrial items was probably underestimated due to the lower taxonomic resolution of the ingested terrestrial invertebrates as many could not be reliably identified beyond the level of Order due to fragmentation of their bodies and a lack of taxonomic keys for the region. Nevertheless the input of terrestrial invertebrates was elevated at the second oldest stream, Berg Bay (170 years). At the oldest site, Rush Point Creek (200 years), the proportion of terrestrial invertebrates in the diets of both fish species was lower than at Berg Bay, and similar to Ice Valley (130 years). The data presented in Chapter 2 highlighted that for terrestrial carabid beetles, the taxonomic composition was similar between all sites, and the catch per unit effort for riparian sampling was only slightly higher at the older sites than the youngest. This suggests that other factors may be important in providing increased numbers of terrestrial invertebrates to fish diets at Berg Bay, such as riparian terrestrial habitat complexity.

Riparian vegetation contributes more terrestrial prey to streams than open grassland (Dineen et al., 2007b, but see Romaniszyn et al., 2007), and as all streams sampled in Glacier Bay had riparian forests, it was expected that terrestrial invertebrate prey would be abundant in the diets of the juvenile coho and Dolly Varden. However, there were marked differences between the streams, with very low contribution of terrestrial resources to fish diets at both the oldest and youngest streams, as compared to aquatic invertebrates. Terrestrial vegetation type varied between streams in Glacier Bay, with the younger streams dominated by alder, and older streams bordered by a mixed riparian forest including cottonwood and Sitka spruce. The low contribution of terrestrial invertebrates in the diets of both juvenile coho and Dolly Varden in streams where the riparian vegetation was dominated by alder compared to other vegetation types contrasts with the findings of Wipfli (1997). Instead, the highest contribution of terrestrial invertebrates to the diets of juvenile coho and Dolly Varden were found at sites bordered by mixed riparian vegetation (including cottonwood, alder, and spruce) and with coarse woody debris present in the stream channel. These findings also contrast to those of Allan et al. (2003), who found that there was no difference in terrestrial invertebrate prey number or biomass in coho salmon diets between old- and young-growth forests. The oldest site, which has a conifer-dominated forest, contributed low numbers of terrestrial invertebrates to fish diets, partly supporting the findings of Wipfli (1997, see also Romero et al., 2005, Syrjänen et al., 2011). The complexity of the riparian forest would appear to be important for the provision of terrestrial invertebrates to streams, rather than the dominant tree species.

The diversity of diet was highest for the mid-aged sites, Ice Valley and Berg Bay. This was supported by the findings of a complementary study using stable isotope analysis, which found that the greatest dietary breadth occurred for both juvenile coho and Dolly Varden at Berg Bay (see Chapter 5). During sampling, it was observed that channel morphology in Berg Bay was more complex (greater sinuosity and a more mobile channel), with larger quantities of coarse woody debris than at the other sites (*personal observation*, see also: Klaar et al., 2009, 2011). Some of the terrestrial invertebrates identified in the stomach contents of fish at Berg Bay were wood-specialists (e.g. Rhizophagidae, Cerambycidae, Scolytidae) normally found under the bark of trees (White, 1983), which may have entered the water column via the input of dead wood, or perhaps trees (or branches) falling into the stream due to, for example, wind action. Lepidopteran larvae were also only found in the stomachs of fish at Berg Bay. This greatly increased the richness of the taxa in the diets of the juvenile salmonids at Berg Bay as these particular terrestrial invertebrates were not found at any other site. The results of this study contrast with the findings of Gustafsson et al. (2014), where the addition of woody debris had no effect on fish diet. However, the woody debris used in the stream habitat manipulation by Gustafsson et al. (2014) was much smaller than that found in the streams in Glacier Bay, where entire trees had fallen into the stream, rather than artificially added small logs and branches 1m or less in length. This emphasises the importance of large, natural, woody debris accumulations in increasing the terrestrial subsidy available to fish.

Interestingly, Allan et al. (2003) found that terrestrial Aphididae, Collembola, and Hymenoptera contributed the largest terrestrial invertebrate input to the diets of coho salmon in coastal southeastern Alaskan streams, whereas in the Glacier Bay streams these taxa only made up a small proportion of the diet. Aphididae were not found in any fish stomachs in Glacier Bay, which may be linked to colonisation patterns: the relatively young substrates in this study may not have been colonised by invertebrate groups found elsewhere in Alaska.

Diets of juvenile coho and Dolly Varden were similar at all sites (Table 3.2), and the proportions of terrestrial invertebrates in their stomach contents were similar between species within the same sites. The high diet similarity suggests that there was no diet partitioning between juvenile coho and Dolly Varden in streams in Glacier Bay. Simpson's index of diversity of diet was also similar between species within sites, with neither fish species having a consistently more diverse diet. Fish inhabiting the same streams have been found to partition resources between species in other studies. Dineen et al. (2007a) found that Atlantic salmon consumed more terrestrial prey than brown trout. Similarly, in a study in Kamchatka, Eberle and Stanford (2010) found that terrestrial resources comprised a much greater proportion of the diet of coho when compared to Dolly Varden, particularly in late summer and early autumn. This did not occur in any of the streams in Glacier Bay. Dietary overlap was very high in all streams, although it was slightly reduced at Berg Bay, where dietary diversity was highest. It may be the case that in these streams resources were not limited for juvenile coho and Dolly Varden, and so there was no advantage to partitioning of resources, or that both fish were opportunistic feeders not limited to bottom, or top feeding modes.

3.6 Conclusion

Sites of intermediate age, with a rich riparian forest and inputs of coarse woody debris, provided the greatest input of terrestrial invertebrates to the diets of juvenile salmonids in streams in Glacier Bay, Alaska. Increased habitat complexity led to more diversity in salmonid diets, which may be beneficial to juvenile fish if stochastic events (e.g. floods; Milner et al., 2013) lead to a decrease in a particular prey item.

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4

STREAM FOOD WEB DYNAMICS IN CATCHMENTS OF DIFFERENT AGES

Abstract

Aquatic food webs have been much studied in a variety of systems, from lowland, temperate streams, to geothermal springs, and glacial meltwaters. However, no study has yet examined the structure of food webs in streams over multi-decadal timescales. This study used space for time substitution to examine food web structure in streams ranging from 55 to 200 years old. Food webs were dominated by generalist feeders, but although taxonomic richness varied marginally over time, food web connectivity increased. The increase in connectivity was driven by habitat stability, which had a bottom-up effect on food web structure by increasing the availability of basal resources to consumers. This is likely to positively influence food web stability in the older stream systems.

4.1 Introduction

By highlighting the feeding and competitive linkages between taxa through studies of food webs, an enhanced understanding of the functioning of communities can be attained. Stream food webs have been relatively well studied, particularly in lowland, temperate environments. (e.g. Jaarsma et al., 1998, Townsend et al., 1998, Woodward and Hildrew, 2001, Schmid-Araya et al., 2002a, Thompson and Townsend, 2003, Layer et al., 2010, Brown et al., 2011), but work, albeit limited, has also been undertaken in glacier-fed alpine systems (e.g. Clitherow et al., 2013). Worldwide, glaciers are receding, new streams are forming and others are increasing in length (Robinson et al., 2014); however, the focus on lowland, temperate streams without a recent history of glaciation means that there is a lack of food web research that addresses the changes in community interactions over time as new streams form, and hence the effects of climate change and glacial recession on stream community functioning is not fully understood.

Food web structural patterns have been investigated across different types of stream systems (e.g. lowland temperate: Townsend et al., 1998, mesocosms: Brown et al., 2011, Ledger et al., 2013, glacial: Clitherow et al., 2013, and geothermal: O'Gorman et al., 2012). Connectance food webs, based on the analysis of consumer gut contents, are the basis for the determination of many structural properties of food webs. These include basic properties such as number of taxa present in the food web (S), and the number of links between taxa (L), as well as the relationships between these, such as linkage density (L/S) and directed connectance (L/S^2). Linkage density (L/S) has been found to increase with S, but connectance ($C=L/S^2$) declines with increasing S (Riede et al., 2010). The relationship between taxonomic richness of the food web (*S*) and some topological features have been described by power-law equations (Equations 1a-c, p144, Riede et al., 2010), suggesting commonality between food webs in different systems. Clitherow et al. (2013) found that linkage densities (*L/S*) in a glacier-fed stream in Austria were comparable to 62 other reviewed studies, although the number of taxa (and consequently the number of links) was lower than in more stable stream systems. Nevertheless, the relationship between these values ($\log_{10}L$ and $\log_{10}S$) across all the streams in their review followed a strong and positive linear relationship (see also Schmid-Araya et al., 2002b). Maximum food chain length also varies between the ecosystems studied, but for streams, the global average is 3.5 trophic levels (Vander Zanden and Fetzer, 2007, McHugh et al., 2010), although this can increase with ecosystem size, and decrease with high flow variability (Sabo et al., 2010, McHugh et al., 2010). Food webs often also display properties of ‘small worlds': Williams et al. (2002) showed that in large communities (*S*=25-92) almost all components of the food web are within three links of one another. The same remained true for the species-poor Austrian glacial streams (Clitherow et al., 2013), although these were even more closely linked. Such ‘small-world’ properties, with individuals separated by just ‘two degrees of separation’ (Williams et al., 2002) emphasise the high connectivity of stream food webs. Some simple structural features may be common across all food webs, despite their contrasting physical habitat properties, some of which may be used to determine changes in food web structure along a gradient of catchments of different biocomplexity (e.g. time since deglaciation).

Some structural patterns have been related to physical conditions rather than simply taxonomic richness, such as the effects of disturbance on food webs. This has relevance for studies of stream development as physical habitat disturbance has been found to decrease as time since deglaciation (stream age) increases as inputs of coarse woody debris enhances sediment stability, and slower flowing stream reaches become more common (Milner et al., 2007, Klaar et al., 2009). Disturbance typically leads to lower species richness or dominance of one or two taxa (Townsend et al., 1998, Death and Zimmermann, 2005), and may shorten food chain length (McHugh et al., 2010). Connectance has been found to be higher in webs that are located in physically harsh stream environments (e.g. acidic: Hildrew et al., 1985, and glacier-fed: Clitherow et al., 2013). Likewise, in a study of streams with different water sources on the North Slope region of Alaska, Parker and Huryn (2013) found that regardless of the size of the food web, streams with higher bed movement were dominated by trophic generalists, which consumed a wide range of the available food resources, and therefore had higher connectance than communities in streams with more benign flow regimes. Food web studies of glacier fed rivers (Zah et al., 2001, Clitherow et al., 2013) have shown higher levels of omnivory and generalist feeding patterns for invertebrate diets, as compared to lowland, temperate streams.

Glacier Bay, in southeast Alaska, provides an ideal location for the study of stream community development over multi-decadal time periods and the influence of this on stream food webs. Previous work in this region has documented and dated glacial retreat, changes in terrestrial vegetation and increases in taxonomic richness of streams with age, as well as taxonomic turnover within communities, as some species are lost and new species colonise (Milner et al., 2000, 2008, 2011). This chronosequence approach provides a unique opportunity to investigate the development and changes in food web attributes as stream systems become more physically complex and the extent and species of terrestrial riparian vegetation respond to catchment age and changing soils.

4.2 Study aim and research questions

The principal aim of the study was to characterise aquatic food webs in streams of different ages in Glacier Bay, Alaska. Although characteristics such as number of nodes will change with stream age as species richness increases along the successional sequence, food webs would be expected to remain highly connected and demonstrate some of the properties of small world systems. It was also expected that stream food web characteristics (such as linkage density) would fall between those of glacier-fed, alpine streams and lowland, temperate systems. The oldest streams were also anticipated to be taxonomically richer than the youngest streams due to the accumulation of species as successional processes occur (Milner et al., 2000).

The following research questions were identified:

- Would taxonomic richness (S), and therefore number of food chain links (L) increase as floodplain age increased?
- Would connectance ($C=L/S^2$), decrease as stream age (and habitat stability) increased? It was expected that the oldest streams would have connectance values similar to the studies of other temperate, lowland stream systems;
- Would there be a decrease in links per species as site age increased? At younger sites taxa were expected to be generalist feeders, whereas at older, more stable sites, specialist feeding habits were expected to develop;
- Did the food webs in Glacier Bay follow the ‘two degrees of separation’ theory, with most taxon pairs separated by <3 links?
- Would there be an increase in diatom morphospecies richness as site age increased?

4.3 Methodology

Glacier Bay National Park and Preserve is situated in southeast Alaska. The area is a unique site for studying ecosystem development following well documented and rapid glacial retreat (Miller, 1964, Milner et al., 2007, Milner and Robertson, 2010). Spanning an area of 11,000km^2, it is a deglaciated landscape over 220 years old (Milner and Robertson, 2010), surrounded by mountains rising to 5000m above sea level and including many kilometres of shoreline, exposed bedrock, unconsolidated glacial sediments and temperate rainforest (Milner et al., 2007). The last glacial maximum occurred around 1700 and glacial recession began (with some regional re-advances) between 1735 and 1785 (Miller, 1964; Figure 4.1). The climate of Glacier Bay is temperate maritime, with mean monthly temperatures ranging from -3°C to 13°C and a mean annual precipitation of 1400mm (Milner and Robertson, 2010).

Table 4.1: Stream floodplains sampled in Glacier Bay, age indicates the length of time the stream mouths have been ice-free

Stream	Code	Age (years)	Longitude	Latitude
Wolf Point Creek	WPC	55	58°59’48.3”	136°10’18.1”
Nunatak Creek	NUN	70	58°58’40.5”	136°5’41.2”
Ice Valley Stream	IVS	130	58°49’10.9”	136°9’49.6”
Berg Bay South Stream*	BB	170	58°30’17.5”	136°14’0.62”
Rush Point Creek	RPC	200	58°28’11.2”	136°06’08.5”

*Berg Bay South Stream hereafter referred to as Berg Bay

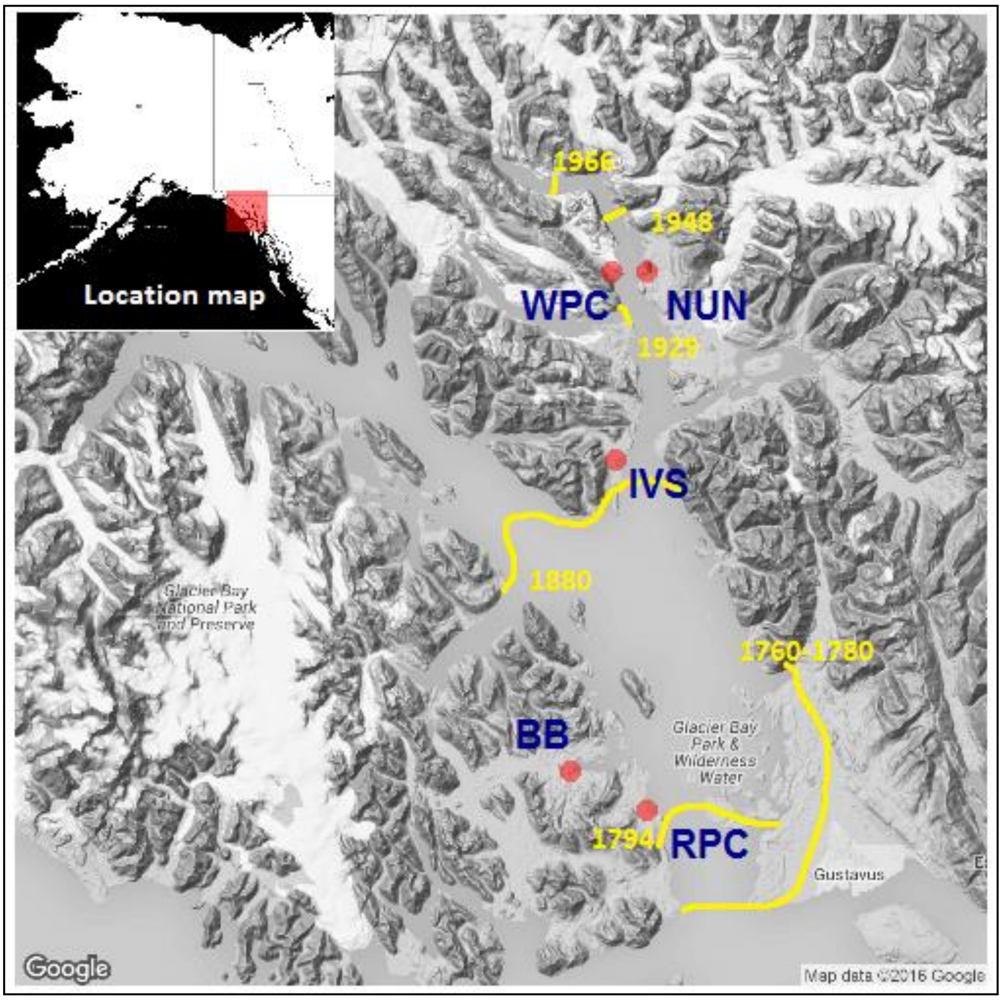

Figure 4.1: Location of field sites in Glacier Bay National Park and Preserve. Site codes correspond to numbers in Table 4.1. Approximate position of glacier termini indicated with dates

4.3.1 Sampling design

Five streams were sampled during the summers of 2013 and 2014 (Figure 4.1; Table 4.1) to represent a range of floodplain ages (55-200 years since glacial retreat). For each stream one reach (c.10m long) was selected, approximately 0.75km from the stream mouth (*sensu* Milner et al., 2008). Each reach consisted of a non-meandering stretch of the stream, and an unvegetated gravel bank, with riparian forest behind.

4.3.2 Sample collection

Aquatic macroinvertebrates were collected using a modified Surber (250µm, 0.1m^2) from June-August in 2013 and 2014. Each site was visited up to four times in 2013 and three times in 2014. Although this mesh size did not retain meiofauna, gut contents analysis showed the absence of meiofauna, thereby indicating this group formed an insignificant part of the diatom-macroinvertebrate-fish food web (see also Thompson and Townsend, 2003). Three samples were collected at each stream during each sampling event and were immediately stored in 70% isopropyl alcohol. Additional samples were collected by hand searching. Fish were collected at each stream using minnow traps, baited with fish eggs, which were pre-soaked in betadyne iodine solution. The fish eggs were placed in a perforated plastic 'Kinder egg' container in each minnow trap to prevent consumption and the streams were fished for 90 minutes (Bryant, 2000). Three traps were placed in pools and backwaters of the main stream channel in 2013, and in 2014 ten traps were deployed. Two juvenile salmonid species were present in the streams studied: coho salmon (*Oncorhyncus kisutch*) and Dolly Varden char (*Salvelinus malma*). A maximum of five individuals of each species per stream were permitted to be sacrificed in 2013 and up to twenty in 2014 (as per Alaska Department of Fish and Game permit). These fish were collected for isotopic analysis, and their stomachs were removed for dietary analysis. Additional stomach content samples were collected in 2014 by gut flushing: a blunt-ended syringe filled with stream water was carefully inserted into the mouth of an individual fish and the stomach contents were flushed into a sample bag (Meehan and Miller, 1978). Fish were allowed to recover in a tray of stream water before being released into the areas where captured with no mortality.

In the laboratory, invertebrates were identified to the lowest practicable taxonomic level, which was frequently generic, using the key of Merritt et al. (2008), before being dissected and their guts removed. Invertebrate guts were mounted on to slides using Euparol (as per Clitherow et al., 2013); where possible, ten individuals of each taxon were analysed at each site. Gut contents were examined using a high-powered microscope at x1000 and diatoms present were identified to morphospecies due to a lack of taxonomic keys. Amorphous detritus was present in all the gut contents, and included fragments of rock and unidentifiable plant matter; these were classified as 'detritus'. Fish stomach contents were identified under a dissecting microscope to the lowest practicable level using available taxonomic keys (Lindroth, 1969, White, 1983, Eaton and Kaufman, 2007, Merritt et al., 2008). Due to digestion of the stomach contents of the juvenile coho and Dolly Varden, identification was only possible to generic level. This reduced taxonomic resolution, but using the same level of resolution for each food web thereby allowed comparisons to be made within the present study (see also Parker and Huryn, 2013). At some sites aquatic invertebrate taxa were found in fish stomachs, but were not collected in the benthos. The diets of these individuals were estimated from individuals found in the benthos at other sites and were incorporated into the food web analysis for the sites where they were present in fish stomachs but not Surber samples.

4.3.3 Data analysis

Aquatic food webs were constructed for each of the five streams. Terrestrial invertebrates were found in the stomach contents of the juvenile coho and Dolly Varden at each of these streams, but for calculation of the wholly aquatic food webs, these invertebrates were not included in the food webs. Fish diets were analysed in more detail (including the terrestrial component) in Chapter 3. Data analysis was carried out using the open source statistical software package Cheddar (Hudson et al., 2013, 2014) in R (build v3.1.1; R Core Team, 2014). Summary food web statistics were calculated using Cheddar, namely: number of nodes (*S*, also known as taxon richness), number of links between individuals (*L*), linkage density (*L/S*) and directed connectance ($C=L/S^2$). Further details regarding these statistics can be found in Clitherow et al (2013, see also Pimm et al., 1991, Brown et al., 2011). Mean and maximum chain length, and mean trophic height were also calculated for each stream food web. Chain length is the length of every chain within the food web. Trophic position (used to calculate mean trophic height) was calculated for a species as 1+ the number of individuals preceding it in the food chain and trophic height of an individual is its mean position in all the food chains of which it is a part (Jonsson et al., 2005). The mean trophic height refers to the mean of all species' trophic heights in the food web. Trophic generality was calculated as the mean number of links going into each organism in the food web; it is therefore synonymous with dietary richness. The two degrees of separation theory of Williams et al. (2002) was tested using the 'ShortestPaths' function within the Cheddar package. This function computes the length of the shortest path between two individuals within the food web. The proportions of paths of each length (1 to 4 in these streams) were calculated for each stream.

4.4 Results

Stomach contents of 210 juvenile coho and juvenile Dolly Varden salmonids, and 600 individual aquatic macroinvertebrates were analysed (Table 4.2; yield-effort curves for macroinvertebrate diets are shown in Figure S4.1 in the Appendix). Juvenile coho and Dolly Varden consumed both terrestrial and aquatic invertebrates, alongside unidentifiable detritus, whereas aquatic macroinvertebrates consumed mainly diatoms and amorphous detritus. This detritus consisted of stones and unidentifiable plant fragments, and the majority of taxa consumed only diatoms and detritus. Most diatoms were present in invertebrate diets at all sites, and hence there was no clear turnover of morphospecies with site age (Table 4.3). Some invertebrates were predatory, namely: Simuliidae; the mayflies *Cinygmula* and *Drunella*; the stoneflies *Arcynopteryx*, *Plumiperla*, and *Haploperla*; and the caddisfly *Rhyacophila*. Predatory invertebrates consumed chironomids exclusively, the only exception being *Drunella*, which predated on the baetid mayfly *Acentrella* at Ice Valley, and *Plumiperla* at Rush Point Creek. Some Chironomidae were found to be cannibalistic. Chironomidae comprised the greatest proportion (57-89%) of invertebrates collected at all sites except Ice Valley where *Cinygmula* were the most abundant (50% of assemblage). The second most common invertebrate was frequently *Cinygmula* (>10%; apart from Wolf Point Creek where Simuliidae were highly abundant, and Ice Valley where Chironomidae were second most abundant). Other invertebrate taxa comprised a small proportion of the total invertebrate assemblage (<11%). The mean dietary richness of the two most abundant taxa across the chronosequence showed different patterns with site age (Figure 4.2). Chironomid diet richness was highest at Wolf Point Creek, whereas *Cinygmula* diet richness increased with site age, reaching a maximum at Berg Bay. Overall, Simuliidae had the largest diet breadth (consumed the most diatom taxa) of any invertebrate at all five sites, and the numbers of diatoms consumed varied between invertebrate taxa at each site (Figure 4.3).

Table 4.2: Summary of invertebrate abundance, and numbers of fish and invertebrate stomach contents analysed

	Invertebrate abundance (m^{-2})		**Number of guts analysed**		**Taxon richness**
Site	**2013**	**2014**	**Invertebrates**	**Fish**	**Invertebrates**
WPC	1966	1987	111	40	11
NUN	293	1043	81	27	8
IVS	221	130	125	41	9
BB	932	1278	136	43	13
RPC	855	847	147	59	13

Table 4.3: Diatom morphospecies present at each site, diatoms are differentiated by numbered codes. Presence is indicated by 1 and absence by 0

	Diatom morphospecies																																					
Site	**1**	**2a**	**2b**	**2c**	**2d**	**3a**	**3b**	**3c**	**4a**	**4b**	**5**	**6**	**7**	**8a**	**8b**	**8c**	**9**	**10**	**11**	**14**	**15a**	**15b**	**16**	**17**	**18**	**18b**	**19**	**20**	**21**	**22**	**22b**	**23**	**24**	**25**	**25b**	**26**	**27**	**Sum**
WPC	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	1	0	1	1	1	**32**
NUN	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	0	0	1	1	1	0	0	0	1	1	1	1	**29**
IVS	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	0	1	1	1	0	0	1	1	0	1	0	1	0	0	1	**27**
BB	0	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	**30**
RPC	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	0	1	0	0	0	**28**

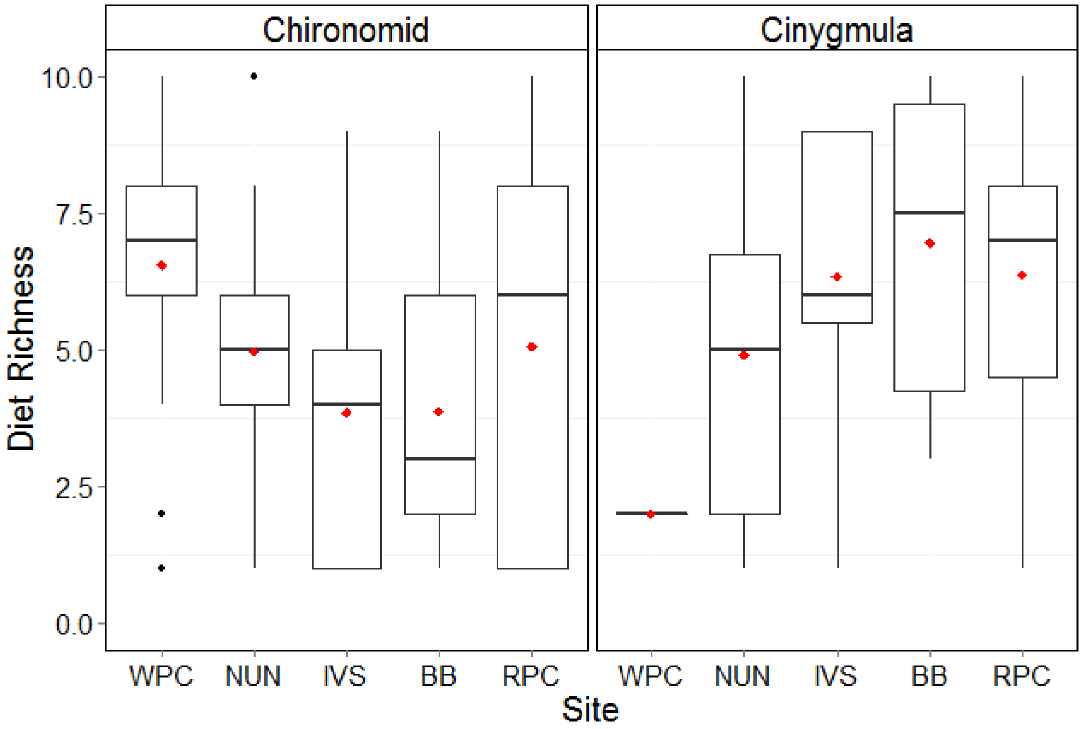

Figure 4.2: Dietary richness of the most abundant macroinvertebrate taxa. Red dots indicate mean values

Food web structure for each stream emphasises their similarity across all sites (Figure 4.4): with the largest proportion of taxa at the lowest trophic levels, and just two taxa occupying the highest trophic position at each site. The number of nodes (taxon richness, *S*) in each food web was similar across all sites, although the highest number of nodes was found at the two oldest sites (Table 4.4). The number of links increased from 158 at the second youngest site to 307 at the oldest site. As a result, linkage density increased with site age, as did connectance. The proportion of top level consumers was highest at the second oldest site, and lowest at the youngest site, whereas the proportion of basal resources decreased with site age. The maximum chain length was the same across all sites except Rush Point Creek (this measure does not include cannibalistic loops, although at all sites the only cannibalistic group present were the Chironomidae). Mean chain length was highest at Rush Point Creek, but varied only slightly between sites, whereas mean trophic height increased with site age. Mean trophic generality also increased with site age, indicating increased dietary breadth. The distributions of path lengths at each site were very similar (Figure 4.5) and the majority (>76%) of components within every food web were connected by ≤2 links. The relationship between *S* and *L* in the Glacier Bay streams and a range of other published studies are shown in Figure 4.6. The Glacier Bay streams fit within the range of reported literature values.

Table 4.4: Food web statistics from the five streams

Site	**WPC**	**NUN**	**IVS**	**BB**	**RPC**
Nodes (*S*)	46	42	45	49	47
Links (*L*)	182	158	202	259	307
L/S	3.96	3.76	4.49	5.29	6.53
C (L/S^2)	0.09	0.09	0.10	0.11	0.14
% Basal	71.74	71.43	64.44	61.22	61.70
% Intermediate	19.57	16.67	24.44	22.45	25.53
% Top level	8.70	11.90	11.11	16.33	12.77
Max. chain length	4	4	4	4	5
Mean chain length	3.234	3.160	3.291	2.998	3.313
Mean trophic height	1.362	1.373	1.458	1.494	1.526
Mean trophic generality	3.957	3.762	4.489	5.286	6.532

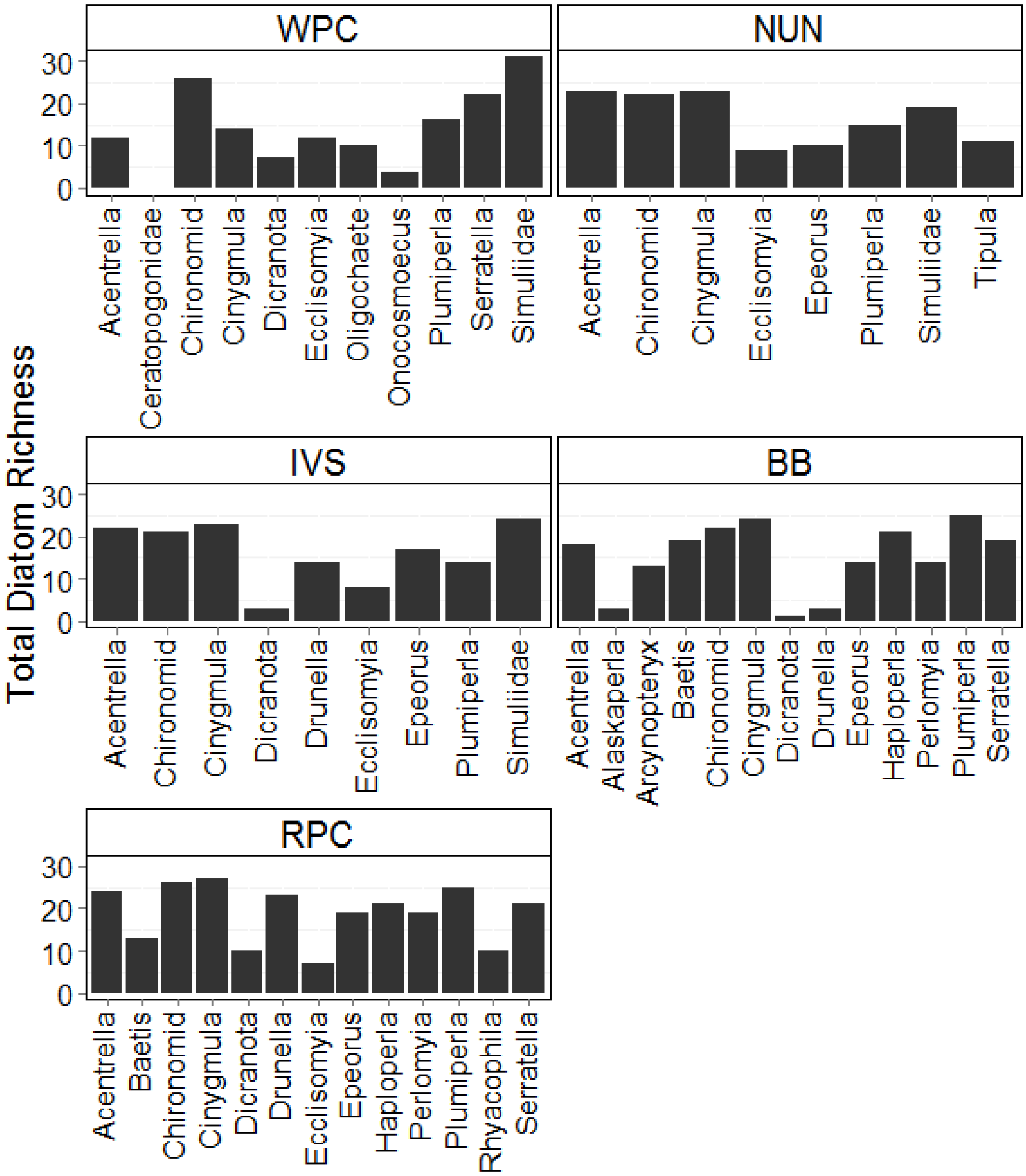

Figure 4.3: Diatom morphospecies richness in the gut contents of macroinvertebrates at each site

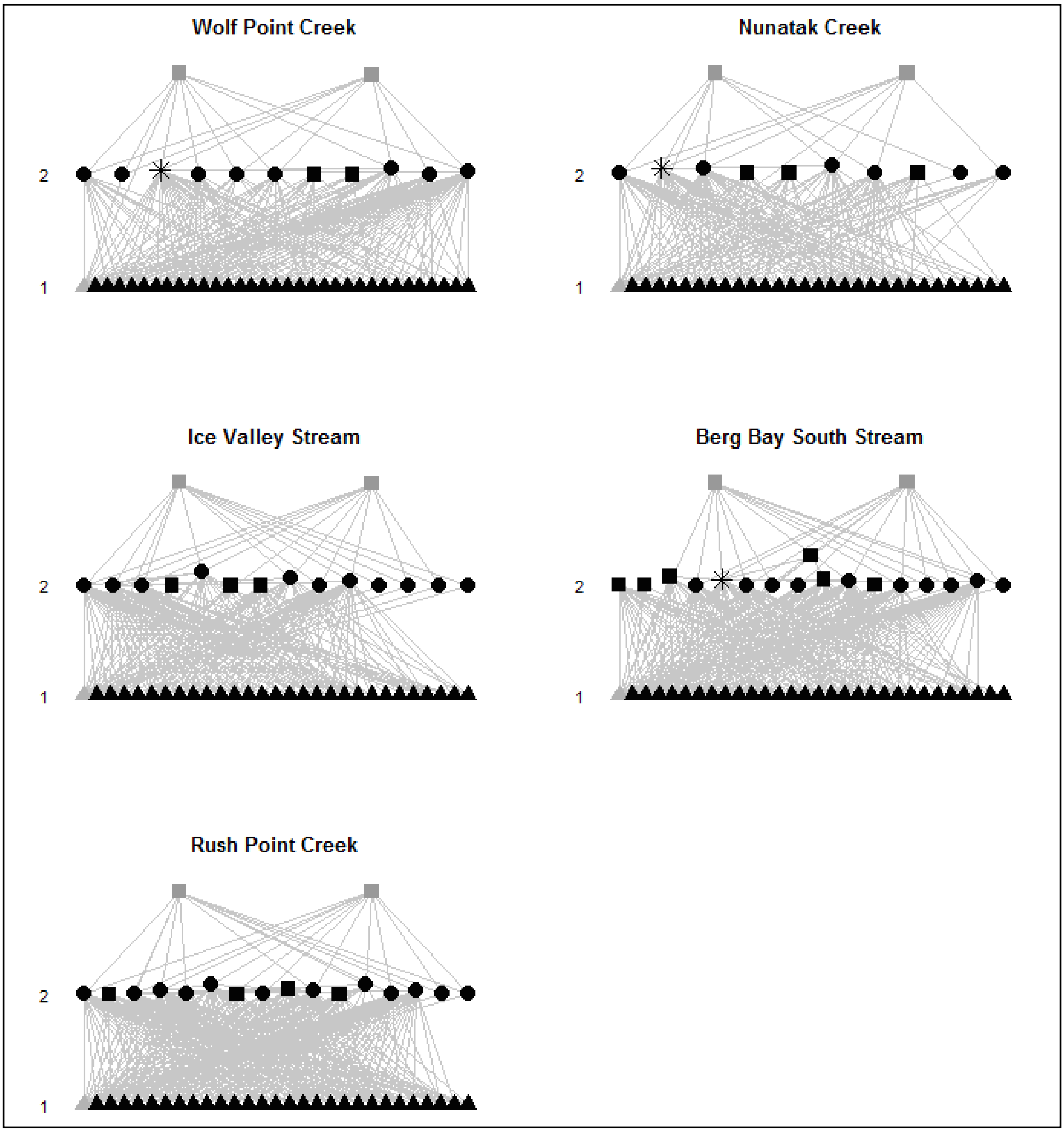

Figure 4.4 Food web diagrams for each stream in Glacier Bay. Consumer height is plotted by chain averaged trophic level. Triangles are basal resources (grey=detritus, black=diatoms), circles are intermediate consumers (invertebrates), squares are top consumers (black=invertebrates, grey=fish), * indicates cannibals (Chironomidae). See also Figure S4.2 in the Appendix

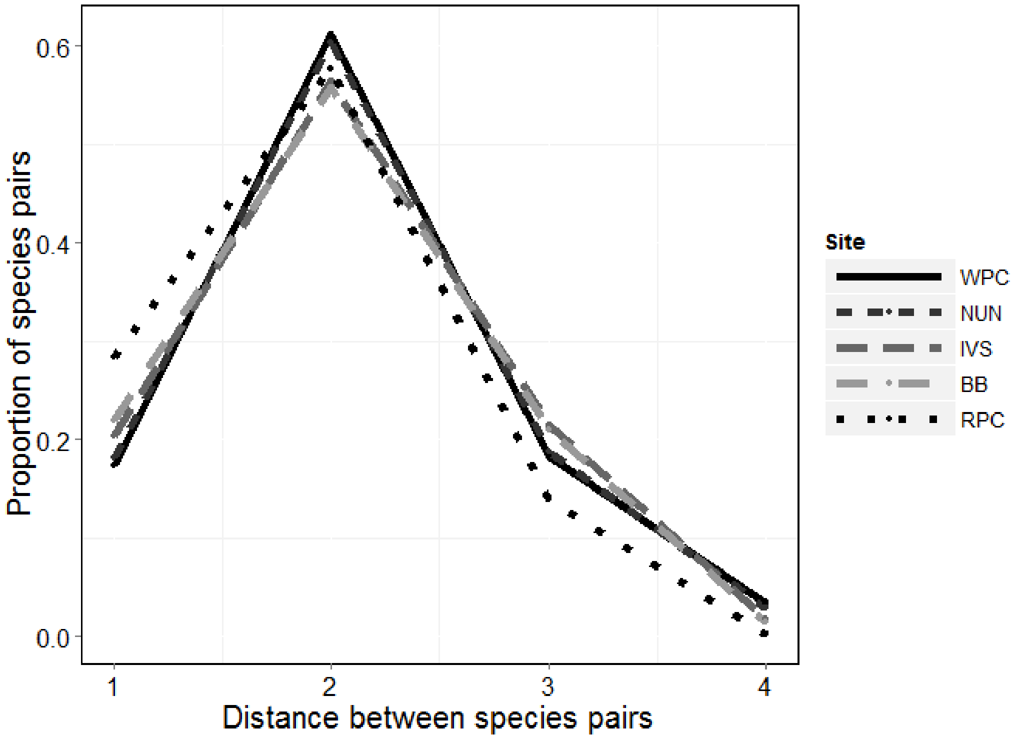

Figure 4.5: Path length distributions for each stream food web

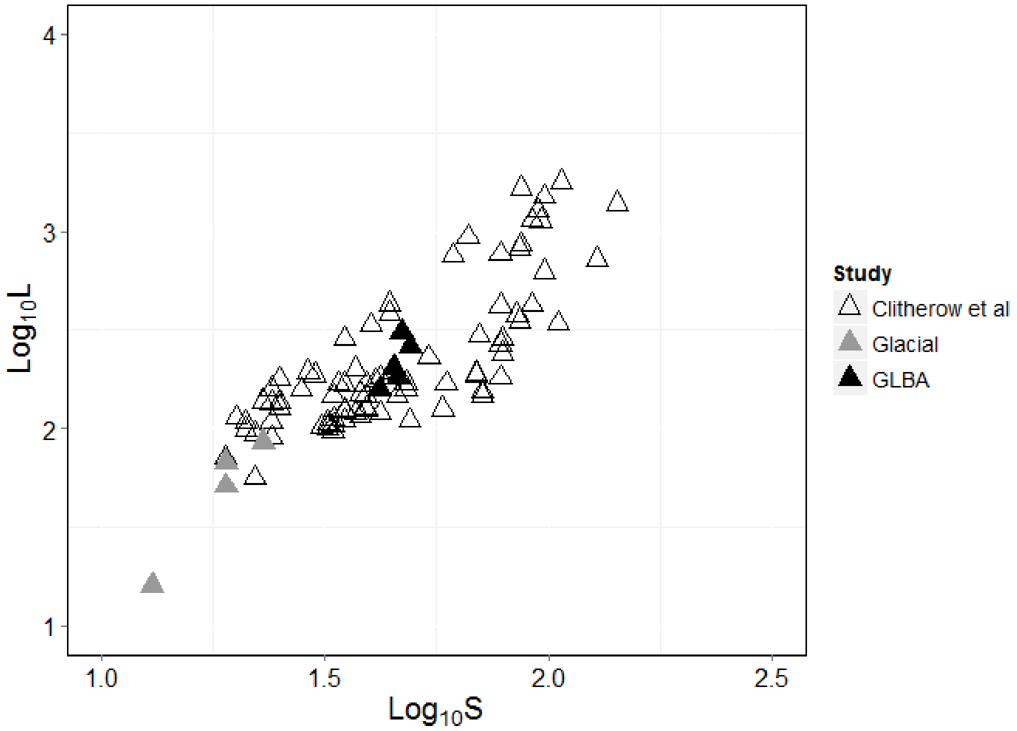

Figure 4.6: Relationship between taxon richness (*S*) and number of links (*L*). Comparisons are drawn between the present study (GLBA, black triangles) and other stream food webs (from Clitherow et al. (2013; open triangles and grey triangles. For full reference list see Table S4.1 in the Appendix)

4.5 Discussion

This study provided the first attempt to describe, using detailed stomach contents analysis of juvenile fish and invertebrates, stream food web development over multi-decadal timescales. There have been many attempts to describe stream food webs using field based methods (e.g. Jaarsma et al., 1998, Townsend et al., 1998, Woodward and Hildrew, 2001, Schmid-Araya et al., 2002a, Thompson and Townsend, 2003, Layer et al., 2010, Brown et al., 2011, O'Gorman et al., 2012, Parker and Huryn, 2013) but as yet, to my knowledge, none have used catchment age as a factor influencing web development.

Individual taxa within all the study streams in Glacier Bay were closely connected, reflected in their generalist type feeding patterns and the small distances between species pairs. All streams supported a similar community assemblage consisting of juvenile coho and Dolly Varden at the highest trophic levels, followed by an invertebrate assemblage consisting of Diptera, Ephemeroptera, Plecoptera and Trichoptera, and with a range of diatom taxa at the base of the food webs, which were comparable across all sites. Contrary to what was expected, food web taxonomic richness did not increase with site age, instead, many of the same taxa persisted across the spectrum of site ages. However, the number of links between the taxa, as well as dietary richness (trophic generality) increased, which suggested that there was a greater abundance of food resources at older sites and consumers were therefore able to utilise a wider range of available resources; this was perhaps indicative of greater habitat stability as catchment age increased. The most abundant macroinvertebrates in the streams were the Chironomidae, which decreased their diet richness with site age, whereas the next most abundant organism, *Cinygmula* sp. increased their diet richness over time. Chironomidae are typically filter feeders, whereas *Cinygmula* are more mobile grazers, and their differing dietary responses to site age may be as a result of different feeding modes: in young sites with unstable substrates and faster flowing water, diatoms may be more easily detached from the substrate and were therefore available in the water column to filter feeding invertebrates. Benthic organic material increased with stream age, and stable (often older) streams have been found to have greater autochthonous production (Milner et al., 2000), therefore in the slower flowing waters of the older streams (Klaar et al., 2009), grazers, such as *Cinygmula*, may be more able to utilise the increased resources, and hence increase their diet breadth with site age.

The increase in mean diet richness across the chronosequence occurs despite a relative decrease in the proportion of basal resources, suggesting that abundance, rather than number of different resources may be important in structuring food webs. Mean food chain length was slightly lower and maximum length slightly higher than the global estimate of around 3.5 for streams (Vander Zanden and Fetzer, 2007), which suggests that the food webs did include the full range of trophic levels that could be expected. The relationship between number of nodes and number of links fitted within the range of literature values, and was higher than found in glacier fed streams, but lower than many temperate lowland systems.

No attempt to sample meiofauna was made in this study, although they are known to exist in streams in Glacier Bay (Milner et al., 2000, 2011, 2013). Schmid-Araya et al. (2002a) found that small chironomids consumed meiofauna in their streams, but no evidence of meiofauna was found in any of the invertebrate digestive tracts in this study. This was interesting as it appeared to suggest that two food webs are acting independently in the Glacier Bay streams: macroinvertebrate and meiofauna dominated webs. Schmid-Araya et al. (2002a) found that 70% of benthic species in their food webs were meiofaunal (<500µm in size) and this therefore contributed significantly to a much higher number of taxa and links in their food webs than in the Glacier Bay webs. Despite this, structural features such as linkage density were comparable between the two studies (*L/S* was very similar at the mid-aged site, Ice Valley Stream, to that of Schmid-Araya et al. (2002a)). Connectance was lower in the food webs presented by Schmid-Araya et al. (2002a) and this may have been at least in part due to the inclusion of the meiofauna normally excluded from food web studies. Inclusion of meiofauna in the Glacier Bay food webs would certainly lead to a higher taxonomic richness (*S*), but as it would appear that macroinvertebrates were not consuming them, this may decrease overall connectance values, perhaps giving values similar to those of Schmid-Araya et al. (2002a, see also Schmid-Araya et al., 2002b).

Macroinvertebrate specialist feeders were not present in any of the Glacier Bay streams studied. At all sites macroinvertebrates ingested a range of diatoms and detritus, similar to other studies (Füreder et al., 2003, Clitherow et al., 2013). The mode of feeding for these invertebrates would appear to follow a rule ‘if it fits, it’s food’ (*sensu* Elton, 1927), meaning that if an item is small enough to fit in an individual’s jaws, then it can be eaten. Beside diatoms, this also included a variety of detritus such as unidentifiable plant material, but also rock fragments. The mayfly *Drunella* was the largest invertebrate collected, which may account for it being the only predatory taxon to consume items other than chironomids. Invertebrate predators were very rare, and those taxa which were represented by predatory individuals, also had individuals in the assemblage with no evidence of predatory diets. This was surprising, given that in other studies the proportion of predatory taxa within a food web was quite high. In a tropical stream predators comprised 39% of total species richness (Cheshire et al., 2005) and predators dominated the assemblages in the temperate streams studied by Thompson and Townsend (2003). The low numbers of invertebrate predators in Glacier Bay streams may reflect a harsher physical environment than these other studies, in which both opportunistic and generalist feeding strategies were advantageous, a pattern seen in the mesocosm-based drought study by Ledger et al. (2013). It might also be the case that invertebrate densities were lower, or patchier than in other systems, and therefore predatory encounter rates would be low (neither of the aforementioned studies present invertebrate abundance data).

Fish consumed individuals of the majority of invertebrate taxa, and neither juvenile coho nor Dolly Varden displayed diet specialisation, thereby suggesting that these species were opportunistic predators, selecting prey when encountering something small enough to consume. Juvenile coho and Dolly Varden also consumed terrestrial invertebrates, which were not included in the calculations of the aquatic food web statistics. Food webs often need to be acknowledged as subsets of greater networks, in this case defined by a focal habitat: the stream (Winemiller and Layman, 2005). The entire diet of the juvenile coho and Dolly Varden was further explored in Chapter 3.

Habitat stability was likely the driving force behind the structural differences in the food webs presented here, rather than site age alone. Biotic factors, such as richness of macroinvertebrate taxa, were positively related to habitat stability in Glacier Bay streams, but stability is not linearly related to stream age and may be affected by other physical characteristics of the catchment such as the presence of lakes (Milner et al., 2000). One confounding factor in the chronosequence of streams in this study is the presence of a lake in the Wolf Point Creek system. Lakes act to stabilise streams (Milner et al., 2000), and this may explain why the youngest stream had higher taxonomic richness compared to Nunatak Creek and Ice Valley, neither of which have lakes. The oldest two streams also have no lakes, but the effect of this on stream stability may be mitigated by the other features of older streams, such accumulations of coarse woody debris stabilising the stream channel and more slow flowing stream reaches (Klaar et al., 2009).

Taxonomic composition was very similar between sites at all trophic levels, suggesting that site colonisation was not a limiting factor 55 years or more since glacier recession. The number of links and connectance, however, increased with site age, which may be linked to increased habitat stability at the oldest sites (Milner et al., 2007, Klaar et al., 2009). Substrate movement, a measure of disturbance, can influence linkage density and connectance, both of which have been found to decline with increased bed movement (Parker and Huryn, 2013), which is in line with these results showing lower connectivity and linkage density in the youngest streams. Disturbance leads to lower algal biomass (Death and Zimmermann, 2005, Herrmann et al., 2012), which reduces the basal resources available to consumers. In an unstable stream, the distribution of resources and consumers may be patchy, which leads to a lower encounter rate of a consumer with any given food type. Even if the full range of possible food items are present at the disturbed site, spatial patchiness reduces the probability that a consumer will encounter the full range of possible food items during any given unit of time (see also Townsend et al., 1998). Therefore the number of links in the food web is lower than in a more stable stream, where resources are more evenly distributed and any given consumer has a higher probability of encountering any of these items. Food webs with higher connectance suffer fewer secondary extinctions when species are removed (Dunne et al., 2002), suggesting that in the Glacier Bay streams, the food webs characteristic of the oldest sites will be more robust to perturbations than the less highly connected younger streams.

4.6 Conclusion

Aquatic food webs, when described using identical methodologies, provide an opportunity to explore community interactions across temporal scales (i.e. across a 200 year gradient of glacial recession) and different catchment characteristics. The evidence presented here suggested that between 55-200 years since glacial recession, stream communities were similar and dominated by generalist feeders. Food web structural differences were therefore driven by abundance and patchiness, rather than taxonomic composition. This in turn was driven by the physical habitat template, with the relative ‘harshness’ or disturbance of the stream influencing the basal resource distribution and abundance, which had a bottom-up effect on food web connectivity where consumers have generalist feeding modes. This promotes stability and persistence of the same taxa across the chronosequence.

4.7 References

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5

THE ROLE OF RECIPROCAL SUBSIDIES ACROSS FLOODPLAINS OF DIFFERENT AGES

Abstract

Reciprocal subsidies between the stream and riparian zone have been well documented in various studies. However, no study has yet determined whether these fluxes change over multi-decadal timescales. This study used stable isotope analysis to assess the importance of the reciprocal flux of subsidies for consumers on floodplains ranging from 20-200 years old in Glacier Bay, Alaska. Results indicated that juvenile coho salmon and Dolly Varden diets were strongly coupled to the riparian zone, with more than half their diet sourced from terrestrial invertebrates. Meanwhile, riparian beetles and spiders utilised the reciprocal aquatic subsidy flux to a lesser extent. Prey body size was an important factor for both aquatic and terrestrial consumers, with larger sized prey a dominant food source.

5.1 Introduction

Riparian zones are unique and complex habitats, acting as an ecotone linking terrestrial and stream ecosystems (Naiman and Décamps, 1997). Nutrient movements across riparian zones are termed 'subsidies' because the movement of resources provides additional nutrients to the recipient habitat (Polis et al., 1997, Richardson and Sato, 2014). Examples include leaves from riparian vegetation and terrestrial invertebrates falling into streams, and adult aquatic insects emerging into the terrestrial environment. Stream and riparian zones are excellent systems to study such subsidies because of their high edge ratio (Richardson et al., 2010), which enhances resource exchange. Seminal work by Polis and Hurd (1995, 1996) on desert island ecosystems highlighted the importance of incorporating the focal habitat into the wider spatial heterogeneity of other habitats and showed that high densities of consumers can be maintained in relatively unproductive environments by such movements of subsidies (see also Power, 2001, Fausch et al., 2002). These 'spatial couplers' (*sensu* Hagen et al., 2012) provide the link between the aquatic and terrestrial ecosystems and *vice versa*.

Research on subsidies associated with lotic systems has mainly concentrated on the terrestrial input to streams, such as leaves and invertebrates (e.g. Cloe III and Garman, 1996, Wipfli, 1997, Bridcut, 2000, Kawaguchi and Nakano, 2001, Nakano and Murakami, 2001, Allan et al., 2003, Kawaguchi et al., 2003, Baxter et al., 2004, Romero et al., 2005, Rundio and Lindley, 2012, see also reviews by Baxter et al., 2005, Richardson and Sato, 2014). This is a natural focus, as subsidies generally gravitate towards low points of the physical environment, which are most frequently bodies of water (Leroux and Loreau, 2008). The River Continuum Concept (Vannote et al., 1980) identified the importance of headwater streams for the terrestrial to aquatic subsidy flux as channels are relatively narrow and closely linked to their riparian zone. This is in comparsion to higher-order, wider rivers which are often less tightly coupled to their riparian zone due to their lower surface area to volume ratio. The consumption of allochthonous (i.e. terrestrial) subsidies by fish has been widely documented and includes a range of invertebrate taxa (e.g. beetles, spiders, true bugs, wasps, and various flies; Jellyman, 1979, Hubert and Rhodes, 1989, Garman, 1991, McDowall et al., 1996).

Subsidies are not unidirectional: nutrients also move from the aquatic to the terrestrial (riparian) environment. Examples of terrestrial consumers utilising emerging aquatic insects include beetles (Hering and Plachter, 1997, Paetzold et al., 2005, Paetzold et al., 2006, Henshall et al., 2011, O'Callaghan et al., 2013), spiders (Collier et al., 2002, Sanzone et al., 2003, Paetzold et al., 2005, Paetzold et al., 2006, Burdon and Harding, 2008, including those that hunt directly from the water surface: Greenwood and McIntosh, 2008), lizards (Sabo and Power, 2002a, 2002b), bats (Fukui et al., 2006) and birds (Nakano and Murakami, 2001, Murakami and Nakano, 2002, Iwata et al., 2003, Uesugi and Murakami, 2007). Bears and wolves also actively target anadromous spawning salmon thereby transferring marine derived nitrogen (MDN) to the terrestrial environment via salmon carcass deposition, and through urine and faeces (Helfield and Naiman, 2006). Terrestrial invertebrates may also consume fish, which become stranded on stream edges after spawning, or are removed and partially consumed by vertebrate predators (Naiman et al., 2002).

The riparian habitat itself can act as a modifying filter for subsidies moving between the stream and the riparian zone in either direction. Studies indicate that increasing complexity (e.g. overhanging tree branches) acts to strengthen the linkages between the stream and riparian zone. For example, Kawaguchi and Nakano (2001) found grassland streams contributed fewer terrestrial invertebrates to the diets of salmonids as compared to forested streams, and England and Rosemond (2004) found that deforestation led to decreased terrestrial invertebrate input. The type of vegetation can also have an effect: younger, alder dominated riparian vegetation contributed greater quantities of terrestrial invertebrates to salmonid diets in coastal Alaskan streams than old growth, conifer-dominated riparian forests (Wipfli, 1997, see also Allan et al., 2003). Riparian vegetation can also act as a barrier to emerging aquatic insects by restricting lateral dispersal (Greenwood, 2014). Spiders foraging at the stream edge were found to have sourced a greater proportion of their diet from aquatic sources than those further from the stream, particularly in open (grassland) habitats as opposed to shrub land (Greenwood, 2014). Typically, the aquatic subsidy is important only very close to the stream edge (<1.5m from the stream; Muehlbauer et al., 2014) indicating the effect of terrestrial filters (such as vegetation) on aquatic insect dispersal. Terrestrial predators, such as beetles and spiders, therefore aggregate at the stream edge (Paetzold et al., 2005), with some species being stream-edge specialists (Langhans and Tockner, 2014), which presumably also increases the probability of individuals entering the water column and becoming a subsidy themselves, for example by being washed into the stream if water levels rise.

Subsidy size may also have an effect on its utilisation by consumers. Salmonids, and many other fish species, are visual foragers (Hynes, 1970, Fraser and Metcalfe, 1997), and hence the typically larger size of terrestrial invertebrates, as compared to aquatic invertebrates, means they provide an important food source for foraging fish (Nakano et al., 2001). The large, dark shape of a terrestrial invertebrate silhouetted against incoming light is more visible on the water surface than more cryptic aquatic invertebrates, which are frequently well camouflaged on the stream substrate, or seek refuge in interstitial spaces. Terrestrial invertebrates also have a higher calorific value compared to aquatic invertebrates (Cummins and Wuycheck, 1971), which means that they are also a much higher quality resource for fish. Evidence regarding the preference of terrestrial invertebrates for prey taxa of a certain size is limited in the aquatic to terrestrial subsidy literature. However, extensive work on beetles on alpine floodplains showed that the relatively large carabid beetle *Nebria* fed on larger prey than the smaller *Bembidion* (Hering and Plachter, 1997). Hering and Plachter (1997) also found that *Nebria* consumed more individuals of the larger stonefly *Isoperla* than the more abundant, but smaller, stonefly *Leuctra*, suggesting a preference towards larger food items.

The two-way exchange of resources was the focus of this study. Most research into resource subsidies have emphasised small spatial scales (such as single streams or rivers) and only a few address temporal variability (e.g. Paetzold et al., 2005, O'Callaghan et al., 2013). To our knowledge, large scale spatio-temporal studies examining how floodplain succession influences resource subsidies have not been attempted. Glacier Bay, in southeast Alaska, is relatively undisturbed by anthropogenic activities and provides a unique opportunity to fulfil this research gap as this ‘natural laboratory’ has a long history of research into ecosystem development following glacial retreat. Firstly, the area has been well studied in terms of the development of vegetation as glaciers have receded over a period of c.250 years (Cooper, 1923, Chapin et al., 1994). Numerous studies have also been undertaken which describe how the aquatic community has developed over time since streams have been released from glacial influence (e.g. Milner, 1994, Flory and Milner, 2000, Milner et al., 2008, Milner and Robertson, 2010, Milner et al., 2011). Habitat complexity has also been found to change as floodplains age: there is an increase in complexity on floodplains over time, with mid-aged sites having the highest in-stream habitat complexity (Klaar et al., 2009). Older sites also support a mixed riparian forest containing cottonwood, willow and conifers (as opposed to the young streams which are almost entirely bordered by dense alder forest), which may decrease the permeability of the riparian zone to emerging aquatic insects.

5.2 Study aim and research questions

The aim of this study was to determine whether aquatic and riparian communities become more tightly coupled, in terms of a greater reliance on aquatic and terrestrial resources (by terrestrial and aquatic consumers respectively) as they develop along a successional gradient in Glacier Bay, Alaska. It was anticipated that prey size would also be important in terms of the utilisation of subsidies, with larger prey being more important to consumers due to their greater visibility and higher calorific value. However, consumer size constraints are likely to be a major factor, with fish less gape-limited than riparian invertebrates due to their relatively larger size compared to their potential prey. Therefore an additional aim of this study was to determine if larger prey items comprised a greater proportion of consumer diets than smaller taxa. The specific research questions addressed were:

- Would the contribution of terrestrial sources to the diet of juvenile coho and Dolly Varden be highest at the oldest sites where floodplain development (e.g. increased stability of the riparian zone and greater number of different habitats as vegetation develops) supports more terrestrial invertebrates?

- Would riparian beetles source the largest proportion of their diet from aquatic resources and would this be highest at the oldest streams due to increased aquatic invertebrate richness and abundance with floodplain age?
- Would riparian spiders source the largest proportion of their diet from aquatic resources and would this be highest at the oldest streams due to increased aquatic invertebrate richness and abundance with site age?
- Do larger aquatic or terrestrial prey form a greater proportion of the total diet of terrestrial or aquatic consumers respectively compared to smaller prey as they are energetically more favourable food items?

5.3 Methodology

Glacier Bay National Park and Preserve, in southeast Alaska, is a unique area for studying ecosystem development following well documented and rapid glacial retreat (Miller, 1964, Milner et al., 2007, Milner and Robertson, 2010). Spanning an area of 11,000km^2, it is a deglaciated landscape over 220 years old (Milner and Robertson, 2010), surrounded by mountains rising to 5000m above sea level and including many kilometres of shoreline, exposed bedrock, unconsolidated glacial sediments and temperate rainforest (Milner et al., 2007). The last glacial maximum occurred around 1700 and glacial recession began (with some regional re-advances) between 1735 and 1785 (Miller, 1964; Figure 5.1). The climate of Glacier Bay is temperate maritime, with mean monthly temperatures ranging from -3°C to 13°C and a mean annual precipitation of 1400mm (Milner and Robertson, 2010).

Table 5.1: Stream floodplains sampled in Glacier Bay, age indicates the length of time the stream mouths have been ice-free

Stream	Code	Age (years)	Longitude	Latitude	Dominant riparian vegetation	Large woody debris present in stream channel
Upper Muir 1	UM*	<20	59°04’43.1”	136°19’10.8”	*Dryas* sp.	No
Upper Muir 2	UM*	<20	59°04’02.5”	136°17’09.9”	*Dryas* sp.	No
Wolf Point Creek	WPC	55	58°59’48.3”	136°10’18.1”	Alder, some cottonwood	No
Nunatak Creek	NUN	70	58°58’40.5”	136°5’41.2”	Alder, cottonwood	No
Ice Valley Stream	IVS	130	58°49’10.9”	136°9’49.6”	Alder, spruce	Yes
Berg Bay South Stream**	BB	170	58°30’17.5”	136°14’0.62”	Alder, spruce, cottonwood	Yes
Rush Point Creek	RPC	200	58°28’11.2”	136°06’08.5”	Spruce	Yes

*Samples from Upper Muir 1 and 2 were combined as one site for the analysis due to low sample number
**Berg Bay South Stream hereafter referred to as Berg Bay

5.3.1 Sampling design

Five streams were sampled during each of the summers of 2013 and 2014 (Figure 5.1; Table 5.1). Streams were selected to represent a range of floodplain ages and complexity. For each stream, one reach (c.10m long) was selected, approximately 0.75km from the stream mouth (*sensu* Milner et al., 2008). Each reach consisted of an unvegetated gravel bank, with riparian forest behind. Two streams, additional to the main five, in Upper Muir inlet were sampled once in 2014. Access to this part of Glacier Bay by motorized boat was not permitted for much of the field season, hence the single field visit. The data presented from these two sites are limited, but included for comparison.

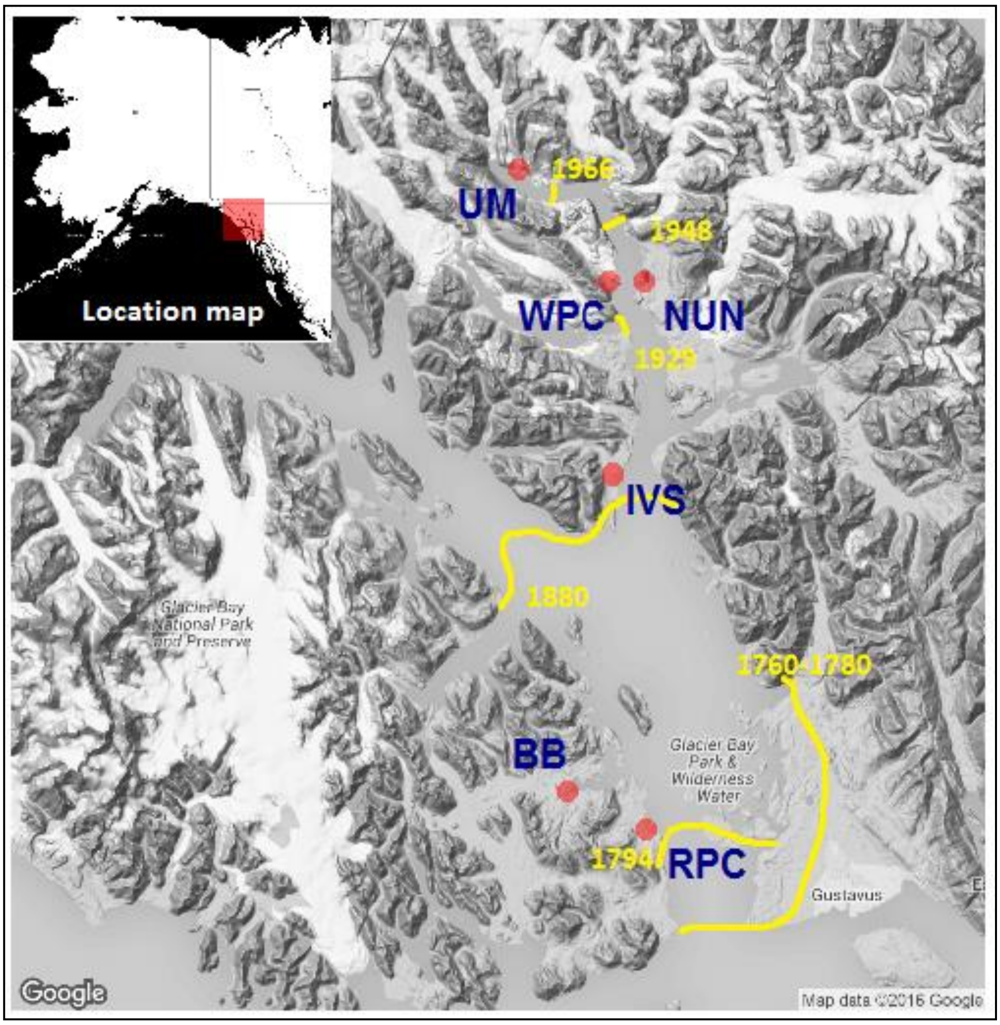

Figure 5.1: Location of field sites in Glacier Bay National Park and Preserve. Sites codes correspond to names in Table 5.1

5.3.2 Sample collection

Terrestrial and aquatic consumers were collected twice at each site (in summer 2013 and 2014) along with their food sources. Carabid beetles and spiders constituted the terrestrial consumers, and juvenile coho (*Onchorhynchus kisutch*) and Dolly Varden charr (*Salvelinus malma*), as the only fish species collected, were the aquatic consumers. End members for each consumer were identified *a priori* (*sensu* O'Callaghan et al., 2013). Aquatic macroinvertebrates and riparian invertebrates were used as autochthonous and allochthonous food sources respectively for the juvenile coho and Dolly Varden. No aquatic macrophytes were present in any of the streams and algae were present in low abundance. For the terrestrial consumers (beetles and spiders), food sources were aquatic macroinvertebrates, and terrestrial leaves collected from the dominant riparian vegetation. Riparian beetles were included as a third end member for spiders. Terrestrial prey for beetles and spiders includes small invertebrates, such as aphids, mites and Collembola (Lovei and Sunderland, 1996, O'Callaghan et al., 2013), but none were collected in pitfall traps or found when hand searching, so basal resources (leaves) were substituted into the analysis as a surrogate; leaves have been used as basal resources for terrestrial consumers in other studies (Paetzold et al., 2005).

Three replicate samples of aquatic macroinvertebrates were collected using a modified Surber (0.1m^2, mesh size 250µm) at each site. Invertebrates were held in containers of stream water for at least 24h to empty their digestive tracts. Additional macroinvertebrate samples were collected by hand searching under stones in the stream. Juvenile salmonids were collected at each stream using minnow traps, baited with salmon eggs (pre-soaked in Betadyne iodine solution) held in a perforated plastic ‘Kinder egg’ capsule. Streams were fished for 90 minutes on each sampling occasion (Bryant, 2000). Three traps were placed in pools and backwaters of the main stream channel in 2013, and ten traps were used in 2014. A maximum of five individuals were sacrificed for stable isotope analysis in 2013 and up to twenty in 2014 (as per the Alaska Department of Fish and Game permit). Surplus trapped fish were released back into the stream. No unintended fish deaths occurred during the course of the study.

Terrestrial invertebrates were collected using live (i.e. without preservative) pitfall traps: 500ml plastic cups with diameter 9cm, which was within the recommended diameter range of 6.5-11.2cm suggested by other studies (Woodcock, 2008, Hancock and Legg, 2012). Traps were covered by wire mesh to prevent entry by small mammals, particularly shrews. Mesh size was 2cm, but enlarged to 3cm in length at the trap edges (see Chapter 2). Traps were placed at the edge of the stream channel (<50cm from the stream edge) for 24h. Attempts were made to also collect invertebrates in the riparian forest for comparison, but traps were unsuccessful (frequently catching <3 individuals of any species). Invertebrates were removed and kept alive for at least 24h to empty their digestive tracts, and were then frozen. Additional samples were collected by hand searching. Samples of leaves were collected from each dominant riparian tree species at each site, and were frozen until further processing.

5.3.3 Sample processing

To determine if fish preferred larger sized terrestrial invertebrates, the body length of beetles was measured using an eye-piece graticule as the length from the tip of the labrum to the apex of the elytra. Beetles were then identified to generic level using Lindroth (1969). Aquatic invertebrates were identified to Order. It was assumed that aquatic insects were consumed as adults by riparian predators, and as no adults were collected, measurements of body length could not be taken (body length of aquatic larvae would not be representative of adult size as the population would likely contain several instars of varying sizes). Samples were then dried at 60°C for 24 hours (Chaloner et al., 2002, O'Callaghan et al., 2013), ground into a powder, and weighed (animal matter: 0.7 ± 0.1mg; plant matter: 1.5 ± 0.1mg) before combustion. Smaller invertebrate samples comprised multiple individuals, whereas for larger individuals, sub-samples of the whole animal or plant were used. Samples were analysed simultaneously for ^{13}C and ^{15}N using a Thermo Delta V isotope ratio mass spectrometer (IRMS) interfaced with a Costech ECS 4010 elemental analyser (EA) in 2013 and a Thermo Delta XP isotope ratio mass spectrometer (IRMS) interfaced with an Elementar Pyrocube elemental analyser (EA) in 2014. Isotopic analysis was carried out at the SUERC facility in East Kilbride, Scotland. Analytical precision was ± 0.07 $\delta^{13}C$ and ± 0.09 $\delta^{15}N$ (2013 runs), and ± 0.07 $\delta^{13}C$ and ± 0.11 $\delta^{15}N$ (2014 runs) calculated from in-house standards.

5.3.4 Data analysis

Data were first assessed for outliers using Cleveland dot plots and tested for normality (Zuur et al., 2010). Where fewer than three individuals were collected from a habitat, taxa were not included in the analysis. Data were not normally distributed; therefore the statistical differences between groups (isotopic values of end members) were calculated using the non-parametric Mann-Whitney U test. All analyses were undertaken using R (build v.3.1.1; R Core Team, 2014) and the SIAR package (Parnell et al., 2008). SIAR plots consumers and dietary sources to visually represent trophic positions in the riparian and aquatic food webs. SIAR can also be used to model estimated proportional diet sources of consumers using Bayesian statistics and a Markov Chain Monte Carlo (MCMC) method (Layman et al., 2011, Parnell and Jackson, 2013). The MCMC model was run with 500,000 iterations.

Separate models of dietary composition were created for fish and terrestrial invertebrates. For construction of the initial model, the food sources were grouped together as ‘aquatic’ or ‘terrestrial’ (with ‘beetles’ included for spiders as a third source). After this, food sources were analysed in more detail, with sources separated into Family- or Genus-level groups. Shifts in isotope ratios may occur between trophic levels due to differential fractionation of the carbon and nitrogen isotopes during metabolic processes (such as the preferential uptake of the lighter isotope). This is called the 'trophic shift' and in order to account for these processes, the mixing models used to calculate dietary source proportions incorporate literature values for these shifts. Trophic shift values calculated by McCutchan et al. (2003) for terrestrial invertebrates ($\Delta\delta^{13}C$: 0.5 ± 0.19; $\Delta\delta^{15}N$: 2.3 ± 0.24), aquatic organisms ($\Delta\delta^{13}C$: 0.4 ± 0.17; $\Delta\delta^{15}N$: 2.3 ± 0.24) and terrestrial plants ($\Delta\delta^{13}C$: 0.4 ± 0.28; $\Delta\delta^{15}N$: 2.4 ± 0.42) were incorporated into the models used here.

5.4 Results

A total of 962 samples were included in the analysis. Mean values of isotopic N and C for food web components at each site are summarised in Table S5.1 in the Appendix. Sources (terrestrial vs. aquatic) differed significantly in terms of their isotopic composition (Table 5.2) for each site (terrestrial invertebrates and juvenile salmonids as consumers).

Table 5.2: Mann-Whitney U tests for significant differences between isotope values of terrestrial vs. aquatic food sources. Food sources (terrestrial and aquatic) included different taxa for each consumer type and are hence separately analysed for juvenile salmonids and terrestrial invertebrates. Fish were not collected in the Upper Muir streams

	Consumer			
	Juvenile salmonids		**Terrestrial invertebrates**	
Site	**$\delta^{13}C$**	**$\delta^{15}N$**	**$\delta^{13}C$**	**$\delta^{15}N$**
UM			*	*NS*
WPC	**	**	**	**
NUN	**	**	*	**
IVS	**	**	**	*NS*
BB	**	**	**	**
RPC	**	**	**	**

**<0.001; *<0.01; *NS* non-significant

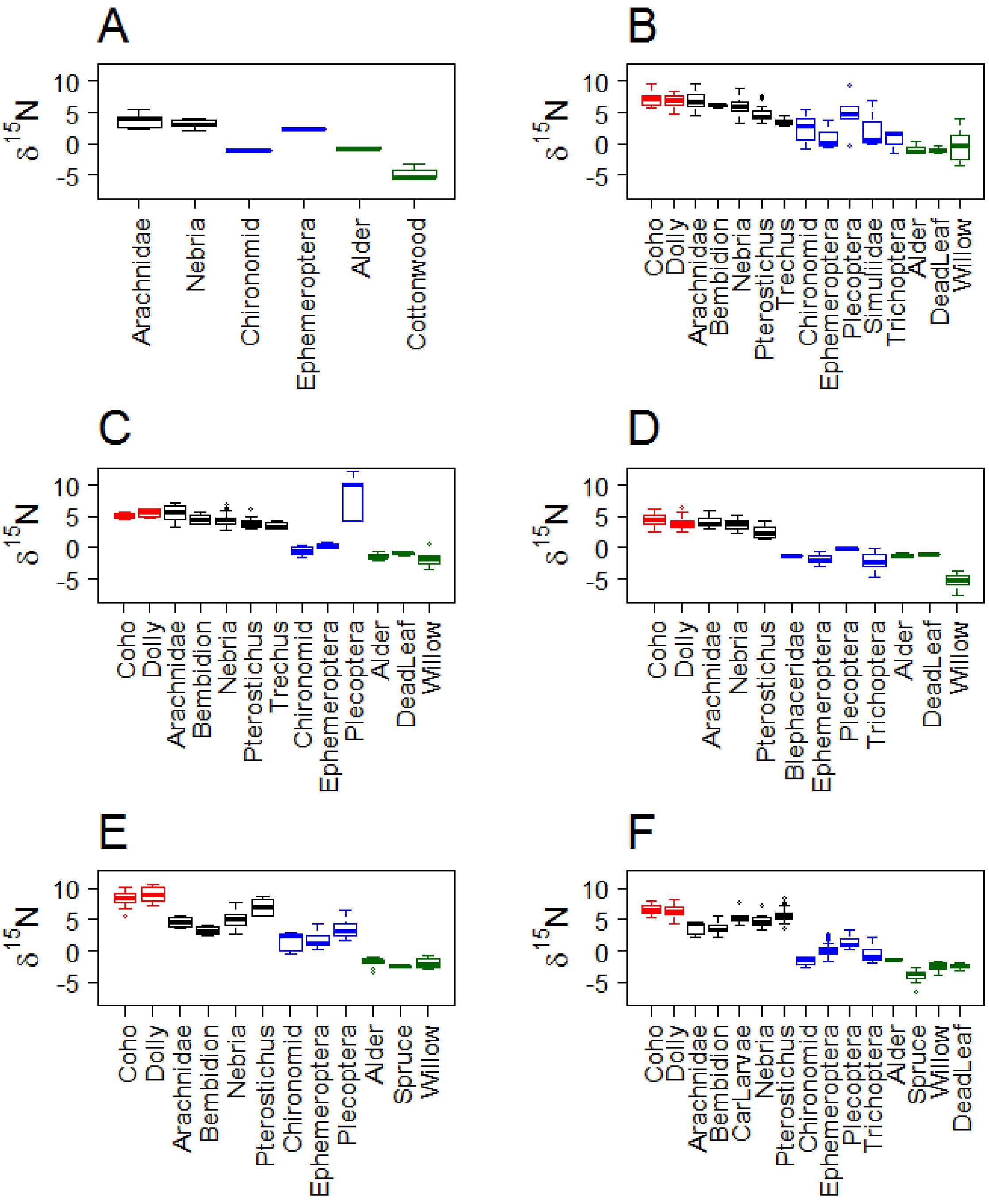

Figure 5.2: Trophic position for taxa at each site (**A**: Upper Muir Streams, **B**: Wolf Point Creek, **C**: Nunatak Creek, **D**: Ice Valley Stream **E**: Berg Bay **F**: Rush Point Creek). Colours indicate the type of taxon (red: juvenile salmonids, black: terrestrial invertebrates, blue: aquatic invertebrates, green: terrestrial leaves. (CarLarvae=Carabid larvae)

5.4.1 Trophic position

δ^{15}N values for consumers and potential sources were compared for each site. Trophic height for the three oldest sites (Figures 5.2D, E, F) were clearly structured, with juvenile coho and Dolly Varden occupying the highest trophic level, indicated by the highest δ^{15}N values, followed by terrestrial invertebrates with a slightly lower mean trophic level, and then aquatic invertebrates. Terrestrial plants occupied the lowest trophic levels at all sites. At Nunatak Creek and Wolf Point Creek spiders (Arachnidae) had a similar isotopic δ^{15}N signature to the fish, and riparian beetles had only slightly lower mean δ^{15}N values (Figures 5.2B-C). Of the aquatic invertebrates, Plecoptera occupied the highest trophic level, most noticeably at Nunatak Creek (Figure 5.2C). Juvenile salmonids were not collected from the Upper Muir streams and terrestrial invertebrates occupied the highest trophic levels at these sites (Figure 5.2A).

Table 5.3: Dietary composition of juvenile salmonids at each site, with beetles separated by genus

		Dietary Proportion (%)						
Taxon	**Site**	**Aquatic**	**Spider**	**Bembidion**	**Nebria**	**Diplous**	**Pterostichus**	**Trechus**
Coho	WPC	28.98	12.67	11.51	27.55	-	13.44	5.84
Dolly Varden		35.57	7.83	9.35	25.02	-	14.94	7.29
Coho	NUN	39.41	7.91	11.01	19.71	-	10.75	11.20
Dolly Varden		27.20	11.85	14.17	17.65	-	14.43	14.69
Coho	IVS	30.37	17.99	-	34.58	-	17.06	-
Dolly Varden		43.42	7.33	-	42.98	-	6.26	-
Coho	BB	12.52	10.27	7.07	16.80	53.34	-	-
Dolly Varden		2.27	12.50	6.06	11.88	67.29	-	-
Coho	RPC	5.57	21.74	19.68	25.81	27.20	-	-
Dolly Varden		14.01	16.17	17.59	22.98	29.26	-	-

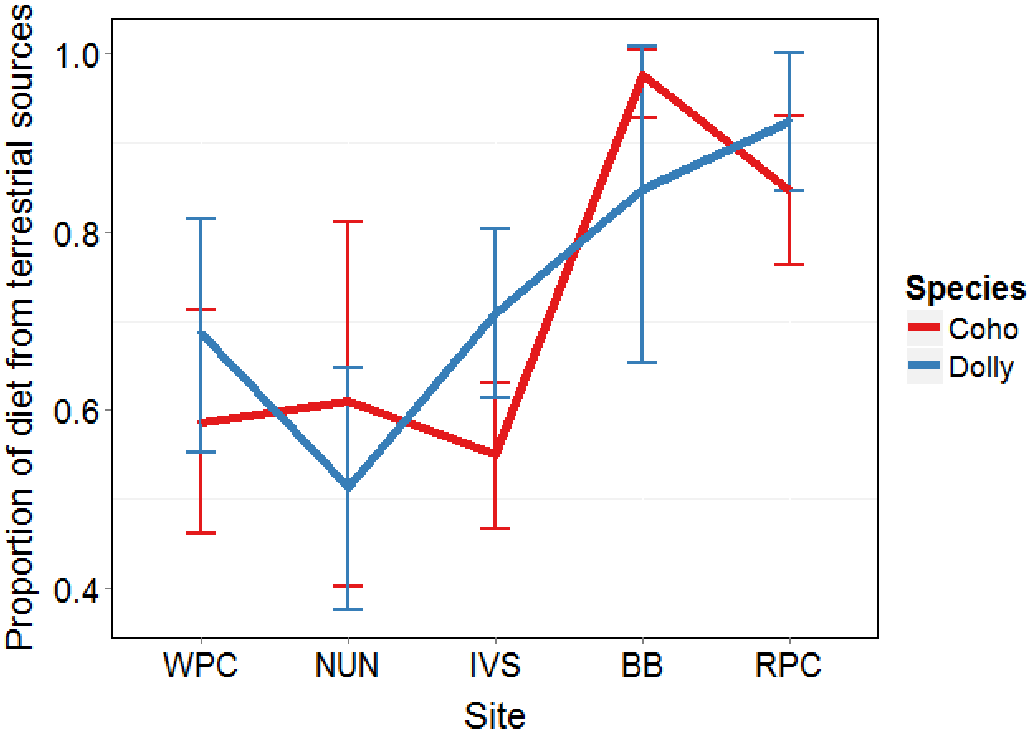

Figure 5.3: Proportional contribution of terrestrial sources to the diet of juvenile coho and Dolly Varden based on Bayesian probabilities. Error bars indicate 95% confidence intervals for the estimated diet source

Table 5.4: Mean body sizes (±1 standard deviation) of riparian beetles collected in Glacier Bay

Genus	Body length (mm)
Bembidion	3.85 (±0.58)
Diplous	9.5 (±0.53)
Nebria	10.26 (±1.10)
Pterostichus	8.09 (±0.43)
Trechus	4.30 (±0.18)

5.4.2 Diets of juvenile coho and Dolly Varden

The mixing model estimated that over half of the diet of both juvenile coho and Dolly Varden was sourced from terrestrial invertebrates (Figure 5.3). Terrestrial invertebrate contribution to diet generally increased with site age, although for juvenile coho terrestrial input was lower at the oldest site. As terrestrial sources made the greatest contribution to diet of juvenile salmonids, these were analysed in more detail (Table 5.3). This analysis showed that *Nebria* and *Diplous* comprised the greatest proportion of juvenile coho and Dolly Varden diet, frequently contributing >25% (except at Nunatak Creek). Other beetles and spiders comprised <20% of the diet for all fish at all sites (except juvenile coho at Rush Point Creek). The mean body sizes of the terrestrial beetles collected on floodplains in Glacier Bay are summarized in Table 5.4. The largest beetles, *Nebria* and *Diplous*, comprised the largest proportion of the diets of juvenile coho and Dolly Varden.

5.4.3 Diets of riparian invertebrates

At most sites, the diets of beetles were estimated to comprise mostly terrestrial food sources (Figure 5.4, Table 5.5), although the proportions varied for each taxon. *Nebria*, the only carabid beetle present at all sites, increased its consumption of aquatic food sources from 13% at the very youngest (Upper Muir) site to approximately 30% at the two oldest sites. However, consumption of aquatic sources by *Nebria* was estimated to be over 70% at Wolf Point Creek, far higher than at any other site. Wolf Point Creek was the only site where most beetles sourced more than half their diet from aquatic sources. At the very youngest Upper Muir sites, the only beetle present, *Nebria*, consumed almost entirely terrestrial foods, and the same was true of spiders at this site. Spiders consumed mostly riparian beetles at most sites, with very low proportions of their diet from aquatic sources (Table

5.5). The aquatic proportion of the spider diet showed some increase with site age from Wolf Point Creek (Figure 5.4), whilst the proportion derived from beetles decreased. The exception for the spider data were the Upper Muir streams, where the aquatic proportion of the diet was relatively high compared to the other young streams (Table 5.5), although the small sample size reduced confidence in this result.

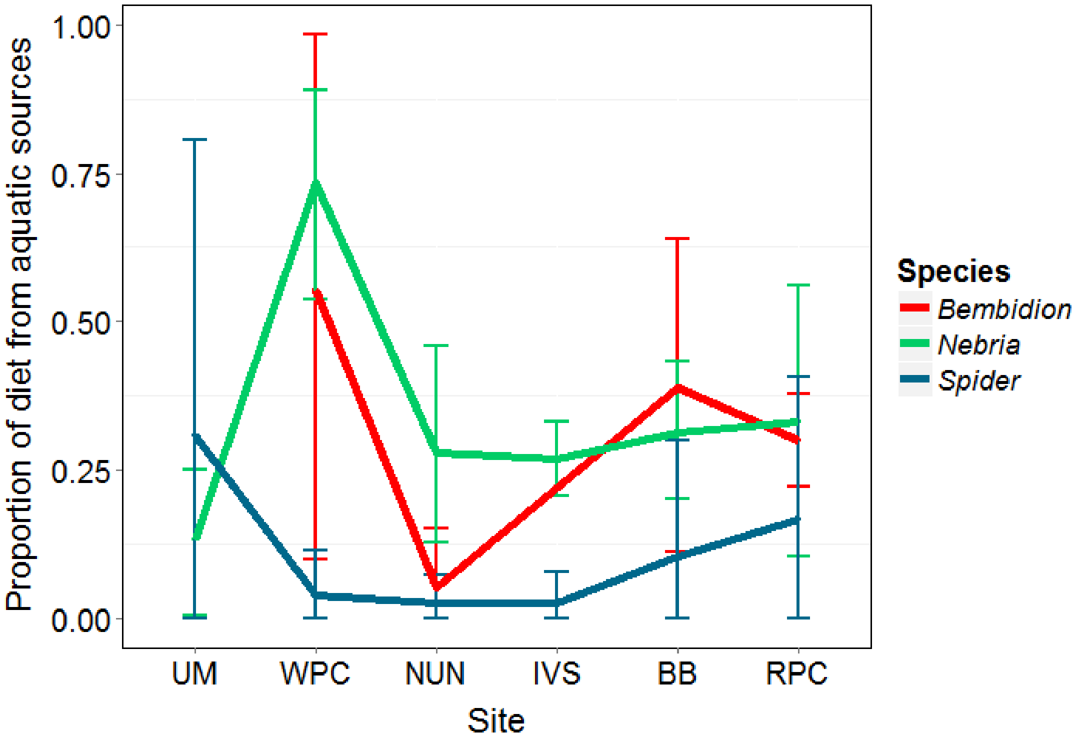

Figure 5.4: Proportional contribution of aquatic sources to the diet of the most widespread riparian invertebrates based on Bayesian probabilities. Error bars indicate 95% confidence intervals for the estimated diet source

Table 5.5: Dietary composition of riparian invertebrates at each site

	Dietary Proportion (%)												
Taxon	***Bembidion***		***Nebria***		***Diplous***		***Pterostichus***		***Trechus***		**Spider**		
Site	**Aquatic**	**Terrestrial**	**Aquatic**	**Terrestrial**	**Aquatic**	**Terrestrial**	**Aquatic**	**Terrestrial**	**Aquatic**	**Terrestrial**	**Aquatic**	**Terrestrial**	**Beetle**
UM	-	-	13.24	86.76	-	-	-	-	-	-	14.08	32.21	53.71
WPC	55.22	44.78	73.44	26.55	-	-	58.11	41.89	40.83	59.17	3.86	11.62	84.52
NUN	5.07	94.93	27.77	72.23	-	-	2.98	97.02	26.06	73.94	2.72	17.40	79.88
IVS	-	-	26.78	73.22	-	-	9.98	90.02	-	-	2.63	26.14	71.23
BB	38.75	61.24	31.42	68.58	41.25	58.75	-	-	-	-	10.54	40.69	48.77
RPC	29.91	70.09	33.22	66.78	44.24	55.76	-	-	-	-	16.75	38.66	44.58

Table 5.6: Dietary composition of riparian beetles at each site, with aquatic invertebrates separated by family. Upper Muir beetle diets could not be separated further due to a lack of multiple sources (the aquatic component consisted of mostly chironomids and only one Ephemeroptera). The terrestrial component refers to riparian leaves

		Dietary Proportion (%)						
Taxon	**Site**	**Blephariceridae**	**Chironomidae**	**Ephemeroptera**	**Plecoptera**	**Simuliidae**	**Trichoptera**	**Terrestrial**
Bembidion	**WPC**	-	17.90	16.22	21.42	15.30	14.71	14.45
Nebria		-	34.66	9.72	35.05	7.30	7.21	6.06
Pterostichus		-	20.38	15.92	29.10	4.95	7.75	21.89
Trechus		-	16.40	17.48	13.90	14.81	17.23	20.18
Bembidion	**NUN**	-	5.24	3.57	33.27	-	-	57.93
Nebria		-	7.92	5.46	32.90	-	-	53.71
Pterostichus		-	2.62	1.79	27.71	-	-	67.88
Trechus		-	19.86	16.97	22.49	-	-	40.68
Nebria	**IVS**	0.87	-	1.11	49.53	3.00	7.10	38.39
Pterostichus		6.78	-	8.35	24.12	15.12	19.63	26.01
Bembidion	**BB**	-	8.85	10.79	34.44	-	-	45.91
Nebria		-	2.70	3.34	67.42	-	-	26.54
Diplous		-	10.76	13.07	43.77	-	-	32.40
Bembidion	**RPC**	-	1.42	1.05	83.60	-	3.60	10.33
Nebria		-	11.45	8.60	35.35	-	19.95	24.65
Diplous		-	2.38	3.19	88.51	-	3.99	1.93

Table 5.7: Dietary composition of riparian spiders at each site, with aquatic invertebrates separated by family and beetles by genus, Upper Muir spider diets could not be separated further due to a lack of multiple sources (the aquatic component consisted of mostly chironomids and only one Ephemeropteran). The terrestrial component refers to riparian leaves

	Dietary Proportion (%)											
Site	**Blephaceridae**	**Chironomidae**	**Plecoptera**	**Simuliidae**	**Trichoptera**	**Ephemeroptera**	**Terrestrial**	**Bembidion**	**Nebria**	**Diplous**	**Pterostichus**	**Trechus**
WPC	-	3.34	3.38	2.00	2.55	3.12	3.99	29.88	7.80	-	12.49	31.43
NUN	-	2.25	5.95	-	-	1.60	11.94	17.08	7.90	-	25.31	27.97
IVS	1.15	-	4.03	2.49	4.57	1.48	8.89	-	58.76	-	58.76	-
BB	-	9.00	11.09	-	-	9.37	24.63	18.26	15.37	12.28	-	-
RPC	-	11.06	12.62	-	12.60	9.23	15.25	13.59	13.44	12.21	-	-

The diets of terrestrial consumers, beetles (Table 5.6) and spiders (Table 5.7), were analysed in more detail by separating the aquatic component of the diet into individual families. As the terrestrial component was inferred through the use of riparian leaves, it was not possible to resolve this element further. For spiders, the beetle component of the diet was also separated into genera (Table 5.7). Plecopterans were the most important aquatic component of beetle diets, comprising >20% (except *Trechus* at WPC). Dipterans formed a smaller proportion of the beetle diets, particularly at the oldest sites. Terrestrial food sources were most important for beetles at Nunatak Creek, and at Wolf Point Creek diets were split more evenly between the different food sources than at any other site. For spiders, Plecoptera comprised a smaller proportion of the diet than for beetles (Table 5.7). *Pterostichus*, *Trechus*, and *Bembidion* were the most important food sources for spiders at Wolf Point and Nunatak Creeks, whereas at the two oldest sites, spider diets were more evenly split between food sources. More detailed analysis could not be carried out on the Upper Muir streams due to insufficient data.

5.5 Discussion

This study has provided evidence for reciprocal subsidy flows across the riparian-stream interface on floodplains of different ages, with terrestrial invertebrates forming the largest component of fish diets and emerging aquatic invertebrates being consumed by riparian beetles and spiders. There was also evidence that prey body size was important, as larger invertebrates contributed more to the diets of both aquatic and terrestrial consumers than smaller taxa.

5.5.1 Trophic structuring

This study was the first to investigate food web linkages in relation to reciprocal subsidy movement across catchments of different ages. Results indicated that although stream physical characteristics may differ between sites, trophic structuring remained relatively stable over time. Juvenile coho and Dolly Varden occupied the highest trophic levels, followed by aquatic invertebrates and plants, consistent with the findings of other studies (Doucett et al., 1996, Collier et al., 2002, Coat et al., 2009). Riparian invertebrates occupied a similar trophic level to the juvenile salmonids, suggesting a mainly predatory diet, shown to be comprised of both aquatic and terrestrial prey. The higher $\delta^{15}N$ signature of juvenile Dolly Varden and coho compared to riparian beetles, particularly at the older sites, suggested feeding on carabid beetles (especially *Nebria* and *Diplous*), as well as aquatic invertebrates. This was supported by the isotope mixing model results for both juvenile coho and Dolly Varden, which estimated that carabid beetles were a dominant food source. The relatively high $\delta^{15}N$ values for Plecoptera, as compared to other aquatic insects, could indicate that this group was predatory on other aquatic invertebrates. Gut content analysis of stonefly individuals from these streams provided evidence that individuals had consumed chironomids whereas other invertebrate diets were dominated by diatoms (Chapter 4), which supported the findings from the stable isotope analysis. The $\delta^{15}N$ values for alder leaves were close to 0, consistent with alder being a nitrogen fixer (Johnston et al., 1997; cited by Chaloner et al., 2002). The differences between the $\delta^{15}N$ values for different food web components (i.e. between carabid beetles and terrestrial leaves) exceeded the isotopic enrichment factors put forward by both DeNiro and Epstein (1981) and McCutchan et al. (2003). This suggested that some intermediate steps may have been excluded from the system presented here, for example, between terrestrial leaves and riparian carabid beetles there may be intermediate terrestrial invertebrates (e.g. Collembola) which consumed basal terrestrial resources and were then predated on by riparian beetles. These findings emphasise the limitations of using stable isotope dietary analysis as it is often difficult to sample all end members in a community, although it was clear that this remains a useful method for determining the overall trophic structure of a community.

5.5.2 Food source

The diet of juvenile coho and Dolly Varden at all sites was predominantly of allochthonous (terrestrially derived) origin. The terrestrial proportion of diet increased with site age for juvenile Dolly Varden from Nunatak Creek to Rush Point Creek. Juvenile coho sourced the greatest proportion of their diet from terrestrial resources at the second oldest site, Berg Bay. Stomach contents analysis of the same individuals from a complementary study found that the proportion of terrestrial invertebrates in the stomachs of juvenile coho and Dolly Varden increased with site age up until Berg Bay, before declining at the oldest site (Chapter 3). Observations of large quantities of woody debris in the stream channel at Berg Bay suggested that an increase in site complexity led to increased terrestrial invertebrate input to diet, especially as fish stomachs also contained wood-specialist beetles found at Berg Bay and not at any other sites (Chapter 3). The close agreement between the results of two different methods for assessing fish diets provided strong evidence that fish were utilising allochthonous resources as part of their diet, which agreed with the findings from other studies (e.g. Hubert and Rhodes, 1989, Nakano and Murakami, 2001, Allan et al., 2003).

Juvenile coho and Dolly Varden in streams in Glacier Bay successfully utilised terrestrial invertebrates which entered the water column across the range of streams sampled, either from invertebrates falling in from riparian vegetation or those washed in from the stream edge. Although successional processes have not been previously examined in terms of changes in subsidy fluxes, differences in riparian vegetation have been investigated formerly and found to influence fish diets; for example, riparian vegetation contributes more terrestrial prey to streams than open grassland (Dineen et al., 2007b). However, in contrast to Wipfli (1997), the younger streams in Glacier Bay, which were dominated by alder, were found not to provide greater quantities of terrestrial invertebrates than the older, conifer dominated streams. It could be that diversity of vegetation was more important in the provision of allochthonous resources to streams than stream age alone. Vegetation diversity was not quantified here, but Glacier Bay streams could have a more diverse riparian forest than the streams studied by Wipfli (1997), or that they contain more woody debris accumulations (particularly at Berg Bay). The streams in the study by Wipfli (1997), although also situated in southeast Alaska, had a history of logging activity, which Glacier Bay does not, and this could be a confounding factor when comparing these results to Wipfli's study.

The results of the more detailed dietary analysis for juvenile coho and Dolly Varden suggested that prey size is an important factor as larger food resources contributed more to diet, as was expected. The large beetles, *Nebria* and *Diplous*, frequently contributed >25% to the diet of the juvenile salmonids. These larger invertebrates could be more mobile and therefore have an increased probability of falling or being washed into the stream. Alternatively, as salmonids often feed by sight (Hynes, 1970, Fraser and Metcalfe, 1997) larger beetles may be more visible targets for foraging fish. Spiders typically comprised a smaller proportion of the diet than the large beetles. Although most of the spiders collected appeared to be large, highly mobile wolf spiders (Lycosidae), their diets indicated a reliance on carabid beetles rather than aquatic invertebrates, in contrast to the findings of Paetzold et al. (2005). The spiders occupying the riparian zones of the Glacier Bay streams may therefore be active in the riparian zone in order to hunt for beetles, but if they are not actively feeding on emerging aquatic invertebrates, they may be distributed further from the stream edge, and therefore are less likely to fall or be washed into the stream. Spiders, particularly at the younger sites, also occupied similar trophic levels to the juvenile salmonids, which reinforced the conclusion that they did not fall into the stream and become food sources for fish, but in fact were consuming similar resources (riparian beetles). The low contribution of spiders to fish diets supported the stomach contents analysis (Chapter 3) carried out on the juvenile coho and Dolly Varden, which also showed spiders to be rarely ingested.

Although the diets of the fish in the sampled streams indicated a high reliance on allochthonous resources, the riparian consumers were not so strongly coupled to the reciprocal subsidy flux. The diets of beetles were predominantly comprised of terrestrial food sources at all sites apart from Wolf Point Creek. Emergence timings were not taken into account in this study (emergence traps were placed on the streams in 2013, but were damaged during high flow events and could not be redeployed), and sampling of terrestrial invertebrates may have missed the peak availability of aquatic resources, although sampling did occur over most of the summer season. Stenroth et al. (2015) estimated that overall, aquatic food sources contributed 43% to the diets of the beetles in their study, which is within the range of some of the estimations in this study, but contrasts to the highly (>80%)

aquatic-based diets of beetles in a study by Paetzold et al. (2005). Aquatic productivity was not measured directly in this study and nor was it recorded in Paetzold et al. (2005), which means that it is uncertain whether differences in aquatic food source utilisation between this study and that by Paetzold et al. (2005) are due to production or utilisation differences. At the youngest sites (Upper Muir Inlet) there were very few aquatic invertebrates, and the few that were present were predominantly Chironomidae. The restricted abundance and diversity at these sites could explain the low proportion of aquatic sources in the diets of the terrestrial invertebrates. The high proportion of beetle diets sourced from aquatic items at Wolf Point Creek could be due to lower abundances of terrestrial food items, which would agree with the fish diets, where aquatic sources were more important than at older sites. As site age increases, and terrestrial resources perhaps increased in abundance, consumers (riparian beetles and juvenile coho and Dolly Varden) were likely to consume these resources instead of aquatic items, which may be less available (e.g. aerial adult life stages would mostly not be available to ground predators).

The more detailed analysis of the diets of the carabid beetles indicated that Plecoptera were frequently a more important food source than all other aquatic invertebrates. Even where the terrestrial proportion of beetle diets exceeded the aquatic, Plecoptera comprised more than 20% of the beetles' diets (except *Trechus* at Wolf Point Creek). This may be related to size, with adult Plecoptera larger than adult Dipterans, and therefore potentially a higher quality food source, or were perhaps easier to predate (due to higher visibility as a result of a larger body size). Plecoptera often emerge on to land prior to their last moult and are hence vulnerable to predation by riparian invertebrates during this time (Hering and Plachter, 1997). *Pterostichus, Trechus,* and *Bembidion* collected at these sites are small beetles (c. 8mm, c. 4mm, and c. 4mm body length respectively at these sites), so it is surprising that the large Plecoptera comprised a significant proportion of the diet of these beetles. This contrasts to the findings of Hering and Plachter (1997) where chironomids were most important to the diets of riparian *Bembidion*. *Nebria* and *Diplous*, meanwhile, were large (c.10mm) so consumption of Plecoptera would be expected, and Hering and Plachter (1997) showed similar diets for *Nebria picicornis* on alpine floodplains in Germany. Stenroth et al. (2015), meanwhile, found that riparian carabid beetle abundance was related to the abundance of Diptera (Nematocera) and terrestrial insect biomass, which contrasted to this study, where Diptera contributed very little to carabid beetle diets compared to Plecoptera and terrestrial food sources.

Riparian spiders predominantly consumed carabid beetles at all sites, contrary to what was anticipated. However, the proportion of diet sourced from aquatic invertebrates, although low, increased for spiders with site age (excluding the Upper Muir streams), and led to a consequent decrease in the proportion of the diet sourced from beetles; however beetles remained the dominant food source. The large *Nebria* comprised <20% of spider diets at most sites, often less than the smaller beetles, which suggested that prey size might have some impact on spider diets. The spiders were observed to be much larger at the four youngest sites where beetles formed a larger proportion of spider diets, as compared to Berg Bay and Rush Point Creek, suggesting that it was the larger spider taxa which were more likely to consume relatively large prey, such as terrestrial beetles. Unfortunately no keys to the spider taxa of this region were available for identification, but it was likely that larger spiders were Lycosidae (wolf spiders) and the smaller were Linyphiidae. Differences in spider guilds can lead to different resource utilisation (Collier et al., 2002), therefore further investigation of spider diets at the generic or specific level in Glacier Bay is certainly warranted.

The low proportions of aquatic-derived food in the spider diets contrasts with the findings of Collier et al. (2002), who reported that more than 50% of spider diets in the riparian zone of a New Zealand stream were aquatic in origin (see also Sanzone et al., 2003, Paetzold et al., 2005). In an exclusion experiment in the coastal rainforest of British Columbia, spider abundance declined alongside stream reaches in which aquatic insect emergence had been experimentally reduced (Marczak and Richardson, 2007, see also Kato et al., 2003) and spider biomass was positively related to the resource pool of aquatic insects in New Zealand (Burdon and Harding, 2008, see also Stenroth et al., 2015), suggesting again that spiders were reliant upon aquatic invertebrates. Spider webs can effectively collect emerging aquatic insects (Power and Rainey, 2000) and web-building spiders may source more of their carbon from aquatic insects compared to free-living spiders (Collier et al., 2002, Sanzone et al., 2003, Stenroth et al., 2015). However, the spiders collected in Glacier Bay were collected in pitfall traps or by hand searching the exposed gravel bars. Therefore it is likely that the individuals analysed were free-living and did not build webs, hence the low proportion of aquatic food items in their diet.

5.6 Conclusion

Reciprocal movement of subsidies occurred in streams of different ages in Glacier Bay, Alaska. Juvenile coho salmon and Dolly Varden, which were only present in streams >50 years old, predominantly consumed terrestrial food sources, particularly large riparian carabid beetles. The proportion of terrestrial sources in the diets of juvenile coho and Dolly Varden increased with site age, which can be linked to greater riparian habitat complexity. Riparian carabid beetles utilised aquatic resources, but were not strongly coupled to the aquatic subsidy flux, and terrestrial sources dominated overall. Plecoptera, which were absent at the very youngest sites, were the most important aquatic subsidy for riparian carabid beetles at older sites, which was likely linked to their larger size. Riparian spiders predominantly predated upon riparian beetles and utilised aquatic invertebrates to a lesser extent.

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6

DIETARY BREADTH OF AQUATIC AND RIPARIAN COMMUNITIES ON FLOODPLAINS OF DIFFERENT AGES AND COMPLEXITY

Abstract

Recent advances in stable isotope analysis provide a new approach to studying the dietary breadth of consumers. Coupled with a space-for-time substitution, food web structural changes and resource utilisation can be analysed across ecologically long timescales. This study showed that both floodplain age and habitat complexity were important factors determining the dietary breadth of consumers. Food web structure of aquatic communities was driven by the consumption of allochthonous resources, which increased as habitat complexity increased, but were only utilised by the top consumers (juvenile coho and Dolly Varden). Riparian communities, meanwhile, were driven by opportunistic feeding strategies and body size constraints, as well as stochastic influences on resource availability.

6.1 Introduction

The niche concept is a fundamental theory of community ecology. The niche of an organism was first defined by Elton (1927, p64) as 'its place in the biotic environment, its relations to food and enemies'. Hutchinson (1957) expanded the definition further to describe a niche as an 'n-dimensional hypervolume', with each dimension defined by an ecological factor of importance to the organism in question. If the niches of individual components within a community can be defined, then it follows that the structure of the community, in terms of interactions between organisms, can be better understood. Hutchinson's niche is largely hypothetical as the number of dimensions could be almost infinite; the niche under this definition is therefore referred to as the 'fundamental niche'. Many niche studies choose to focus on a specific aspect of an organism's fundamental niche, such as considering only the trophic niche. Research relating to the niche concept has expanded in recent years with refinement of stable isotope techniques (Bearhop et al., 2004).

Stable isotopes of carbon (^{13}C) and nitrogen (^{15}N) are often used in studies of dietary sources (Doucett et al., 1996, Chaloner et al., 2002, Hood-Nowotny and Knols, 2007, O'Callaghan et al., 2013; see also Chapter 5). ^{13}C is typically used to estimate the range of food sources as it can vary by food type, whereas ^{15}N is used to estimate trophic height as it varies predictably up the food chain due to differential uptake of heavier and lighter isotopes. These can therefore be used to describe the range of food sources and the trophic height of the consumer respectively (Chaloner et al., 2002, Finlay and Kendall, 2007). The isotopic signatures of consumers can be plotted in an x-y space, typically with the x-axis defined by ^{13}C and the y-axis by ^{15}N values. These can therefore be used to define two axes of

Hutchinson’s niche hypervolume on a continuous scale, thereby giving a ‘realised niche’ (as opposed to the hypothetical fundamental niche). As stable isotope signatures are a product of both habitat and food consumed (Newsome et al., 2007), they can provide information regarding both biotic and abiotic factors of an individual’s realised niche.

The recent refinement of stable isotope techniques has led to the creation of a number of metrics that can be used to quantify niche space in terms of areas that can be compared between taxa or communities, as well as a host of community metrics that describe food web structural properties (Layman et al., 2007). Based on the x-y plot of ^{13}C and ^{15}N, the area occupied by a group of consumers (e.g. individuals of the same species or trophic group) can be calculated by several means. Convex hulls and standard ellipses are minimum area calculations which encompass all (or a proportion of) the isotope signatures of individuals of a taxonomic group within a community in order to quantify niche size of that group (Layman et al., 2007, Jackson et al., 2011). Layman et al. (2007) also described the following metrics of trophic diversity: δ^{15}N range, δ^{13}C range, and mean distance to the δ^{15}N-δ^{13}C centroid. Measurements of trophic redundancy within the community were also proposed by Layman et al. (2007) and use a further two metrics: mean nearest neighbour distance, and standard deviation of nearest neighbour distance.

Further work by Jackson et al. (2011) suggested that the original Layman metrics do not incorporate variability within the community, therefore these authors proposed an alternative approach in which Bayesian methods are used to facilitate comparisons between communities where sample sizes vary, whilst also incorporating an indication of uncertainty in the data. These Bayesian estimates of isotopic niche area and food web structure of communities allow for comparisons between systems, thus their utility as a means for addressing changes in community structure along gradients (e.g. time, complexity) are clear. The Bayesian method is relatively new, and hence has been little used in the literature (but see Jackson et al., 2012, Abrantes et al., 2014).

The Bayesian methods for comparing isotopic niches may be used to quantitatively compare similar communities in different locations, such as estuarine communities (Abrantes et al., 2014), or changes in community structure over time. Glacier Bay, in southeast Alaska, provides an ideal opportunity to test these methods. A well-dated history of glacial retreat has provided the opportunity to study community composition over a successional sequence spanning 200 years (Milner, 1994, Milner et al., 2000, 2007, 2008). The food sources of consumers on floodplains of different ages have already been determined using stable isotope techniques as outlined in Chapter 5, but the changes in niche breadth as communities develop across a chronosequence of different floodplain ages have not previously been investigated.

6.2 Study aim and research questions

The aim of this study was to utilise the measurements of niche width and community-wide metrics of niche variation to explore how dietary breadth and food web structure changes over ecologically long time scales (c.200 years). The aim was to investigate communities on stream floodplain catchments of different ages (defined as time since deglaciation), and therefore sampled both aquatic (instream) and terrestrial (riparian) consumers. This complements a parallel study investigating the dietary sources of these terrestrial and aquatic stream communities (Chapter 5). The specific research questions addressed were:

- Would trophic diversity ($\delta^{13}C$ range) increase with catchment age? More food resources were anticipated to become available to consumers in both aquatic and terrestrial communities as catchment age increased, such as an increased input of allochthonous subsidies to older streams;
- Did the numbers of trophic levels ($\delta^{15}N$ range) in aquatic communities increase with catchment age? Utilisation of allochthonous resources (see Chapter 5) would potentially lead to an increase in trophic height of aquatic consumers in older streams;
- Did the numbers of trophic levels remain constant over time for the terrestrial communities? Carabid beetles and spiders are generalist predators or omnivores (Lindroth, 1969) consuming both terrestrial food and emerging aquatic invertebrates, and were therefore expected to have similar diet breadths at all sites;
- Would isotopic niche width increase with catchment age as more food resources became available to consumers over time?
- How would trophic redundancy be impacted by increasing catchment age? Older sites are likely to be more stable than younger sites and therefore have a greater range of resources, supporting a range of individuals with similar diets, thereby increasing redundancy.

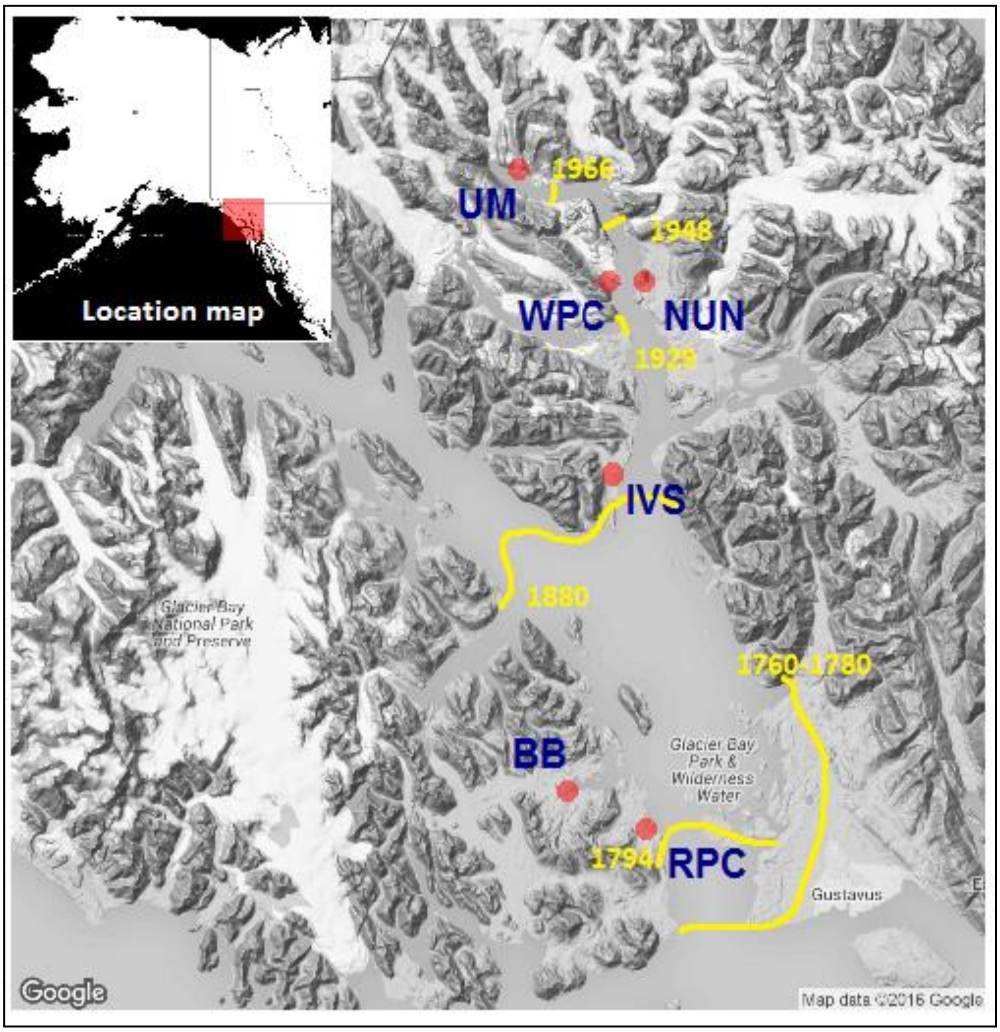

Figure 6.1: Location of field sites in Glacier Bay National Park and Preserve. Sites codes correspond to names in Table 6.1

6.3 Methodology

Glacier Bay National Park and Preserve is situated in southeast Alaska. The area is a unique site for studying ecosystem development following well documented and rapid glacial retreat (Miller, 1964, Milner et al., 2007, Milner and Robertson, 2010). Spanning an area of 11,000km^2, it is a deglaciated landscape over 220 years old (Milner and Robertson, 2010), surrounded by mountains rising to 5000m above sea level and including many kilometres of shoreline, exposed bedrock, unconsolidated glacial sediments and temperate rainforest (Milner et al., 2007). The last glacial maximum occurred around 1700 and glacial recession began (with some regional re-advances) between 1735 and 1785 (Miller, 1964; Figure 6.1). The climate of Glacier Bay is temperate maritime, with mean monthly temperatures ranging from -3°C to 13°C and a mean annual precipitation of 1400mm (Milner and Robertson, 2010).

6.3.1 Sampling design

Five streams were sampled up to four times during each of the summers of 2013 and 2014 (Figure 6.1; Table 6.1) to represent a range of floodplain ages and complexity. This is space-for-time substitution, as different sites indicated different stages of ecosystem development. For each stream, one reach (c.10m long) was selected, approximately 0.75km from the stream mouth (*sensu* Milner et al., 2008). Each reach consisted of an unvegetated gravel bank, with riparian forest behind. Two streams, additional to the main five, in Upper Muir inlet were sampled once in 2014. Access to this part of Glacier Bay by motorized boat was not permitted for part of the field season, hence the single field visit. The data presented from these two sites were therefore limited, but were included for comparison.

Table 6.1: Stream floodplains sampled in Glacier Bay, age indicates the length of time the stream mouths have been ice-free

Stream	Code	Age (years)	Longitude	Latitude	Dominant riparian vegetation	Large woody debris present in stream channel
Upper Muir 1	UM*	<20	59°04’43.1”	136°19’10.8”	*Dryas* sp.	No
Upper Muir 2	UM*	<20	59°04’02.5”	136°17’09.9”	*Dryas* sp.	No
Wolf Point Creek	WPC	55	58°59’48.3”	136°10’18.1”	Alder, some cottonwood	No
Nunatak Creek	NUN	70	58°58’40.5”	136°5’41.2”	Alder, cottonwood	No
Ice Valley Stream	IVS	130	58°49’10.9”	136°9’49.6”	Alder, spruce	Yes
Berg Bay South Stream**	BB	170	58°30’17.5”	136°14’0.62”	Alder, spruce, cottonwood	Yes
Rush Point Creek	RPC	200	58°28’11.2”	136°06’08.5”	Spruce	Yes

*Samples from Upper Muir 1 and 2 were combined as one site for the analysis due to low sample number

**Berg Bay South Stream hereafter referred to as Berg Bay

6.3.2 Sample collection

Terrestrial invertebrates were collected at each site using live (i.e. without preservative) pitfall traps: 500ml plastic cups with a 9cm diameter (as suggested by Woodcock, 2008, Hancock and Legg, 2012). Traps were covered by 2cm wire mesh (with holes enlarged up to 3cm in length at the trap edge, Chapter 2) to prevent entry by small mammals, particularly shrews. Traps were placed at the edge of the stream channel (<50cm from the stream edge) for 24h. Attempts were made to also collect invertebrates in the riparian forest for comparison, but traps were unsuccessful (frequently catching <3 individuals of any species). Invertebrates were removed and kept alive for at least 24h to evacuate their digestive tracts. Additional terrestrial invertebrates were collected by hand searching along the stream margin.

Three replicate samples of aquatic macroinvertebrates were collected using a modified Surber (0.1m^2, mesh size 250μm) at each site. Invertebrates were held in containers of stream water for at least 24h to evacuate their digestive tracts. Additional macroinvertebrates were removed from larger substrate by hand searching. Juvenile salmonids were collected at each stream using minnow traps, baited with salmon eggs (pre-soaked in Betadyne iodine solution) held in a perforated plastic 'Kinder egg' capsule. Sites were fished for 90 minutes (Bryant, 2000). Three traps were placed in pools and backwaters of the main stream channel in 2013 and in 2014 ten traps were placed in the stream. Two salmonid species were present in the streams studied: coho salmon (*Oncorhyncus kisutch*) and Dolly Varden char (*Salvelinus malma*). A maximum of five individuals were permitted to be sacrificed for stable isotope analysis in 2013 and up to 20 in 2014 (as per Alaska Department of Fish and Game permit). Remaining fish were released back into the stream and no unintended mortalities occurred during the study.

6.3.3 Sample processing

Samples were frozen on returning from the field. Beetles were sorted and identified to generic using Lindroth (1969) and aquatic macroinvertebrates to Order, the samples were dried at 60°C for 24h (Chaloner et al., 2002, O'Callaghan et al., 2013). Due to a lack of taxonomic keys for this geographical area spiders were not identified beyond Order level. Juvenile coho and Dolly Varden were dried whole, although their stomachs were removed to be used in a separate study of their diet. Dried samples were ground into a powder by hand using a pestle and mortar. Individual samples were weighed (0.7 ± 0.1mg) into tin cups before combustion. Some small invertebrate samples were made up of multiple individuals, whereas for larger individuals, sub-samples of the whole animal were used. Samples were analysed simultaneously for ^{13}C and ^{15}N using a Thermo Delta V isotope ratio mass spectrometer (IRMS) interfaced with a Costech ECS 4010 elemental analyser (EA) in 2013 and a Thermo Delta XP isotope ratio mass spectrometer (IRMS) interfaced with an Elementar Pyrocube elemental analyser (EA) in 2014. Isotopic analysis was carried out at the SUERC facility in East Kilbride, Scotland. Analytical precision was ± 0.07 δ^{13}C and ± 0.09 δ^{15}N (2013 runs), and ± 0.07 δ^{13}C and ± 0.11 δ^{15}N (2014 runs) calculated from in-house standards, which were run alongside the samples.

6.3.4 Data analysis

The original isotopic measurement of trophic niche area was the convex hull. Convex hulls can be used to quantify the size of the niche in terms of 'trophic area' (Layman et al., 2007) by describing the smallest possible area in which all of the data points are encompassed (Syväranta et al., 2013). However, convex hull area is affected by sample size: the addition of more data points can lead to a larger hull area skewed by much smaller or larger values. Standard ellipses were then suggested as a preferred choice instead of convex hulls for estimating niche area (Jackson et al., 2011). Standard ellipse areas (SEA) are comparable to standard deviations, and include only around 40% of the data points, and are hence less affected by extreme values, giving more robust estimates of niche area, particularly for small sample sizes (Jackson et al., 2011, Syväranta et al., 2013). Bayesian statistics are also incorporated into the calculations of SEA to give a range of estimates of ellipse size and therefore include an indication of the natural variability in the data.

The additional community metrics put forward by Layman et al. (2007) to describe community-wide food web structural characteristics are based on the mean isotopic signatures of different consumers within a defined community, and include four measures of trophic diversity ($\delta^{15}N$ range, $\delta^{13}C$ range, total area as a convex hull, and mean distance to the $\delta^{15}N$-$\delta^{13}C$ centroid) and two of trophic redundancy (mean nearest neighbour distance, and standard deviation of nearest neighbour distance). However, different sample sizes can lead to biased results for community metrics, which would rule inter-community comparisons invalid (Jackson et al., 2011, Abrantes et al., 2014). Jackson et al. (2011) suggested the original Layman metrics give only a single point estimate and do not incorporate variability within the community. These authors proposed an alternative approach in which Bayesian methods are used to facilitate comparisons between communities (or individuals within the same community) where sample sizes vary, whilst also incorporating an indication of uncertainty in the data.

Data were first assessed for outliers using Cleveland dot plots and tested for normality (Zuur et al., 2010). Where fewer than three individuals were collected, taxa were removed from the data set: a total of 773 samples were included in the analysis. All analysis was carried out in the open-source statistical software package R (build v3.1.1, R Core Team, 2014). Data were analysed using SIAR v4 (Parnell et al., 2008) and used the SIBER analysis part of this package ('Stable Isotope Bayesian Ellipses in R', Jackson et al., 2011). Firstly, isotopic niche space size was estimated for each taxon at each site. This was estimated from the stable isotope data using Bayesian standard ellipses and the areas of these ellipses were compared for the same taxa over time, as well as for individuals within communities. Secondly, analyses of whole communities at each site were carried out to compare food web structure. Bayesian versions of the Layman metrics were calculated for the terrestrial and aquatic communities using SIBER: $\delta^{15}N$ and $\delta^{13}C$ range, mean distance to centroid (MDC), mean nearest neighbour distance (MNND), and standard deviation of nearest neighbour distance (SDNND). The metrics were plotted graphically and the overlap of the confidence intervals were visually analysed to assess the level of (dis)similarity between sites (see Abrantes et al., 2014). Data which are significantly different therefore have non-overlapping confidence intervals. The Layman metric ‘total area’, which uses convex hulls, was not included in the analysis; standard ellipses were calculated for the whole communities instead.

6.4 Results

Nebria sp. was the only carabid beetle present at all sites and its isotopic niche width (standard ellipse area) increased with site age, reaching a maximum at Berg Bay (Figure 6.2). The second most widespread beetle was *Bembidion*, which in contrast did not increase in isotopic niche width with site age. Isotopic niche width varied within sites: at the youngest sites, niche width was similar and small for all taxa; however at the oldest sites niche widths of *Nebria* and *Diplous* were larger than that of *Bembidion*. Isotopic niche width of riparian spiders decreased from the youngest sites to Ice Valley Stream, and then a clear increase with site age was evident for the two oldest sites (Figure 6.3). For juvenile coho and Dolly Varden, niche width increased with site age, reaching a maximum at the second oldest site, Berg Bay (Figure 6.4). Isotopic niche width of Dolly Varden exceeded that of coho at all sites apart from Berg Bay and Wolf Point Creek. Plecoptera declined in isotopic niche width with site age (Figure 6.5), whereas Chironomidae and Ephemeroptera declined from Wolf Point Creek to Nunatak, followed by an increase to Rush Point Creek. The isotopic niche width of Trichoptera was similar at all sites where this group was collected.

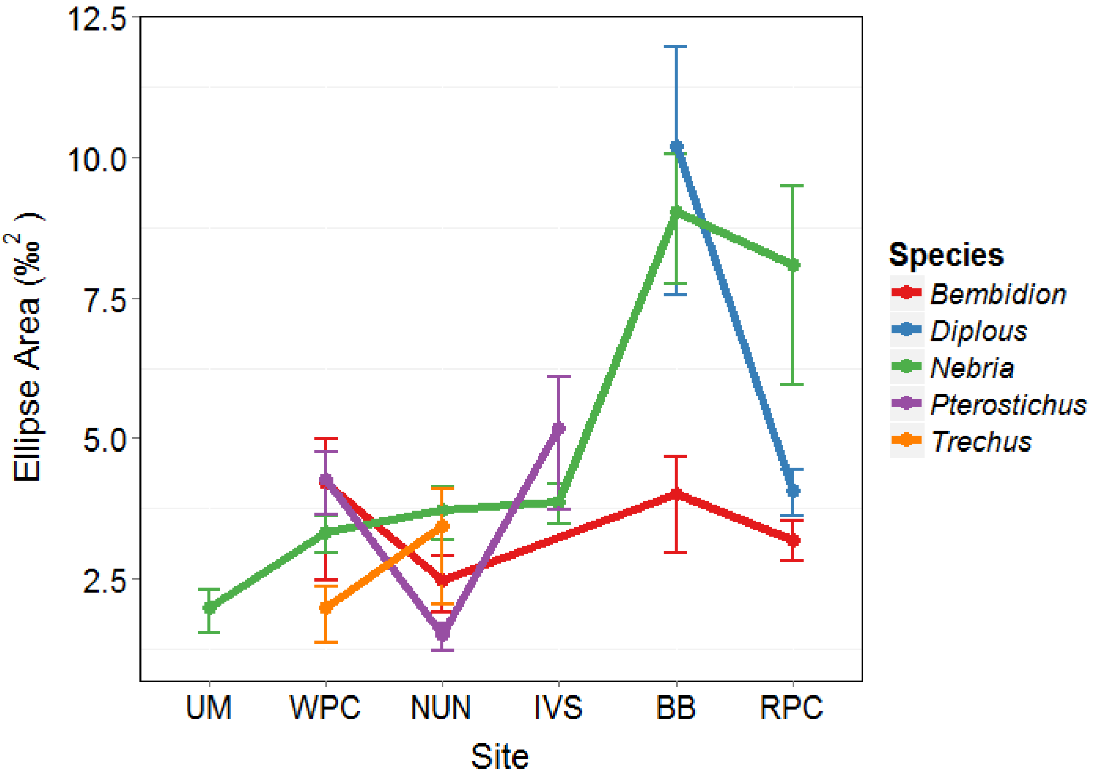

Figure 6.2: Isotopic niche width (standard ellipse area) of riparian beetles. Error bars indicate interquartile ranges of niche estimates

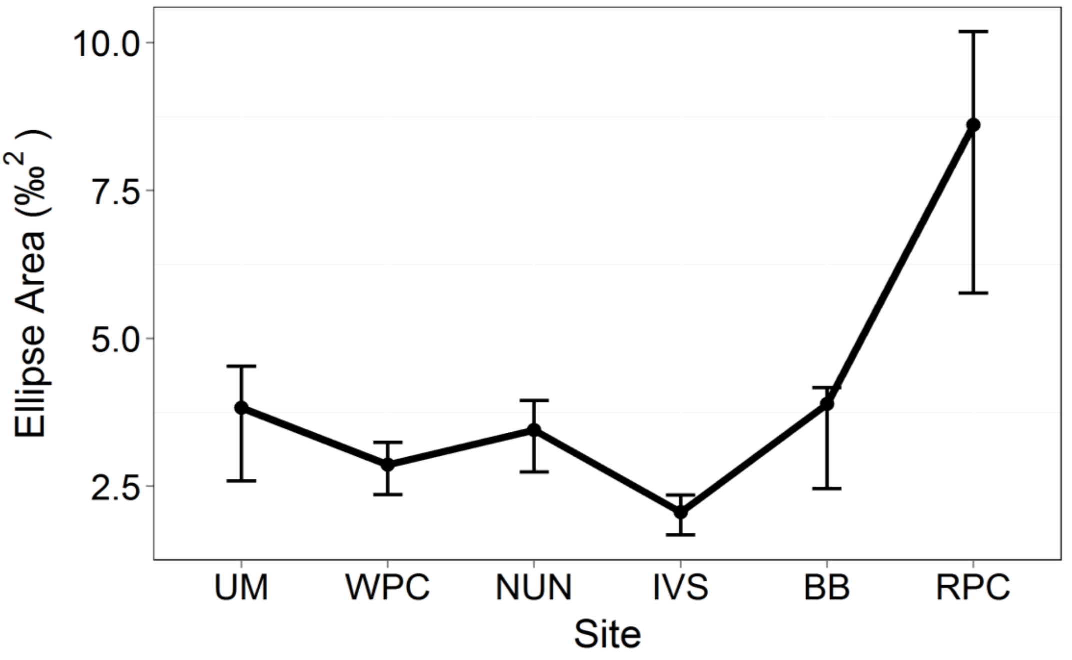

Figure 6.3: Isotopic niche width (standard ellipse area) of riparian spiders. Error bars indicate interquartile ranges of niche estimates

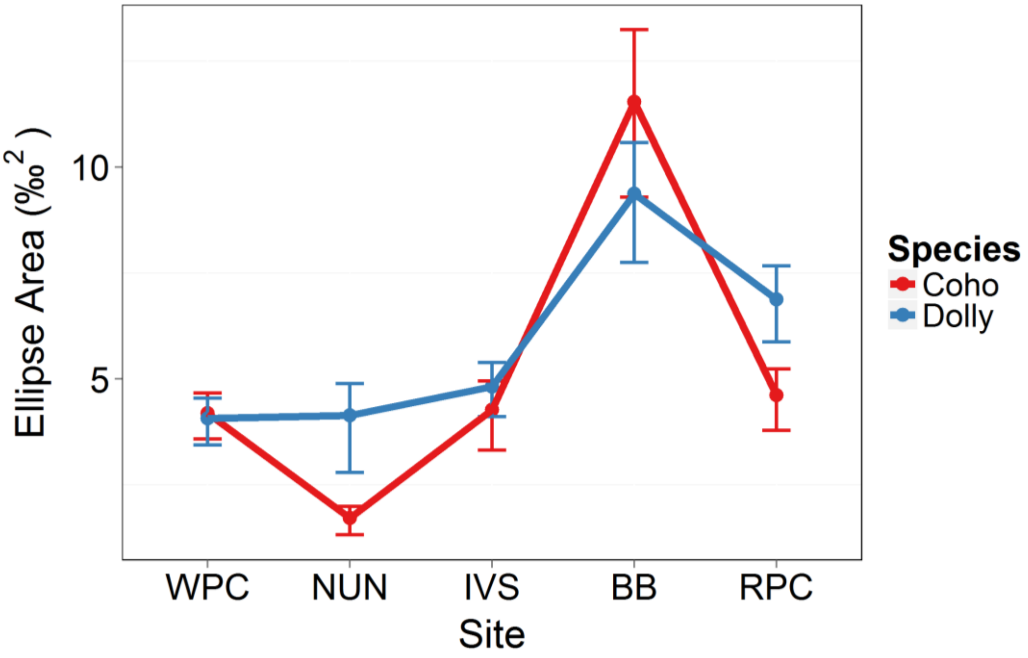

Figure 6.4: Isotopic niche width (standard ellipse area) of juvenile coho and Dolly Varden. Error bars indicate interquartile ranges of niche estimates

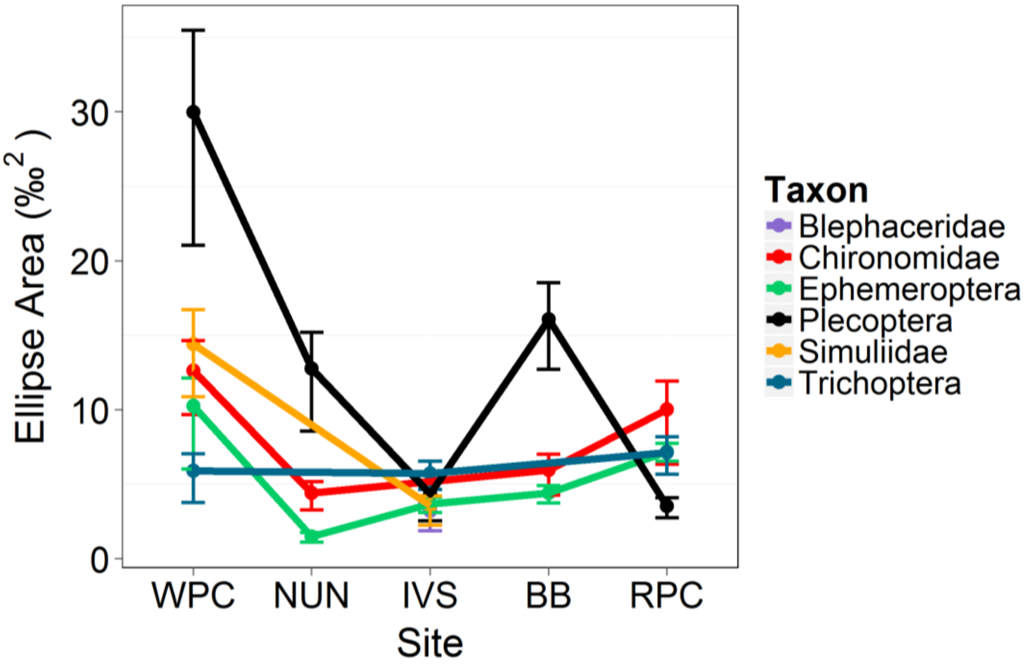

Figure 6.5: Isotopic niche width (standard ellipse area) of aquatic invertebrates. Error bars indicate interquartile ranges of niche estimates

For the terrestrial communities, the $\delta^{15}N$ range was highly variable between sites, with mean values lowest at the youngest site, Upper Muir, and highest at Berg Bay (Figure 6.6A). There was no overlap in $\delta^{15}N$ range credible intervals between the Upper Muir data and those data from Wolf Point Creek, Berg Bay and Rush Point Creek, suggesting that these are significantly different. The $\delta^{15}N$ range was very similar at Nunatak Creek and Ice Valley, and was larger than at Upper Muir, but lower than at all other sites. $\delta^{13}C$ range and MDC did not significantly differ between sites (credible intervals overlap, Figure 6.6B, C). Standard ellipse area was significantly higher for Berg Bay than at all other sites, and the area at Rush Point Creek was significantly larger than the Upper Muir streams (Figure 6.6D), but ellipse areas were similar for other streams. MNND declined along the age gradient from Upper Muir to Nunatak, but increased at Ice Valley and then declined again to Rush Point Creek. All sites showed some degree of credible interval overlap (Figure 6.6E), suggesting differences were insignificant. There was no difference in SDNND between sites (Figure 6.6F; insufficient data were available from the Upper Muir streams to determine MDC).

For the aquatic communities, $\delta^{15}N$ range increased slightly with site age, although the only significant difference was between Ice Valley and Rush Point Creek where the credible intervals did not overlap (Figure 6.7A). $\delta^{13}C$ range increased from Wolf Point Creek to Ice Valley and then declined to Rush Point Creek (although the decline was less significant for the oldest sites as overlaps still occurred for the credible intervals; Figure 6.7B). MDC and standard ellipse area both increased with site age and older sites were more similar to each other than the youngest sites (Figures 6.7C, D). MNND increased from Wolf Point Creek to Ice Valley and then declined, although only Wolf Point Creek and Ice Valley were significantly different (Figure 6.7E). SDNND increased marginally at the two oldest sites, but this was not significant (Figure 6.7F).

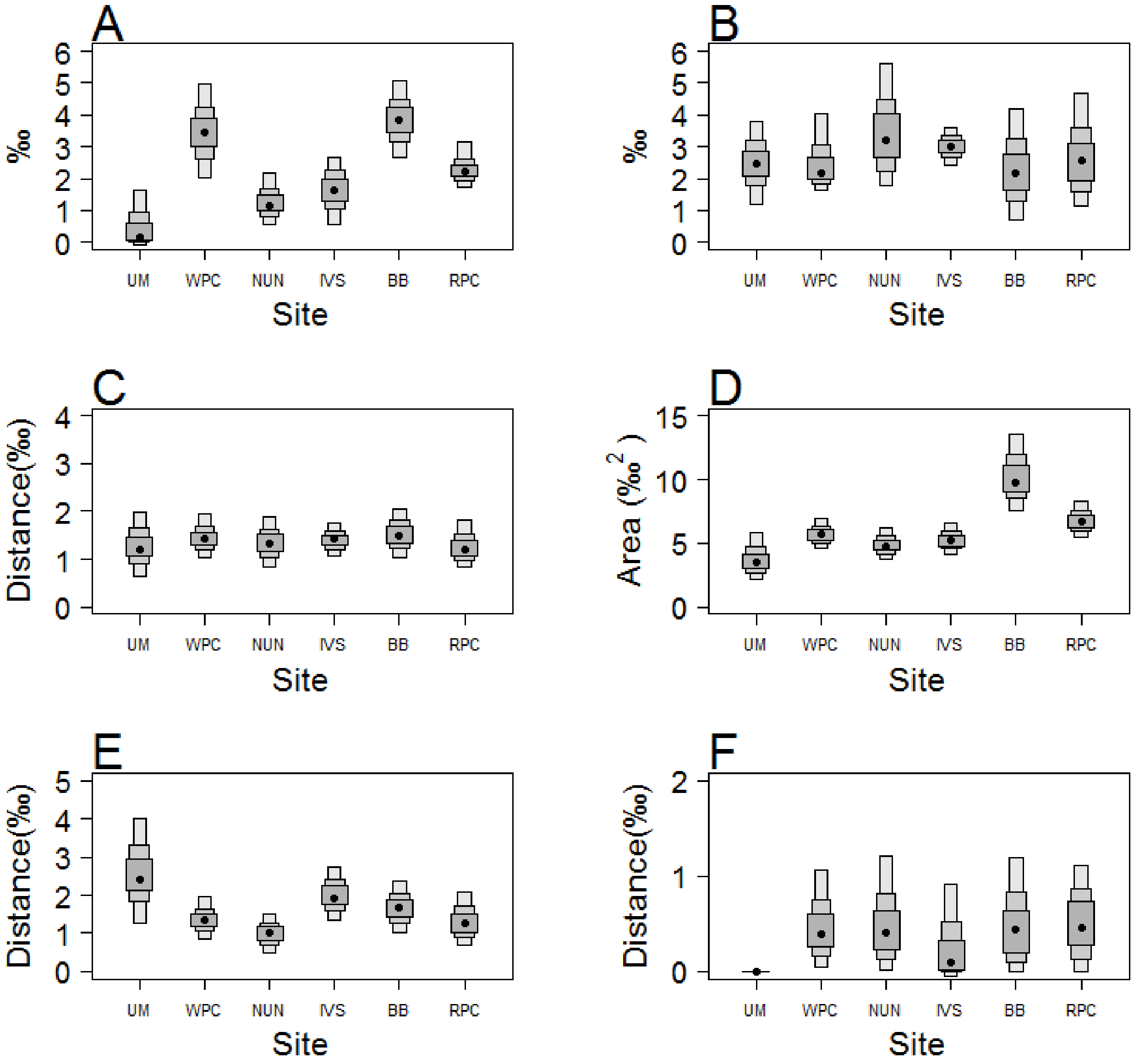

Figure 6.6: Bayesian estimates for the community-wide Layman metrics for terrestrial communities. Black dots indicate the mode (‰) and boxes indicate the 50%, 75%, and 95% credible intervals **A:** δ^{15}N range, **B:** δ^{13}C range, **C:** mean distance to centroid (MDC), **D:** standard ellipse area (SEA), **E:** mean nearest neighbour distance (MNND), **F:** standard deviation of mean nearest neighbour distance (SDNND)

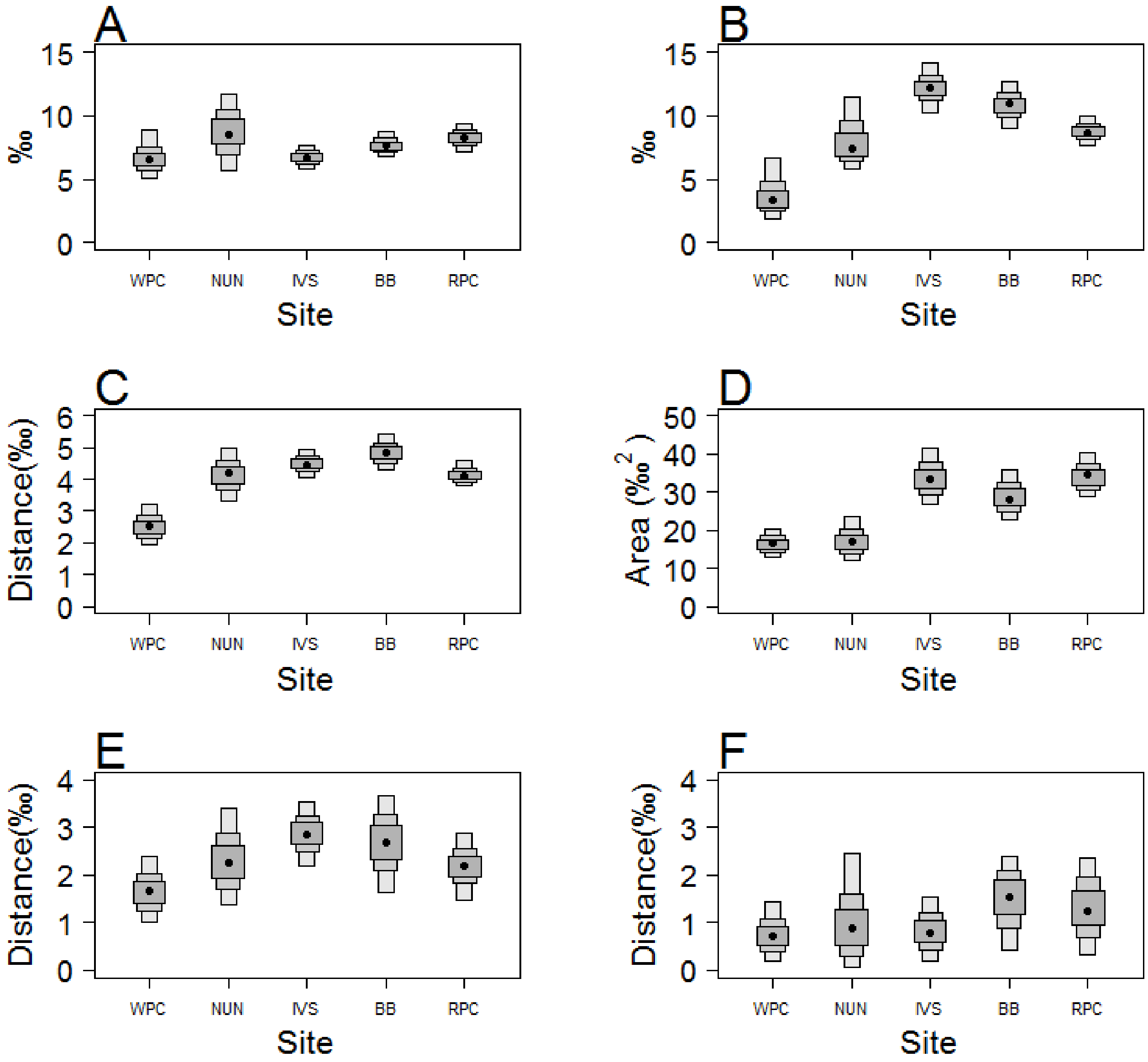

Figure 6.7: Bayesian estimates for the community-wide Layman metrics for aquatic communities. Black dots indicate the mode (‰) and boxes indicate the 50%, 75%, and 95% credible intervals **A:** δ^{15}N range, **B:** δ^{13}C range, **C:** mean distance to centroid (MDC), **D:** standard ellipse area (SEA), **E:** mean nearest neighbour distance (MNND), **F:** standard deviation of mean nearest neighbour distance (SDNND)

6.5 Discussion

To my knowledge this was the first attempt to examine how community food web structure and niche width changes over time, and one of the few studies to use the Bayesian approach of Jackson et al. (2011) to estimate isotopic niche widths at both the individual and community level (see also Abrantes et al., 2014, Catry et al., 2015). The research questions were addressed using a space-for-time substitution field-based study of streams with catchments of different ages in Glacier Bay, Alaska.

The initial research questions centred around whether increasing catchment age would lead to an increase in isotopic niche width, which is analogous to diet breadth. This occurred for the riparian carabid beetle *Nebria* spp. and spiders, both of which were found at all sites, and increased in niche width with age. For the other common carabid beetle, *Bembidion* spp., this was not the case. The other riparian invertebrates were found at fewer than four sites and so any changes in niche width over time could not be determined accurately. *Nebria* are much larger than *Bembidion* (Lindroth, 1969, see also Chapter 2) and so their larger body size, and consequent larger gape width may allow *Nebria* to utilise a wider range of resources available at the older sites, which could lead to an increased diet breadth over time. In contrast, the smaller *Bembidion* are gape-limited, restricting their diet to smaller food items, and therefore also reducing the range of items that could be consumed, which constrains diet breadth.

Unlike the terrestrial invertebrates, fish in these streams were not gape-limited as they are many times larger than their invertebrate prey. Niche width for juvenile coho and Dolly Varden increased until Berg Bay, but then declined at the oldest site. This finding can be linked to terrestrial subsidies in their diet: at Berg Bay in particular there was an increase in the proportion of diet sourced from allochthonous resources (see Chapters 3 and 5), which increased the range of food items consumed, and was therefore reflected in the increased isotopic niche width of these fish. At the younger and the oldest sites terrestrial input to diet was less evident, and niche width was narrower. Habitat complexity likely increased the resources available to fish in mid-aged sites. In stream habitat complexity has been shown to be maximum at mid-aged sites (Klaar et al., 2009), and although riparian habitat complexity has not been quantified, it also appeared to be higher at these same sites, with a diverse riparian forest and much coarse woody debris present in the stream channel. Some of the additional food items in the fish diets at Berg Bay were wood specialist beetles (Chapter 3) and therefore it was likely that woody debris accumulations in the stream channel contributed to an increased diet breadth through the provision of more diverse invertebrate prey.

Although niche width was expected to increase for the aquatic invertebrates, the highest niche width of most taxa occurred at the youngest site, Wolf Point Creek. For Chironomidae and Ephemeroptera there was an increase in niche width from the second youngest to the oldest site, whereas for Plecoptera the smallest niche width was found at the oldest site. For Trichoptera, and to some extent Ephemeroptera and Chironomidae, similar dietary breadth over time agreed with complementary gut contents analysis, which found that diets were similar for most aquatic invertebrates and was predominantly sourced from diatoms (see Chapter 4). The decrease in Plecopteran isotopic niche width remains unexplained, as gut contents indicated consumption of a similar range of diatoms to the other aquatic invertebrates, but also predation on Chironomidae larvae at most sites. The larger niche width for Plecoptera compared to other taxa at three of the five main sites may be due to the additional food source (Chironomidae). However, niche width narrowed significantly at Nunatak Creek and Rush Point Creek, which was surprising given that gut contents analysis showed Chironomidae and diatoms were in the diet of Plecoptera at these two sites. Aquatic invertebrates consume large quantities of detritus (Füreder et al., 2003, Clitherow et al., 2013), the origins of which are often unidentifiable in gut contents analysis. The changes in diet breadth may, therefore, be a result of different detrital food sources available to aquatic invertebrates. This could be affected by a combination of factors, such as retention of detritus instream, and the particular sources of detritus, for example, riparian vegetation, which differs between sites.

6.5.1 Spatial variability in trophic diversity

Trophic diversity of terrestrial communities did not increase with site age. δ^{13}C range, which indicates the diversity of basal resources (Layman et al., 2007), remained similar across sites for terrestrial communities, and although there was a slight increase for the mid-aged sites, this was not significant; similarly, MDC was almost identical across all sites. Standard ellipse area did not significantly differ between five of the sites, but was elevated at the second oldest site, Berg Bay. The increased ellipse area at Berg Bay may be a result of an elevated δ^{15}N range at this site, and was also the site where *Nebria* and *Diplous* had the largest ellipse areas. This suggested that rather than an increase in the diversity of the trophic base with site age, similar resources were being utilised by the riparian consumers at all the sites, independent of site age. However, there may be differences in terms of consumption by different taxa, leading to genus-level variation in niche width, hence the elevated niche width for two beetle taxa, as well as the effects of a potentially more complex riparian habitat at Berg Bay, which provided more food resources at this site.

For the aquatic communities, δ^{13}C range and MDC increased with site age to the mid-aged sites, but declined at the oldest site. Although standard ellipse area was greatest at the three oldest sites, rather than just at the mid-aged sites, the overall pattern of the trophic diversity metrics indicated that rather than increasing with site age, the basal resource pool for the aquatic communities was greatest at intermediate aged sites. Stomach contents analysis of juvenile coho and Dolly Varden at these sites indicated a much higher diversity of diet at Ice Valley and Berg Bay, as well as a greater proportion of allochthonous food consumed as compared to the younger and older sites (see Chapter 3), which agreed with the findings here: overall diet breadth was widest at mid-aged streams. Aquatic invertebrate diet breadth did not increase over time, so it was clear from these results that juvenile coho and Dolly Varden had a greater influence over the community-level isotopic metrics, perhaps because they were able to also utilise allochthonous resources, whereas aquatic invertebrates predominantly consume autochthonous food items (e.g. diatoms).

There was a trend of increasing δ^{15}N range for the aquatic communities, suggesting a greater number of trophic levels present at the oldest sites, however this was not significant. Although the top predators (juvenile coho and Dolly Varden) in the described food webs did not change over time, the contribution of terrestrial sources to their diets increased (Chapter 5), which likely contributed to an increase in trophic levels as these allochthonous resources were consumed by the fish. The terrestrial portion of the diet in these streams contains riparian beetles (see Chapter 3), which are often generalist predators (Lindroth, 1969), and therefore themselves relatively high in the food chain, which in turn increases the trophic level of their consumers (juvenile coho and Dolly Varden). The trophic positions of the other terrestrial prey items are unknown.

In contrast to what was anticipated, the number of trophic levels in the terrestrial communities ($\delta^{15}N$ range) was highly variable between sites. The reasons for this finding are unclear, particularly as the range of food sources ($\delta^{13}C$ range) remained relatively constant across all sites. However, diet breadth alone does not give an indication of diet identity. Beetles consumed varying proportions of terrestrial and aquatic foods across the sites, but the most significant aquatic food source was adult Plecoptera (see Chapter 5). Plecoptera were often found to be predatory (see Chapter 4) and hence would have a higher trophic level than other aquatic invertebrates. At Wolf Point Creek, where the $\delta^{15}N$ range was significantly higher than all other sites apart from Berg Bay, Simuliidae consumed Chironomidae (see Chapter 4), and were themselves consumed by some riparian beetles. Combined with Plecoptera, which were found at all sites, this might explain the increased range of trophic levels at this site compared to most other sites, where Simuliidae were not present. Likewise, the opportunistic nature of carabid diets (Lindroth, 1969) would likely lead to larger beetles consuming smaller beetles. Predators consuming other predators therefore increased the number of trophic levels in a community, without affecting the number of basal resources. Opportunistic feeding by riparian beetles or asynchronous emergence of adult aquatic invertebrates could lead to differential consumption of predatory aquatic invertebrates, which in turn leads to variable $\delta^{15}N$ ranges between sites.

6.5.2 Spatial variability in trophic redundancy

Trophic redundancy for terrestrial communities was variable with site age. MNND values suggested that redundancy was low at the youngest site, but high at Nunatak Creek (third youngest) and the oldest site. At the youngest sites (Upper Muir) aquatic invertebrate abundance and diversity was low (a single Ephemeropteran and few Chironomidae were collected) and riparian vegetation was sparse, suggesting limited food sources. In other studies where food resources become limited, it has been found that consumers have diverging diets. For example, for tropical freshwater fish, niche overlap has been found to decrease as food abundance is reduced during seasonal cycles, and hence the coexistence of multiple species is facilitated by diet partitioning (Correa and Winemiller, 2014), similar results were found for estuarine fish, whose diets differed most when abundance of a dominant food source declined (Feyrer et al., 2003). Riparian invertebrates that inhabit very young substrates possibly have different strategies to collect food thereby partitioning resources and reducing trophic redundancy. At all other sites there was a diverse aquatic invertebrate fauna (which can provide food to riparian consumers when they emerge as adults) and abundant riparian vegetation, both of which likely increased the availability of food and therefore also increased the probability that taxon pairs consumed the same food resources. Therefore at the five main streams trophic redundancy was higher than at the Upper Muir sites. However, the low number of individuals collected on a single sampling occasion at the Upper Muir sites means these conclusions have to be drawn with some caution, especially when compared to Ice Valley, which also showed reduced trophic redundancy, and yet had a similar aquatic invertebrate and riparian vegetation assemblage to the other older sites.

A different pattern of trophic redundancy was evident for the aquatic communities. Here redundancy was highest at the youngest and oldest sites and decreased at mid-aged sites. Stomach contents analysis of the fish in these streams (see Chapter 3) found that the diversity of diet items was considerably higher at Ice Valley and Berg Bay than other streams, with terrestrial food comparatively more important. At Berg Bay, stomach content data also indicated that diets of coho and Dolly Varden were more dissimilar that at other sites, which supported the trophic redundancy results. Aquatic invertebrates had similar diets at all sites (Chapter 4); therefore it would appear that it was the differences in the fish diets which were driving the changes in trophic redundancy. This was likely related to the utilisation of terrestrial resources, such as riparian invertebrates, which were not consumed by aquatic invertebrates.

6.5.3 Bayesian approach to the Layman metrics

This study demonstrated how the Layman metrics may be used to compare similarly defined food webs in different floodplains to investigate how community structure changes over time. Although there are several examples of the Bayesian approach being used to determine standard ellipses, some of which also include the non-Bayesian Layman metrics (e.g. Thomson et al., 2012, Eloranta et al., 2013, Guzzo et al., 2013, Hayden et al., 2013, Hamilton et al., 2014, Yuille et al., 2015), use of the Bayesian approach to calculate the Layman metrics is limited. This is a powerful tool for quantitatively comparing food web structure between systems, such as analysis of communities over long timescales. The same approach can also be used for repeat analysis of the same community sampled on multiple occasions, such as at the scale of multiple seasons or years. This would allow for additional information to be included in long-term monitoring studies, such as those carried out at Wolf Point Creek in Glacier Bay by Flory and Milner (2000) and Milner et al. (2008).

Stable isotope signatures of consumers may be confounded by the longer time scales over which tissue turnover occurs, as compared to stomach contents analysis, and are also subject to spatial and temporal variation (Guzzo et al., 2013). Therefore proper analysis of niche space, diet breadth and redundancy needs to take into account seasonal distributions and diet fluctuations before more robust comparisons can be made between taxa (Yuille et al., 2015). For example, if the diets of fish are dissimilar between seasons (perhaps due to different habitat preferences or food availability) then their isotopic signature, which has a lower turnover than stomach contents (the turnover of fish muscle tissue may be several months; Quevedo et al., 2009), would potentially reflect these differences, whereas the short-term, ‘snap shot’, analysis of stomach contents would only reflect the most recently ingested diet items. In this study, samples were only collected in one season, but seasonality should be considered in future studies. This study highlighted the utility of both isotopic analysis and stomach contents diet analysis as these can often complement each other, as well as explain discrepancies between expected and actual results (i.e. the increased diet breadth for aquatic communities at mid-aged as opposed to older sites was linked to the input of terrestrial subsidies). Isotopic niche space is a useful tool for investigating long term patterns in diet (Guzzo et al., 2013), such as in studies of space-for-time substitution where multi-decadal time scales are used.

6.6 Conclusion

Dietary breadth of top consumers generally increased over time as catchments became more complex. However, site specific differences, and the movement of resource subsidies meant that this pattern was not simple: in fact complex, mid-aged sites (Ice Valley and Berg Bay) supported broader coho salmon and Dolly Varden diet breadths than younger and older sites. Meanwhile, for terrestrial communities, body size constraints meant that dietary breadth only increased for certain taxa. Aquatic communities were therefore driven by the consumption of allochthonous resources, which increased as habitat complexity increased, but were only utilised by the top consumers (juvenile coho and Dolly Varden). Riparian communities, meanwhile, were driven by opportunistic feeding strategies and body size constraints, as well as stochastic influences on resource availability.

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7

SUMMARY

Abstract

The main findings from the research in Glacier Bay are synthesised in this chapter and summarised by conceptual figures. Habitat complexity was suggested as having a major role in structuring communities and their interactions, rather than site age alone, as was initially hypothesised. The presence of coarse woody debris in the streams with highest structural complexity provided more diverse allochthonous subsidies to the diets of juvenile coho and Dolly Varden than less physically complex streams. This has clear implications for stream restoration projects, particularly where juvenile salmonids are present. Limitations to the study are also outlined, and future directions for research are highlighted.

7.1 Reciprocal subsidies and foodweb structure in Glacier Bay

This research examined the reciprocal nature of resource flows between streams of different ages in Glacier Bay, Alaska. The original objectives of the work were to identify the terrestrial invertebrates on gravel bars alongside each stream and to explore the stream and riparian zone linkages. The terrestrial invertebrate fauna of Glacier Bay have not been studied in any detail (the only published work to date is by Goldthwaite et al., 1966), and thus this research offered further insights into these communities. The movement of resources between the stream and the riparian zone has been investigated in many systems worldwide, but this was the first attempt to examine these in the context of a glacial recession chronosequence and across catchments at different stages of development, as well as elucidating aquatic foodweb structure across multi-decadal timescales.

The carabid beetle communities inhabiting gravel bar habitats in Glacier Bay were characterised by highly mobile species (e.g. *Nebria mannerheimi, N. metallica, N sahlbergi,* and *Bembidion quadrifoveolatum*), and large, flightless, specialist beetles (*Scaphinotus* spp.) only appeared late in the chronosequence. Taxa persisted across the chronosequence, following a tolerance model of succession (sensu Connell and Slatyer, 1977, see also Milner et al., 2008), and unlike previous studies of the aquatic macroinvertebrates in Glacier Bay (e.g. Flory and Milner, 2000, Milner et al., 2000, 2008), which show an initial turnover of cold-adapted species and then an increase in taxonomic richness over time, the successional sequence of carabid beetles was less clear. Aquatic invertebrate succession in Glacier Bay is initially driven by deterministic processes, linked to instream physical characteristics (such as water temperature), whereas later successional communities are structured by stochastic processes related to dispersal patterns and life history traits (Milner et al., 2008). Meanwhile, initial terrestrial invertebrate colonisation of gravel bar habitats is likely to be primarily a result of dispersal ability and life history, as opposed to wholly deterministic processes, which was demonstrated by the presence of the highly mobile taxa *Nebria* sp. and *Bembidion* sp. at the youngest (<20 years old) sites. The unstable nature of these stream edge habitats provides a template for colonisation by disturbance adapted taxa, which colonise sites when they encounter them via dispersal. No obvious extirpations occurred in the terrestrial invertebrate fauna across the chronosequence, which suggested that tolerance, rather than facilitation or inhibition, was occurring on gravel bars in Glacier Bay, similar to that observed for macroinvertebrates in streams (Milner et al., 2008).

There is evidence of reciprocal fluxes of nutrients between the stream and the riparian zone across all of the five main floodplains between 55 and 200 years since glacial recession (Figure 7.1). Stable isotope data indicated that juvenile coho and Dolly Varden sourced more than half their diet from terrestrial resources, including carabid beetles inhabiting the riparian zone. Terrestrial invertebrates (carabid beetles and spiders) also consumed the reciprocal subsidy flux from the stream to the riparian zone, but their diet was not dominated by aquatic sources. With increased habitat complexity at the older sites, more food resources became available to top consumers, and juvenile coho and Dolly Varden increased their dietary breadth, which reached a maximum at the second oldest site. Likewise, large beetles (*Nebria* sp.) also increased their diet breadth at the oldest sites. Aquatic foodwebs were dominated by generalist feeding strategies, and this increased with floodplain age as habitats became more stable and foodwebs became more highly connected.

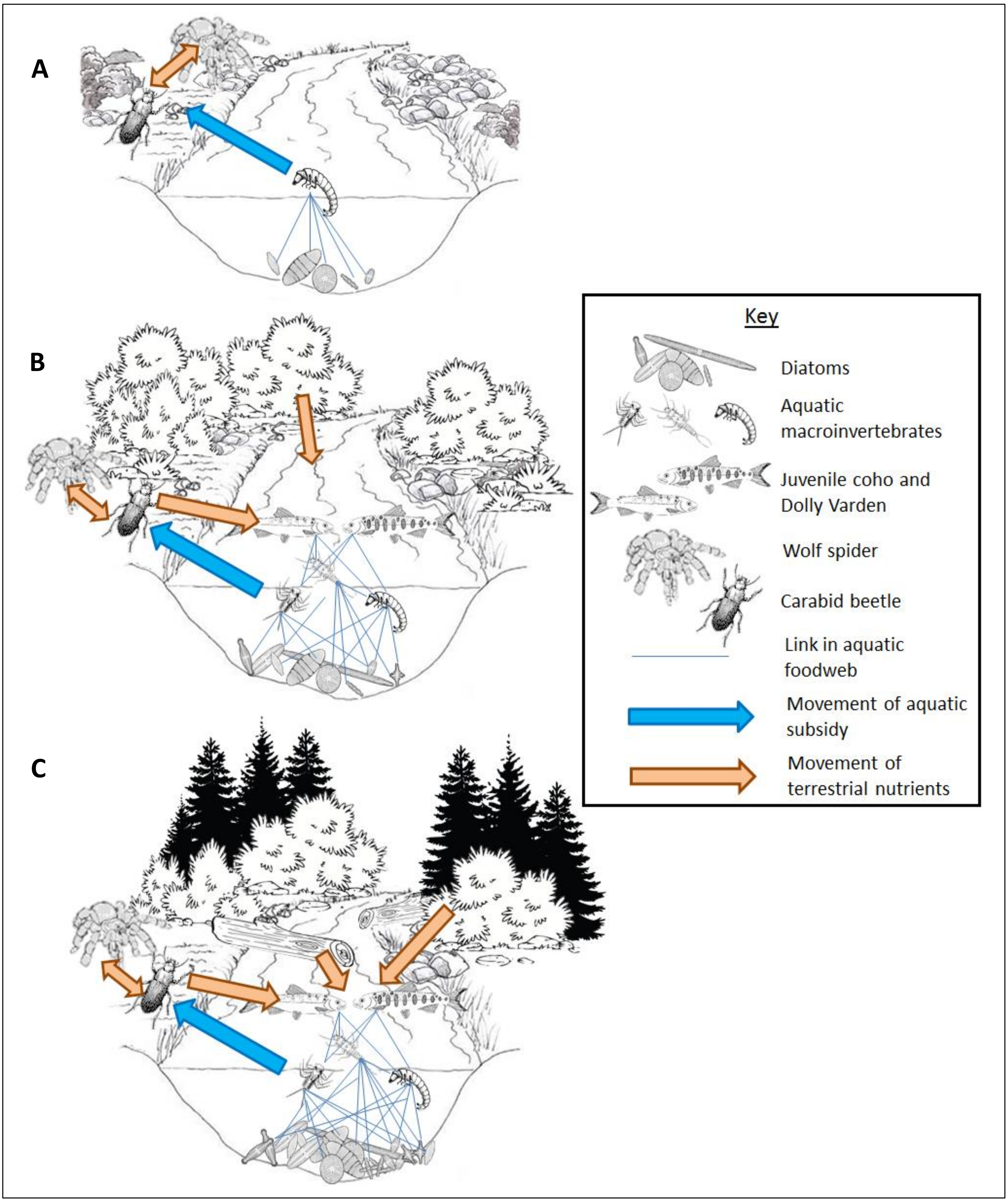

Figure 7.1: Conceptual diagram of the development of linkages between the stream and riparian zone. **A:** Young stream (<50 years) with little riparian vegetation; **B:** 50-70 year old stream with riparian vegetation developing (alder bushes); **C:** Mid-late aged stream (130 years+) with complex physical habitat (coarse woody debris present) and mixed riparian forest. Components of diagrams are not to scale. Aquatic foodweb in the young stream is hypothesised based on the glacial foodwebs of Clitherow et al. (2013).

Contrary to expectations, changes in resource use by juvenile coho and Dolly Varden, and terrestrial invertebrates on floodplains of different ages in Glacier Bay did not increase with floodplain age. Habitat complexity appears to be an important variable in determining resource availability particularly to top consumers (juvenile coho salmon and Dolly Varden, and large riparian beetles; Figure 7.1). Although habitat complexity was not quantified in this study, Klaar et al., (2009, 2011) found Berg Bay (170 years), the second oldest stream, to have the highest instream habitat complexity. Berg Bay was the site with greatest diversity of fish stomach contents (including taxa found at no other stream), the most nodes in the aquatic foodweb, the largest proportion of coho diet sourced from terrestrial sources (Dolly Varden sourced slightly more of their diet from terrestrial sources at Rush Point Creek), and the largest isotopic niche width for both juvenile salmonid species and also for the most common carabid beetle (*Nebria* spp.). Of all the floodplains surveyed, Berg Bay contained the highest quantity of coarse woody debris in the channel (a mixture of tree branches, stumps, and whole trees), as well as a more sinuous channel, and extensive gravel bar habitats, which appeared to have been more recently reworked than at other sites (less vegetation apparent on the bars).

The importance of complexity and not simply site age should be regarded as an encouragement to take into account wider measures of habitat complexity, outside of the stream itself, in future studies of biotic communities in Glacier Bay, as well as further work on reciprocal subsidies elsewhere. Site age is still an important factor, for example, at very young sites (e.g. the Upper Muir streams) it is unlikely that any increase in habitat complexity would have an impact on the fauna present, as these are still constrained by colonisation processes (many taxa have yet to reach these streams). Refugia (areas not glaciated during the Little Ice Age) may have provided the original colonising populations for taxa that eventually reached the floodplains studied, and arrived as these were sequentially uncovered following glacial recession. However, the area is relatively isolated and dominated by high mountains, therefore if the source populations are located a long way from Glacier Bay, such as on the outer coast of southeast Alaska, colonisation could take many years. Colonisation of these streams by aquatic taxa is slower than found for other primary successional studies (Milner et al., 2008), which is as a result of constraints of the physical habitat characteristics. However at older sites (≥55 years since deglaciation), where a diverse community has become established, habitat complexity becomes more important than substrate age.

7.2 Wider implications

Habitat complexity has a great impact on the foodwebs of aquatic and riparian consumers. This research has shown how in physically complex habitats, a greater variety of food resources may be available to consumers. Stability also plays a role, with more stable (older) habitats supporting an abundance of basal resources, which has a bottom-up influence on foodweb resilience, as more highly connected webs are less likely to be deleteriously impacted by stochastic losses of species. Although Glacier Bay is a relatively pristine environment (its status as a National Park reduces anthropogenic disturbance), the conclusions presented here can be utilised in planning and monitoring habitat restoration projects in other stream systems. For example, measures of the success of stream restoration projects often focus on the richness and/or diversity of the biota in the stream/reach that has been restored. Frequently these measures indicate that restoration has been unsuccessful: in a review of 78 independent stream restoration projects where habitat heterogeneity (complexity) was reinstated or increased, Palmer et al. (2010) reported only two studies that found increased invertebrate diversity sufficient to be classed as a biological success. In the five main Glacier Bay streams, the biotic richness and the top predators were found to be similar; however, the interactions between the organisms differed between sites, with physical habitat stability and complexity being key variables in determining resource availability and utilisation, with implications for persistence of the foodweb structure. For successful stream restoration these factors should be taken into account, and to determine if a restoration project has been successful, then perhaps the functioning of the stream should be investigated. Particular reference should be made to the provision of allochthonous subsidies from the riparian zone, especially if the stream restoration involves habitat for juvenile salmonids, as these species may source the majority of their diet from terrestrial invertebrates. In addition, the abundance and richness of diatoms is important, as these provide a food source for aquatic invertebrates.

7.3 Discussion of methods

Two complementary methods were used to analyse foodwebs: direct observations of stomach contents, and stable isotope analysis. Both techniques provide a means to assess the food sources of consumers, but the level of detail of these methods varies. Direct observations of stomach contents show exactly what has been ingested by a consumer near or at the point of sampling, and can give species-level precision regarding these food items if digestion is not too far advanced. Stable isotope analysis is often restricted to more general indications of diet, such as whether a consumer sources its diet from predominantly aquatic or terrestrial resources. If enough potential food sources are sampled then stable isotope analysis can provide strong indications of which resources are likely to make up the bulk of the diet, but this is difficult where diets of consumers can be highly diverse as successfully sampling all possible food sources is unlikely. Stable isotope analysis does have the advantage over gut contents observations for indicating the sources (e.g. aquatic or terrestrial) of unidentifiable food items, such as amorphous detritus, which frequently occur in the diets of aquatic invertebrates and fish.

Gut contents analysis was the method of choice for determining the diets of aquatic invertebrates. Sampling the potential food sources of aquatic invertebrates in order to carry out reliable stable isotope dietary analysis poses a problem as their food sources may be microscopic (e.g. diatoms). Although preservatives can affect isotope signatures (Arrington and Winemiller, 2002, Bicknell et al., 2011), they have no impact on macroinvertebrate gut contents, and hence this technique has a clear advantage where identification of consumers to lower levels (e.g. genus) is not possible in the field. Preparation of slides of invertebrate gut contents can be a time consuming process, but the analysis of invertebrate diets is simple, and even without keys to the diatoms of this area, it was still possible to draw valid conclusions about diet breadth using morphospecies, and these can be compared between sites where the same methods are employed.

Stable isotope analysis was an ideal method to investigate the diets of the terrestrial invertebrates. Gut contents studies of beetle diets are rare (but see Hering and Plachter, 1997), and require a high level of expertise to identify the often heavily fragmented remains of invertebrates within the digestive tracts of the beetles. For spiders, which use extraintestinal digestion, it is almost impossible to carry out meaningful gut contents analysis (Oelbermann and Scheu, 2002, Akamatsu et al., 2004).

Used together, these two methods offer a powerful tool in the analysis of nutrient movements through a system. The work presented here has shown that there is a general agreement in the results of both methods, which is evident from the dietary analysis of the juvenile coho and Dolly Varden. Stomach contents analysis provided a means to explain discrepancies between the actual and expected results from stable isotope analysis (such as the increased diet breadth at Berg Bay occurring as a result of the input of terrestrial invertebrates found nowhere else). Stable isotopes also indicate which resources are assimilated into the consumer's tissues, and this indicated that although terrestrial invertebrates comprised a smaller proportion of items in the stomach contents, carbon and nitrogen from terrestrial sources was preferentially assimilated over aquatic resources.

The new methods for the analysis of stable isotope data outlined by Jackson et al. (2011) offer an exciting prospect for the study of foodwebs. The possibility of comparing foodweb structure of defined communities without the need to exhaustively sample the food sources of consumers is a development which should greatly enhance these studies in systems where basal resources may be difficult to sample, or are currently unknown.

Despite advances in modern techniques such as isotope analysis, quantifying foodwebs via gut contents is still valid and should continue to be used to support the findings from other methodologies. This technique is invaluable for its potential to provide species level identification of food items, and is also considerably cheaper than running stable isotope samples through a mass spectrometer (at least in terms of equipment: gut contents analysis is labour intensive).

7.4 Limitations observed within the research

As with many empirical studies in challenging locations, trade-offs were made in the field campaigns. Additional methodologies which were not carried out are highlighted below, and these may serve as a potential platform for future research in this area:

- Spiders were not identified beyond the order level in this study due to the lack of availability of keys for this region;
- Carabid beetles were only collected from gravel bars, and a short distance into the riparian vegetation. The forest pitfall traps collected too few individuals for stable isotope analysis, and so the permeability (*sensu* Briers et al., 2005, Greenwood, 2014, Muehlbauer et al., 2014) of the riparian forest to aquatic subsidies could not be assessed using stable isotope analysis of forest consumers;
- With stable isotope analysis, the array of potential terrestrial food sources was constrained by the limited range of terrestrial invertebrate food sources which were collected in pitfall traps, or observed during hand searching (Collembola, for example, were notably absent from the assemblage). It is possible that these taxa are not present in Glacier Bay, but the observation of Collembola in the stomach contents of juvenile coho and Dolly Varden indicate their presence somewhere in the stream/riparian system. More thorough sampling using a variety of methods (e.g. vacuum samplers) may have collected a wider range of invertebrates, although a

field team of two restricted the range of sampling methods that could be successfully undertaken.

7.5 Perspectives for future research

This research has suggested that physical habitat complexity has an important role to play in structuring foodwebs and influencing subsidy movements between terrestrial and riparian habitats. Instream complexity has been investigated previously (Klaar et al., 2009), but methods need to be developed to quantify the structure of physical habitats, particularly in riparian zones, and to assess how this influences subsidy movement. Coarse woody debris, as a potential source of allochthonous resources to fish should be assessed, particularly using natural woody deposits (i.e. trees) as opposed to artificial inputs (i.e. small logs, *sensu* Gustafsson et al., 2014).

Glacier Bay offers a unique opportunity to determine how ecosystems develop over time in a pristine environment, and the long history of scientific observation provides a strong basis on which to continue with further investigations. Research should continue on the terrestrial invertebrate communities of Glacier Bay, as this has been little studied. Efforts should certainly be focussed on the more stable habitats, such as the riparian forest, if a wider range of terrestrial invertebrates are to be assessed, which would facilitate a greater understanding of successional processes in this environment.

Spider communities on floodplains in Glacier Bay remain under-explored. Isotope analysis of diet breadth shows a sudden increase in niche width from Ice Valley Stream to Rush Point Creek, and this may indicate a change in spider species with a different mode of food acquisition (i.e. web builders vs. active ground hunters). Additionally, web building spiders along stream margins have been studied previously to determine their utilisation of aquatic subsidies (Kato et al., 2003, 2004, Marczak and Richardson, 2007): in Glacier Bay, sites of different ages offer different physical structures (riparian vegetation species) for web attachment, which may lead to differential resource utilisation. This would build upon this research which suggests that physical habitat complexity is important in determining subsidy use.

Sampling of the diatom fauna of the streams would also be beneficial to link to the findings in the macroinvertebrate diets. There is no apparent turnover of morphospecies with site age, but connectance within the stream foodwebs does increase over time. This is suggestive of higher abundance of diatoms at older sites, such that macroinvertebrates consume a wider range of available basal resources. However, this has yet to be confirmed. Species identification of diatoms would also be informative, but the use of morphospecies allows easy comparison between sites without requiring taxonomic keys, an approach that would be useful in assessing areas where diatom taxonomy has yet to be developed.

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8

APPENDICES

Supplementary information for each chapter is presented here.

2. BEETLE COMMUNITIES ON FLOODPLAINS OF DIFFERENT AGES AND COMPLEXITY IN GLACIER BAY, ALASKA

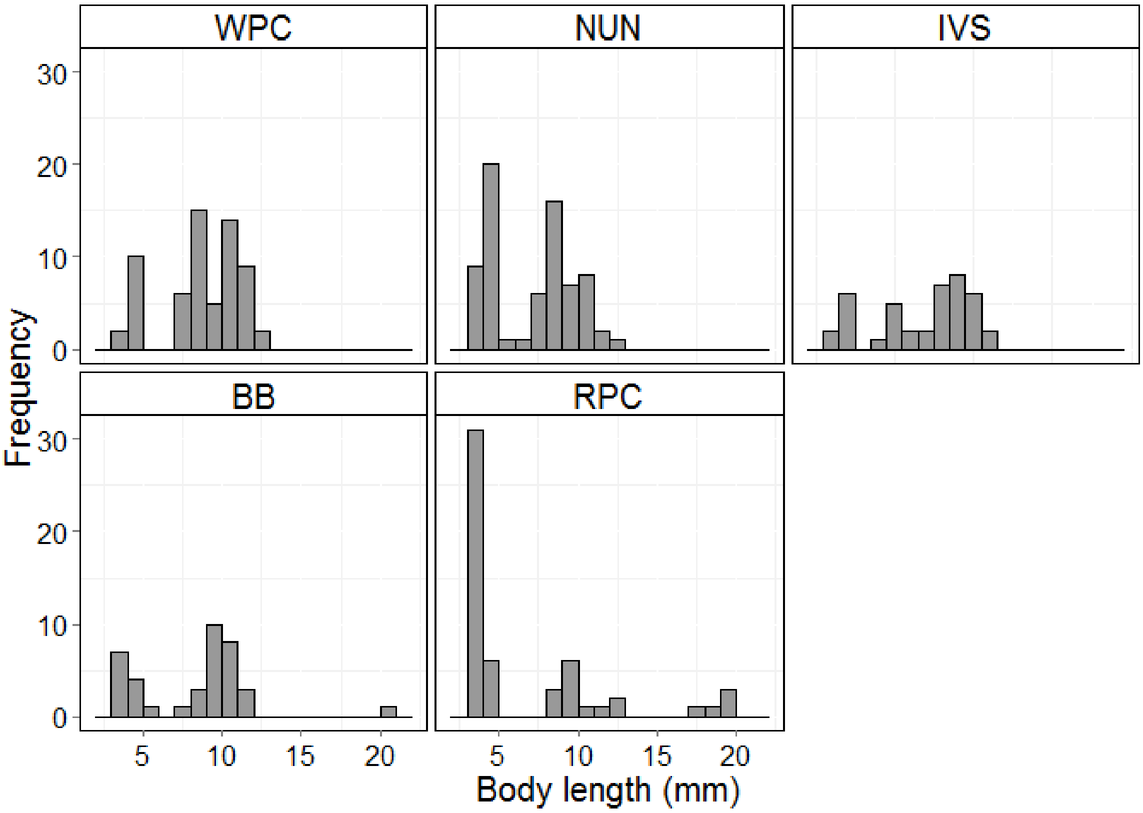


Figure S2.1: Body lengths of carabid beetles collected at sites of different ages. Few beetles were collected from the Upper Muir streams and therefore these were not included here

3. THE ROLE OF TERRESTRIAL INVERTEBRATES IN THE DIETS OF JUVENILE COHO SALMON AND DOLLY VARDEN WITHIN CATCHMENTS OF DIFFERENT AGES

Table S3.1: Invertebrates identified from the stomach contents of juvenile coho and Dolly Varden at each site in Glacier Bay, unID indicates unidentified taxa from a group that has been resolved further for other individuals

		Site where invertebrate was present in fish diet				
Invertebrate	Habitat	WPC	NUN	IVS	BB	RPC
Chironomidae	Aquatic	Y	Y	Y	Y	Y
Simuliidae	Aquatic	Y	Y	Y	Y	Y
Ceratopogonidae	Aquatic	Y	Y		Y	
Tipulidae	Aquatic				Y	
Dicranota	Aquatic	Y	Y		Y	Y
Chelifera	Aquatic			Y	Y	Y
Ephemeroptera (unID)	Aquatic	Y	Y	Y	Y	Y
Serratella	Aquatic	Y		Y	Y	Y
Epeorus	Aquatic				Y	Y
Cinygmula	Aquatic	Y	Y	Y	Y	Y
Baetidae	Aquatic	Y	Y	Y	Y	Y
Drunella	Aquatic			Y		Y
Plecoptera (unID)	Aquatic		Y	Y	Y	Y
Chloroperlidae	Aquatic	Y			Y	
Plumiperla	Aquatic	Y	Y		Y	Y
Trichoptera (unID)	Aquatic	Y	Y	Y	Y	Y
Limnephilidae	Aquatic					Y
Blephaceridae	Aquatic			Y		
Mite	Aquatic	Y	Y	Y	Y	Y
Worm/parasite	Aquatic				Y	
Shrimp	Aquatic					Y
Snail	Aquatic			Y		
Chironomid Adult	Terrestrial	Y	Y	Y	Y	Y
Dipteran Adult	Terrestrial	Y	Y	Y	Y	Y
Mosquito Adult	Terrestrial				Y	
Simuliidae Adult	Terrestrial	Y	Y	Y	Y	
Ephemeroptera Adult	Terrestrial	Y				
Plecoptera Adult	Terrestrial				Y	
Trichoptera Adult	Terrestrial	Y				Y
Lepidopteran Larvae	Terrestrial				Y	
Staphyliniidae	Terrestrial		Y	Y	Y	Y
Carabid (unID)	Terrestrial				Y	Y
Pterostichus	Terrestrial	Y	Y	Y	Y	Y
Bembidion	Terrestrial			Y	Y	Y
Nebria	Terrestrial			Y	Y	
Tachys	Terrestrial			Y		Y

Rhizophagidae	Terrestrial				Y	
Scolitidae	Terrestrial				Y	
Beetle (unID)	Terrestrial				Y	Y
Piercing insect	Terrestrial		Y		Y	
Elateridae	Terrestrial				Y	
Coleoptera Larvae	Terrestrial		Y		Y	
Cerambycidae	Terrestrial				Y	Y
Hymenoptera	Terrestrial	Y		Y	Y	
Arachnidae	Terrestrial	Y	Y	Y	Y	Y
Thysanoptera	Terrestrial	Y	Y		Y	Y
Cicada	Terrestrial				Y	
Hemiptera	Terrestrial				Y	
Collembola	Terrestrial	Y	Y	Y	Y	Y

4. STREAM FOODWEB DYNAMICS IN CATCHMENTS OF DIFFERENT AGES

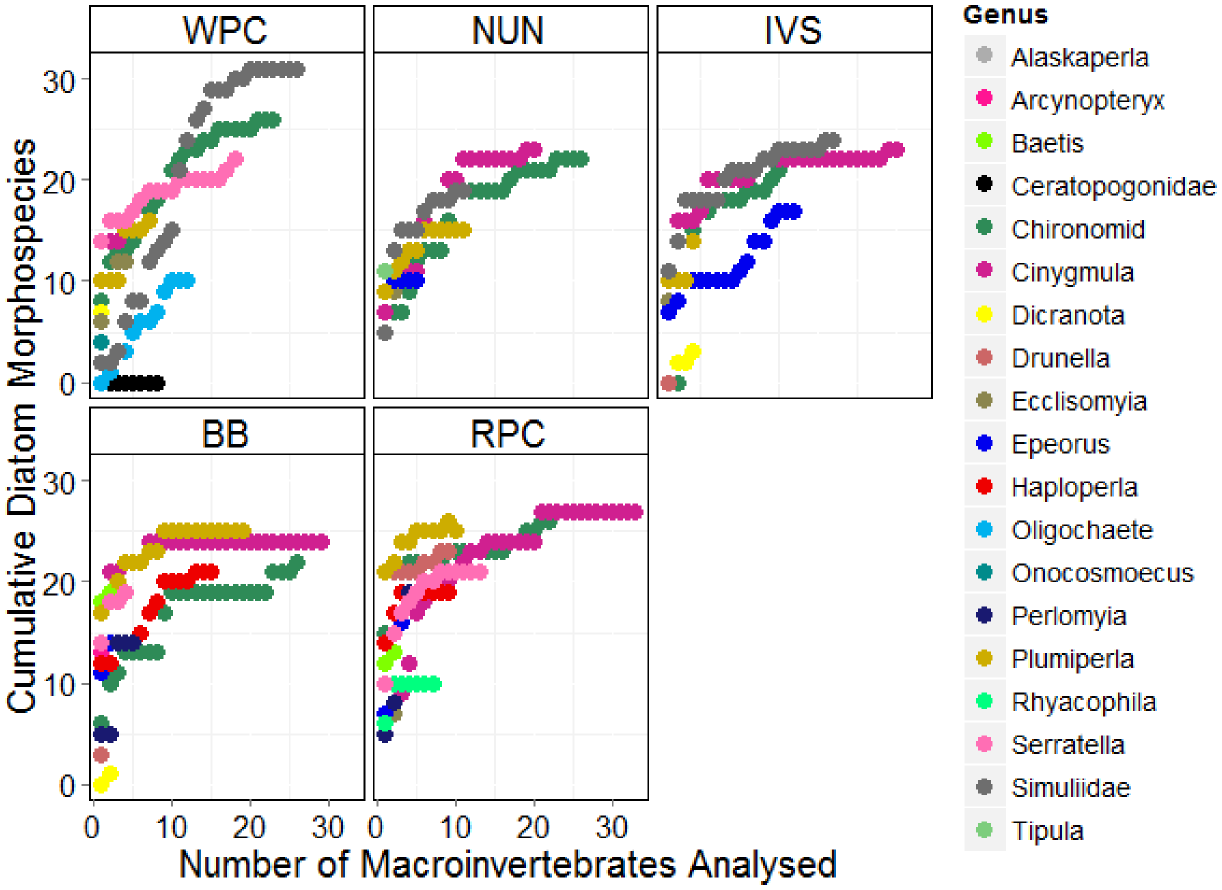
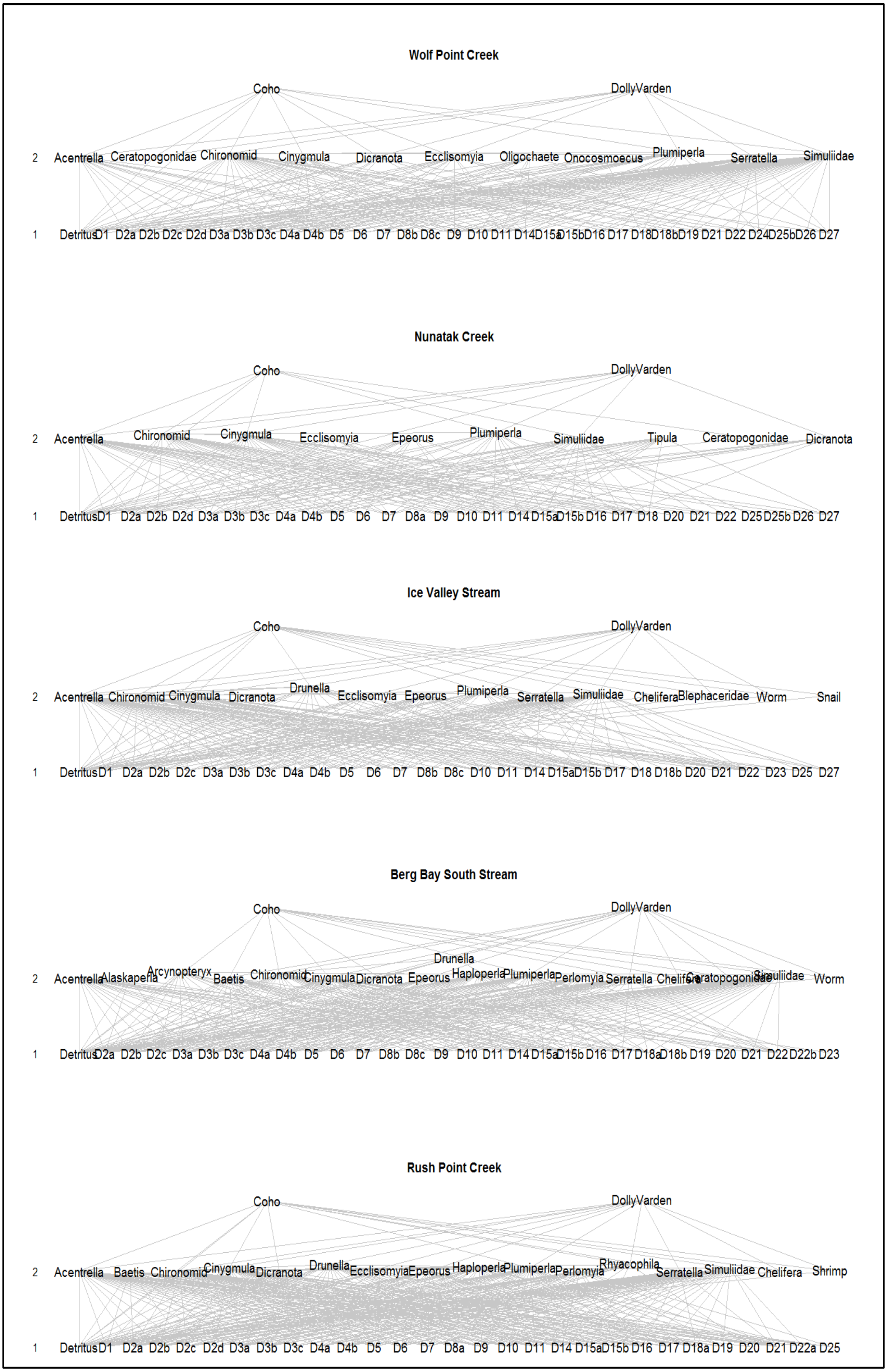


Figure S4.1: Yield-effort curves for diatoms ingested by macroinvertebrates at each sites in Glacier Bay


Wolf Point Creek
Coho
DollyVarden
2
Acentrella
Ceratopogonidae
Chironomid
Cinygmula
Dicranota
Ecclisomyia
Oligochaete
Onocosmoecus
Plumiperla
Serratella
Simuliidae
1
Detritus D1 D2a D2b D2c D2d D3a D3b D3c D4a D4b D5 D6 D7 D8b D8c D9 D10 D11 D14 D15a D15b D16 D17 D18 D18b D19 D21 D22 D24 D25b D26 D27
Nunatak Creek
Coho
DollyVarden
2
Acentrella
Chironomid
Cinygmula
Ecclisomyia
Epeorus
Plumiperla
Simuliidae
Tipula
Ceratopogonidae
Dicranota
1
Detritus D1 D2a D2b D2d D3a D3b D3c D4a D4b D5 D6 D7 D8a D9 D10 D11 D14 D15a D15b D16 D17 D18 D20 D21 D22 D25 D25b D26 D27
Ice Valley Stream
Coho
DollyVarden
2
Acentrella
Chironomid
Cinygmula
Dicranota
Drunella
Ecclisomyia
Epeorus
Plumiperla
Serratella
Simuliidae
Chelifera
Blephaceridae
Worm
Snail
1
Detritus D1 D2a D2b D2c D3a D3b D3c D4a D4b D5 D6 D7 D8b D8c D10 D11 D14 D15a D15b D17 D18 D18b D20 D21 D22 D23 D25 D27
Berg Bay South Stream
Coho
DollyVarden
Drunella
2
Acentrella
Alaskaperla
Arcynopteryx
Baetis
Chironomid
Cinygmula
Dicranota
Epeorus
Haploperla
Plumiperla
Perlomyia
Serratella
Chelifera
Ceratopogonidae
Simuliidae
Worm
1
Detritus D2a D2b D2c D3a D3b D3c D4a D4b D5 D6 D7 D8b D8c D9 D10 D11 D14 D15a D15b D16 D17 D18a D18b D19 D20 D21 D22 D22b D23
Rush Point Creek
Coho
DollyVarden
2
Acentrella
Baetis
Chironomid
Cinygmula
Dicranota
Drunella
Ecclisomyia
Epeorus
Haploperla
Plumiperla
Perlomyia
Rhyacophila
Serratella
Simuliidae
Chelifera
Shrimp
1
Detritus D1 D2a D2b D2c D2d D3a D3b D3c D4a D4b D5 D6 D7 D8a D9 D10 D11 D14 D15a D15b D16 D17 D18a D19 D20 D21 D22a D25

Previous page: **Figure S4.2:** Foodweb diagrams of streams in Glacier Bay with nodes as taxon names

Table S4.1: Richness (*S*) and links (*L*), and references used for Figure 4.6

S	*L*	Reference
24	90	Hildrew et al. (1985)
35	122	Lancaster and Robertson (1995)
39	146	Tavares-Cromar and Williams (1996)
35	110	Tavares-Cromar and Williams (1996)
32	107	Tavares-Cromar and Williams (1996)
31	102	Tavares-Cromar and Williams (1996)
37	120	Tavares-Cromar and Williams (1996)
32	101	Tavares-Cromar and Williams (1996)
33	104	Tavares-Cromar and Williams (1996)
87	858.69	Townsend et al. (1998)
95	1277.75	Townsend et al. (1998)
107	1782.62	Townsend et al. (1998)
86	820.44	Townsend et al. (1998)
96	1130.88	Townsend et al. (1998)
98	1503.32	Townsend et al. (1998)
78	769.86	Townsend et al. (1998)
92	1144.48	Townsend et al. (1998)
37	200	Hall Jr et al. (2000)
35	168	Hall Jr et al. (2000)
41	176	Hall Jr et al. (2000)
35	125	Hall Jr et al. (2000)
24	109	Woodward and Hildrew (2001)
25	128	Woodward and Hildrew (2001)
33	146	Woodward and Hildrew (2001)
34	170	Woodward and Hildrew (2001)
85	378	Schmid-Araya et al. (2002)
86	352	Schmid-Araya et al. (2002)
70	297	Schmid-Araya et al. (2002)
54	229	Schmid-Araya et al. (2002)
128	721	Schmid-Araya et al. (2002)
78	181	Thompson and Townsend (2003)
105	343	Thompson and Townsend (2003)
71	148	Thompson and Townsend (2003)
58	126	Thompson and Townsend (2003)
69	190	Thompson and Townsend (2003)

79	284	Thompson and Townsend (2003)
78	421	Thompson and Townsend (2003)
78	268	Thompson and Townsend (2003)
98	626	Thompson and Townsend (2003)
92	423	Thompson and Townsend (2003)
28	157	Mantel and Salas (2004)
79	240	Thompson and Townsend (2005)
49	110	Thompson and Townsend (2003)
71	155	Thompson and Townsend (2003)
69	187	Thompson and Townsend (2003)
45	193	Parker and Huryn (2006)
42	182	Parker and Huryn (2006)
39	168	Parker and Huryn (2006)
38	150	Parker and Huryn (2006)
46	146	Hernandez and Sukhdeo (2008)
39	126	Hernandez and Sukhdeo (2008)
48	171	Hernandez and Sukhdeo (2008)
42	120	Hernandez and Sukhdeo (2008)
39	127	Hernandez and Sukhdeo (2008)
33	97	Hernandez and Sukhdeo (2008)
48	159	Hernandez and Sukhdeo (2008)
38	116	Hernandez and Sukhdeo (2008)
142	1383	Woodward et al. (2008)
23	137	Layer et al. (2010)
24	159	Layer et al. (2010)
30	187	Layer et al. (2010)
44	427	Layer et al. (2010)
25	136	Layer et al. (2010)
25	178	Layer et al. (2010)
24	135	Layer et al. (2010)
22	94	Layer et al. (2010)
21	99	Layer et al. (2010)
19	71	Layer et al. (2010)
21	108	Layer et al. (2010)
22	56	Layer et al. (2010)
61	759	Layer et al. (2010)
35	285	Layer et al. (2010)
29	194	Layer et al. (2010)
40	335	Layer et al. (2010)
20	114	Layer et al. (2010)

44	384	Layer et al. (2010)
66	940	Layer et al. (2010)
87	1653	Layer et al. (2010)
59	170	Woodward et al. (2010)
33	112	Woodward et al. (2010)
13	16	Clitherow et al. (2013)
19	51	Clitherow et al. (2013)
19	67	Clitherow et al. (2013)
23	85	Clitherow et al. (2013)
46	182	Present study
42	158	Present study
45	202	Present study
49	259	Present study
47	307	Present study

5. THE ROLE OF RECIPROCAL SUBSIDIES ACROSS FLOODPLAINS OF DIFFERENT AGES

Table S5.1: mean $\delta^{13}C$ and $\delta^{15}N$ values for consumers at each site. Site codes refer to names in Table 5.1

			$\delta^{13}C$		**$\delta^{15}N$**		
Site	**Taxon**	**Type**	**Mean**	**SD**	**Mean**	**SD**	**n**
UM	*Nebria*	Riparian	-28.12	0.73	3.24	0.63	11
UM	Arachnidae	Riparian	-25.63	1.07	3.71	1.32	5
UM	Chironomid	Aquatic	-34.07	0.60	-1.08	0.19	3
UM	Ephemeroptera	Aquatic	-34.17	-	2.28	-	1
UM	Alder	Leaf	-27.37	1.00	-0.68	0.12	6
UM	Cottonwood	Leaf	-30.60	0.52	-4.73	1.31	3
WPC	Dolly Varden	Aquatic	-28.94	1.44	6.80	1.02	22
WPC	Coho	Aquatic	-28.67	1.5	7.25	1.09	25
WPC	Arachnidae	Riparian	-26.90	0.53	7.02	1.41	18
WPC	*Bembidion*	Riparian	-27.06	1.56	6.03	0.34	3
WPC	*Nebria*	Riparian	-28.89	0.97	5.95	1.07	42
WPC	*Pterostichus*	Riparian	-28.00	1.16	4.81	1.27	24

WPC	Trechus	Riparian	-26.68	0.62	3.57	0.80	3
WPC	Chironomid	Aquatic	-29.66	2.25	2.59	2.10	10
WPC	Ephemeroptera	Aquatic	-29.30	3.17	1.12	2.34	3
WPC	Plecoptera	Aquatic	-30.10	3.52	4.81	3.16	6
WPC	Simuliidae	Aquatic	-31.44	2.62	2.02	2.70	9
WPC	Trichoptera	Aquatic	-30.11	2.20	0.88	1.57	4
WPC	Alder	Leaf	-27.40	1.38	-0.93	0.73	16
WPC	Cottonwood	Leaf	-30.13	1.29	0.80	1.14	3
WPC	Dead leaf	Leaf	-28.66	0.80	-0.94	0.36	9
WPC	Willow	Leaf	-28.90	1.46	-0.14	2.85	6
NUN	Dolly Varden	Aquatic	-30.11	1.46	3.88	0.95	24
NUN	Coho	Aquatic	-31.44	0.76	5.16	0.43	10
NUN	Arachnidae	Riparian	-26.60	0.74	5.52	1.35	13
NUN	*Bembidion*	Riparian	-27.10	0.82	4.50	0.75	10
NUN	*Nebria*	Riparian	-28.71	1.58	4.46	0.98	26
NUN	*Pterostichus*	Riparian	-26.60	0.58	3.82	0.78	16
NUN	*Trechus*	Riparian	-26.45	0.43	3.50	0.49	5
NUN	Chironomid	Aquatic	-34.30	1.67	-0.53	0.75	8
NUN	Ephemeroptera	Aquatic	-36.90	0.47	0.25	0.37	8
NUN	Plecoptera	Aquatic	-28.96	4.45	8.21	3.75	5
NUN	Alder	Leaf	-27.77	0.87	-1.40	0.41	12
NUN	Dead leaf	Leaf	-29.78	1.21	-1.10	0.20	3
NUN	Willow	Leaf	-28.30	0.84	-1.78	1.30	7
IVS	Dolly Varden	Aquatic	-32.85	2.03	3.88	0.95	24
IVS	Coho	Aquatic	-30.17	1.23	4.47	1.07	11
IVS	Arachnidae	Riparian	-25.97	0.62	4.13	0.85	15
IVS	*Nebria*	Riparian	-28.97	1.56	3.63	0.80	53
IVS	*Pterostichus*	Riparian	-27.34	1.33	2.48	1.16	7
IVS	Blephaceridae	Aquatic	-41.93	0.60	-1.37	0.19	3
IVS	Ephemeroptera	Aquatic	-38.22	1.69	-1.85	0.67	22
IVS	Plecoptera	Aquatic	-31.24	1.67	-0.31	0.13	3
IVS	Simuliidae	Aquatic	-33.67	0.49	-1.08	1.14	4
IVS	Trichoptera	Aquatic	-29.95	1.55	-2.17	1.32	15
IVS	Alder	Leaf	-26.76	1.08	-1.31	0.28	12

IVS	Dead leaf	Leaf	-27.16	0.64	-1.14	0.16	3
IVS	Willow	Leaf	-28.84	1.00	-5.25	1.21	9
BB	Dolly Varden	Aquatic	-28.72	2.61	9.04	1.20	18
BB	Coho	Aquatic	-32.23	3.31	8.46	1.26	14
BB	Arachnidae	Riparian	-28.75	1.05	4.57	0.81	4
BB	*Bembidion*	Riparian	-29.33	1.63	3.20	0.68	8
BB	*Nebria*	Riparian	-30.21	2.15	5.06	1.36	25
BB	*Diplous*	Riparian	-30.80	2.51	7.04	1.34	8
BB	Chironomid	Aquatic	-39.51	1.82	1.52	1.57	7
BB	Ephemeroptera	Aquatic	-38.54	1.95	1.71	1.10	22
BB	Plecoptera	Aquatic	-35.03	4.18	3.55	1.45	12
BB	Alder	Leaf	-27.87	1.38	-1.69	0.67	14
BB	Spruce	Leaf	-29.80	0.14	-2.48	0.12	3
BB	Willow	Leaf	-28.76	1.11	-1.92	0.86	6
RPC	Dolly Varden	Aquatic	-31.81	2.26	6.49	1.03	25
RPC	Coho	Aquatic	-30.91	1.85	6.66	0.74	16
RPC	Arachnidae	Riparian	-29.84	2.58	3.66	1.08	5
RPC	*Bembidion*	Riparian	-30.87	1.27	3.57	0.86	34
RPC	Carabid larvae	Riparian	-32.20	2.39	5.48	1.25	6
RPC	*Nebria*	Riparian	-30.81	2.21	4.81	1.19	8
RPC	*Diplous*	Riparian	-32.36	1.43	5.73	0.91	41
RPC	Chironomid	Aquatic	-35.66	3.95	-1.55	0.78	4
RPC	Ephemeroptera	Aquatic	-39.63	2.27	0.09	1.01	61
RPC	Plecoptera	Aquatic	-32.53	1.05	1.40	1.03	11
RPC	Trichoptera	Aquatic	-33.10	1.96	-0.52	1.36	13
RPC	Alder	Leaf	-27.05	0.85	-1.41	0.14	10
RPC	Dead leaf	Leaf	-29.84	0.46	-2.43	0.47	7
RPC	Spruce	Leaf	-32.30	1.40	-4.02	1.16	9
RPC	Willow	Leaf	-27.90	1.37	-2.48	0.75	11