CAN CONSERVATION STRATEGIES FOR A SINGLE SPECIES BE USED TO INFORM AND GUIDE RESTORATION OF ECOLOGICAL STRUCTURE AND FUNCTION IN FLOODPLAIN PONDS?

by

Margaret Branton

Bachelor of Arts, McGill University, 1990 Master of Environmental Science, Dalhousie University, 1997

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Abstract

Freshwater ecosystems worldwide are degraded by habitat loss, fragmentation and conversion. The practice of ecological river restoration has developed to address degradation, but there has been limited monitoring and assessment of river restoration projects that could be used to improve the science of restoration ecology. I used meta-analysis and studied floodplain ponds restored for juvenile coho salmon (Oncorhynchus kisutch) in southwestern British Columbia, Canada to test ecological and conservation science hypotheses about how restoration projects are planned and assessed. I evaluated the efficacy of the umbrella species concept, which suggests that conservation strategies designed for one species may benefit cooccurring species, using meta-analysis. I empirically assessed the potential for coho to be an umbrella species in restored ponds. I studied the relationship between biodiversity and ecosystem function (i.e., standing biomass) and explicitly considered the role of habitat complexity in mediating that relationship. I evaluated the influence of habitat at different scales (watershed, pond and micro-habitat) on the abundance and biomass of juvenile coho and other aquatic vertebrates. I used standard meta-analytic techniques to assess the umbrella species concept and found conservation strategies designed for umbrella species generally benefit co-occurring species. For the empirical studies, I sampled vertebrates in 17 restored ponds in three watersheds three times over a year. I sampled benthic invertebrates and algae once and documented habitat (e.g., depth, cover) at the pond and trap scale. Coho abundance and biomass, as well as that of other aquatic species, varied across ponds indicating a gradient in response to restoration. There was a positive relationship between species diversity and standing biomass, although that relationship was not consistent across taxonomic groups or with respect to habitat complexity. There was a relationship between watershed-scale habitat features (e.g., landcover, elevation) and the relative abundance and biomass of species present, however, different species responded similarly to micro-habitat types suggesting that watershed scale factors acted as a filter for community composition. This study demonstrated that valuable insight into restoration can be gained by studying patterns from a broad study of restored systems and that restoration designed around a single species can benefit other species.

Preface

A version of Chapter 2 has been published. Branton, M. & Richardson, J. S. (2011) Assessing the value of the umbrella-species concept for conservation planning with metaanalysis. *Conservation Biology*, **25**, 9-20. I conducted all of the analyses and wrote the manuscript with guidance and review from co-author John Richardson.

Check the first page of this chapter to see footnotes with similar information.

The study methods were approved by the University of British Columbia Animal Care Committee (Protocol #A06-0294).

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Sadie and Sack

Chapter 1: Introduction

Habitat loss, fragmentation and conversion have been recognized as the foremost drivers of the loss of biodiversity globally, including ecosystems, biological assemblages, species and populations (Vitousek et al., 1997; Sinclair & Byrom, 2006). Freshwater systems are particularly susceptible to degradation from anthropogenic activities because humans live disproportionately near water and tend to extensively modify riparian ecosystems (Sala et al., 2000; Young, 2000; Palmer, 2009). The conservation of biodiversity is best achieved by setting aside protected areas that include a representative sample of biodiversity, maintain natural processes and viable populations, and exclude threats (Margules & Pressey, 2000). Even at best, however, protected areas are essentially islands of habitat within a larger landscape that are less ecologically intact. Moreover, conservation reserves are often located in areas that are remote or unproductive and do not adequately represent regional or global biodiversity largely due to direct competition between allocation of land for reserves and other human activities such as resource extraction, agriculture and housing and commercial development (Margules & Pressey, 2000; Ehrlich & Pringle, 2008). Given the declining availability of habitat for conservation reserves (Vitousek et al., 1997), strategies for conservation of biodiversity will need to include the restoration of degraded habitats (Dobson, Bradshaw & Baker, 1997; Hobbs & Harris, 2001; Ormerod, 2003; Sinclair & Byrom, 2006; Brudvig, 2011). Restoring habitat in areas that are not typically available for reserves may represent a gain in terms of maintaining or increasing biodiversity and is an important complement to reserve systems (Young, 2000; Hobbs & Harris, 2001; Ehrlich & Pringle, 2008).

Land management practices that can be considered ecological restoration, such as erosion control, reforestation and the improvement of range and other habitat, have been

utilized for decades (Young, Petersen & Clary, 2005). The increasing need for, and practice of, ecological restoration [i.e., interventions to assist the "recovery of an ecosystem that has been degraded, damaged or destroyed" (SER, 2004)] in recent decades has led to the development of the relatively new science of restoration ecology which uses fundamental ecological concepts to guide and address questions stemming from the practice of restoration (Palmer, Ambrose & Poff, 1997; Young et al., 2005). Examples of ecological theory that is relevant to restoration ecology includes, but is not limited to, that related to population dynamics, community assembly and persistence, context dependency of ecological response, ecosystem structure and function and the role of habitat heterogeneity in enhancing species diversity (Lake, Bond & Reich, 2007; Palmer, 2009).

The development of the science to support and inform restoration practices is reflected by the rapid growth in the publication record of articles related to restoration ecology in the 1990s and 2000s with an increase in restoration papers in ecology focused journals of almost 5% between 1990 and 2010 (Young et al., 2005; Brudvig, 2011). Despite this development in restoration ecology, a frequent lament in the literature is that there has been too little interaction between ecologists and restoration practitioners with the result being that the most relevant and current ecological theory does not always get translated to the restoration community in a timely fashion and theoretical ecologists have not taken advantage of the opportunity to test theory using restoration projects (Lake et al., 2007; Temperton, 2007; Palmer, 2009). Some apparent failures of the integration of ecological theory and restoration ecology occur because ecological theory tends to be studied in simplified systems to facilitate the development of theory and generalities and these simplified guiding principles are then applied to ecological restoration in natural systems

which are complex and often highly variable (Hilderbrand, Watts & Randle, 2005). On the other hand, studies of restored systems tend to be site specific, missing the opportunity of producing more generalized theory that may lead to the development of predictable outcomes of restoration (Lake et al., 2007; Palmer, 2009). In other words, to date restoration has not fully provided the "acid test" of ecological theory imagined by Bradshaw (1987). Better incorporation of theory will ideally improve restoration outcomes, help with the development of some general theory, and test ecological theory (Lake et al., 2007).

Notwithstanding the difficulties in aligning theory and practice, there are important examples of ecological theory redirecting ecological restoration and possibly resulting in a paradigm shift such as that related to equilibrium dynamics, thresholds and state changes (Palmer, 2009). Early on the goal of ecological restoration was considered to be the return of ecosystems to a historic condition, generally a "pre-disturbance" state where disturbances were anthropogenic in source. In line with this belief that succession is deterministic, that once the source of degradation is removed the system will essentially reset itself to its former trajectory is the use of reference systems that are supposedly representative of this equilibrium "end" state. However, historic conditions may not be attainable (or even knowable) due to, for example, permanently altered landscapes and climate change or because most restoration projects are implemented on a small scale compared to the scale that a successional paradigm would operate on (Hobbs & Harris, 2001; Hilderbrand et al., 2005; Palmer, 2009). The alternative ecological theory posits that there are multiple stable states, that systems are dynamic and that their development is a function of site history, stochastic events and disturbance (Hobbs & Harris, 2001; Wallington, Hobbs & Moore, 2005; Palmer, 2009). In reality, both equilibrium and non-equilibrium dynamics are likely

present in different systems and now it is not always assumed that a stable end-state should be the goal of all restoration projects. Under this paradigm, instead of identifying an end goal for restoration based on a deterministic concept of ecosystem recovery, the goal becomes precipitating a shift in ecosystem composition, structure, and function to be "within a range that is more desirable than current conditions" (Palmer, 2009).

One of the tensions between the practice of ecological restoration and the testing of ecological theory is, absent large scale manipulations which are not common, stream and floodplain restoration is rarely carried out in a classic experimental framework with before and after studies or test and control sites. In fact, any kind of post-restoration monitoring is rare, and that which is conducted tends to focus on the integrity of physical structures rather than on biological responses to the restoration (Bernhardt et al., 2005; Roni, 2005). Restoration is often conducted opportunistically, where land is available or volunteer groups willing, or on an as needs basis such as in response to large scale and unprecedented events such as the 2010 oil spill in the Gulf of Mexico (Mitsch, 2010).

Though not ideal for cause and effect hypothesis testing, a broad study of restored systems can, and must, be used to reveal patterns that may inform the practice of restoration. Multiple lines of evidence can be used to assess the structure and function of restored ecosystems including those related to populations (e.g., age structure, recruitment), communities (e.g., functional groups, species richness, species dominance, ratio of native to exotic species) and processes (e.g., hydrology, energy flow, nutrient cycling) on both a project-specific and landscape scale (Holl & Cairns Jr., 2002; Holl, Crone & Schultz, 2003). Using quantitative comparisons amongst sites that have undergone similar kinds of restoration, but that vary along environmental gradients or in terms of management practices,

it may be possible to identify the relative importance of specific factors (e.g., hydrology, cover) that may limit or promote restoration (Holl et al., 2003). That being said, wherever possible restoration should be conducted in a more experimental framework and large-scale, replicated manipulative restoration projects are invaluable (Holl et al., 2003). Both a more systematic approach to restoration that incorporates the explicit testing of ecological theory and the publishing of results (success and failures) in a way that makes them amenable to integration in meta-analysis are necessary to strengthen the links between the practice of ecological restoration and the ecological theory that may improve upon the success of restoration while providing real world tests of ecological theory (Holl et al., 2003; Bernhardt et al., 2005).

I used floodplain ponds restored for a single species, coho salmon (*Oncorhynchus kisutch*, hereafter "coho") in southwestern British Columbia to empirically test questions pertaining to ecological theory and the biological response of aquatic vertebrates and invertebrates to restoration. Although restoration of these habitats has been ongoing for over 50 years, there has been a chronic lack of post-project assessment or research studies of the restored habitats. As a result we do not know if the objectives that motivated individual projects have been met or how restoration has affected overall structure and function of the off-channel ponds. This study system, though non-experimental, allows the testing of hypotheses related to the response to restoration of ponds that have undergone similar kinds of treatments but that represent a gradient of pond- and watershed-specific conditions (Holl et al., 2003). In the most general terms, I evaluated if a restoration approach designed to benefit a single species would have discernible benefits for the broader ecological community. I evaluated the effectiveness of using single species to develop conservation and

restoration approaches for the broader community of species present using a meta-analysis (Chapter 2) and a case study with coho (Chapter 3). In Chapter 4, I evaluated the relationship between biodiversity (species richness and evenness) and ecological function in the restored off-channel ponds as well as the role that habitat heterogeneity plays in modifying those relationships. In Chapter 5, I examined variation in abundance and biomass of the most common vertebrate species at watershed, pond and microhabitat scales. A brief description of the study system and an overview of Chapters 2 through 5 are provided below. Throughout this set of studies, wherever possible multiple biological responses (abundance and biomass) were measured as appropriate for all available vertebrate and invertebrate species with the explicit consideration of specific habitat features and complexity. This was done with the intention of assessing the relative sensitivity of biological response and interactions between species and habitat.

1.1 Study System

Riparian corridors are among the most diverse, dynamic and complex systems within terrestrial portions of the earth (Naiman, Decamps & Pollock, 1993). Where rivers are unconstrained there are often braided channels and extensive floodplains resulting in a mosaic of habitat off-channel areas including oxbow lakes, meander bends, floodplain channels (e.g., sloughs, beaver ponds, surface and groundwater fed tributaries), wetland areas and accumulations of wood and riparian vegetation (Pess et al., 2005). Complex river channels provide thermal refugia, nursery and spawning areas and corridors to floodplains for plants, invertebrates, fish, birds, and mammals (Sedell et al., 1990). In British Columbia, and throughout the Pacific Northwest, the disruption, isolation and simplification of the mosaic of river and floodplain systems from activities including urban and agricultural development, flood control, road building and forestry has impacted aquatic and terrestrial communities that rely upon these habitats and their associated resources (e.g., see review in Cederholm et al., 1997; Roni, 2005). Restoration projects have been conducted in British Columbia since the 1950s with the primary goal of improving habitat for salmonids (Johnston & Slaney, 1997) although instream habitat enhancement has a much longer history (e.g. see Roni, Fayram & Miller, 2005). Off-channel floodplain ponds and channels have been restored, created and enhanced (e.g., reconnected hydrologically, instream habitat improvements) (hereafter "restored") over a period of about 20 years specifically to increase the available habitat necessary for coho rearing and spawning and for chum (*O. keta*) spawning (Lister & Finnigan, 1997).

I conducted this study in 17 restored ponds in three watersheds in southwestern British Columbia representing a range of habitat and watershed conditions. These ponds were restored by improving the connectivity of existing ponds to surface water flow and by creating new ponds using groundwater or water diverted from nearby dams, rivers and creeks to flood bermed or excavated areas. Most ponds were either surface- or ground-water fed, though several had a combination of both water sources. Common features of the restoration projects were the addition of wood (root wads or large pieces of wood) and the creation of deep channels. Otherwise the habitat of the restored ponds varied from the watershed- to micro-habitat scale based on local site conditions.

1.2 Chapters 2 and 3

Limited resources and incomplete knowledge about complex ecological systems are chronic issues in the study and practice of conservation biology and restoration. Surrogate species approaches have been developed to make conservation planning and monitoring more efficient when direct assessment of the larger ecological community is not feasible due to technical or financial constraints and/or when benefits accrue from a focus on a single species (Simberloff, 1998; Caro & O'Doherty, 1999; Roberge & Angelstam, 2004). There are five common categories of surrogate species (Favreau et al., 2006; Wiens et al., 2008). Flagship species are charismatic species that can be used to garner public and political support for projects that would otherwise not be supported. *Keystone species* are protected because they have a disproportionate effect on the environment relative to their abundance or biomass and co-occurring species are thought to benefit from their protection (Lambeck, 1997; Simberloff, 1998; Palmer, 2009). Indicator species are generally used either to identify areas with high biodiversity or to monitor changes in the environment (Landres, Verner & Thomas, 1988; Simberloff, 1998). The ecological requirements (or preferences) of umbrella species are used to guide the determination of the minimum size for conservation areas, the selection of sites to be used in reserve networks and setting minimum standards for the composition, structure and processes of ecosystems all with the expectation that conservation efforts on their behalf will confer benefits to co-occurring species as well (Andelman & Fagan, 2000; Caro, 2003; Roberge & Angelstam, 2004). The *focal species* approach, developed from the umbrella species approach, uses a suite of species that are sensitive to specific, threatening processes (e.g., disruption in dispersal, habitat fragmentation) to

determine conservation actions with the assumption that less sensitive co-occurring species will benefit (Lambeck, 1997). Critics argue that surrogate approaches are overly simplistic and may lead to the incorrect assumption that all biota of concern are protected (e.g., higher species diversity, increased density) if the ecological requirements of surrogate species are met (Lindenmayer et al., 2002). In spite of this, single-species surrogate approaches continue to be used and evolve largely because the alternatives are impossible, i.e., direct assessment and management of everything (Sarkar et al., 2006; Rodrigues & Brooks, 2007a), untenable (i.e., to do nothing), or are subject to similar shortcomings (e.g., ecosystem management - Simberloff, 1998; environmental surrogacy - Rodrigues & Brooks, 2007b).

In this study I focused on umbrella species which have potential for use in restoration planning. Lindenmayer (2002) and Roberge and Angelstam (2004) propose that an evaluation of the response of a set of species to restoration actions can be used to test the theory that restoring habitat for a sub-set of taxa is also effective in restoring habitat for other biota. One of the useful aspects of the umbrella species concept is that it can be applied in mixed-use contexts (e.g., some resource extraction, agriculture or habitation) to determine standards of ecosystem composition (e.g., habitat complexity) and structure (e.g., area, dispersal corridors) (Lambeck, 1997; Fleishman, Blair & Murphy, 2001; Roberge & Angelstam, 2004; Gardner et al., 2007).

There have been relatively few empirical tests of the umbrella-species concept and those that have been published report equivocal and context dependent results. In Chapter 2, I use meta-analysis to evaluate if the important characteristics for umbrella species reported in the literature are associated with greater species richness and/or abundance than umbrella species without these important characteristics. The umbrella species concept would be most useful in restoration planning if presumed umbrella and co-occurring species respond similarly to restoration. In Chapter 3 I assess the similarity of response of juvenile coho salmon and co-occurring juvenile and adult vertebrate (fish and amphibians) and benthic invertebrate species to habitat restored for coho. Though the umbrella species concept is generally tested by comparing species richness, and less frequently abundance or density of co-occurring species, in sites with and without umbrella species, I evaluated relationships between the relative abundance and biomass of both coho (the umbrella) and co-occurring species to assess benefits associated with restoration of habitat for the umbrella species. I also assessed habitat as a potential mechanism influencing the congruence in response of coho and co-occurring vertebrate and invertebrate abundance and biomass to restoration.

1.3 Chapter 4

It has been argued that a reduction in biodiversity (i.e., species and functional richness) may result in a decrease in ecosystem function (e.g., productivity, processing rates, water purification). This, has been evoked as a precautionary argument for conserving as much biodiversity as possible (Hooper et al., 2005; Cardinale et al., 2006a). However, it has also been argued that it is not yet appropriate to use biodiversity and ecosystem functioning (BEF) research as the basis of a general argument for the conservation of biodiversity both because important research questions remain unresolved and because the results of BEF research are often context dependent and idiosyncratic (Srivastava & Vellend, 2005; Cardinale et al., 2006a). Evaluating the relationship between biodiversity and key aspects of ecosystem functioning in a restored system where species are being "added" (albeit not experimentally) instead of removed provides a unique opportunity to evaluate some of the

findings of BEF research and also may be useful in informing management decisions related to restoration (Srivastava & Vellend, 2005). To date the majority of BEF studies, particularly those outside of agricultural systems, have tested the relationship between diversity and ecosystem function using simple (e.g., single trophic level) food webs in controlled, experimental environments. Notably a study in several natural environments demonstrated that differences in ecosystem function can be detected along a gradient of habitat heterogeneity (Tylianakis et al., 2009).

The implicit assumptions that the restoration of habitat will result in the return of species, that more heterogeneity in habitat is better than simpler habitat and that increased species diversity will result in enhanced ecological function has had few empirical tests (Lake et al., 2007; Palmer, 2009). In the context of stream restoration this is particularly critical given the number of stream restoration projects with relatively little assessment of the biological response to restoration (Bernhardt et al., 2005; Roni, 2005). I used several measures of vertebrate and benthic invertebrate diversity (i.e., species and functional trait richness and evenness), habitat complexity and interactions between diversity and habitat complexity to evaluate their relative importance for ecosystem function in the study system. Relative standing biomass of vertebrates, benthic invertebrates and algae were used as proxies for ecosystem function.

1.4 Chapter 5

Despite the recognition that watershed-scale factors such as land use are important determinants of processes that may lead to stream degradation or recovery, most stream channel, riparian and floodplain restoration occur as local, small-scale, often one-off

interventions implemented opportunistically rather than strategically within a broader watershed plan (Bernhardt et al., 2005; Lake et al., 2007). Environmental variables at watershed scales may also directly or indirectly influence variables at lower environmental scales including biotic communities, particularly in ecosystems such as floodplains in which function depends on high levels of connectivity (Frissell et al., 1986; Ward, Tockner & Schiemer, 1999; Stephenson & Morin, 2009). While the location of restoration projects within the watershed may act as a filter for species assembly in a newly restored ecosystem, the specific habitat configuration of the restored habitat will also contribute to the biotic environment, for example, by providing substrate for primary productivity and cover for organisms that will mediate inter- and intra- species dynamics. In the stream restoration context, there has been some skepticism as to whether adding structure serves simply to aggregate fish or to actually enhance their production (Palmer, 2009). Assessing the relative condition of organisms congregating around habitat structure in addition to simply enumerating the number of individuals may contribute to a more useful evaluation of the benefit of particular habitat types. From a restoration perspective, if relationships between specific habitat features and project success are known that information can be used in the design of future restoration projects.

The goal of this study was to determine if the presence of pond habitat, whatever its configuration or watershed context, produces coho and other vertebrates in similar numbers and size, or if specific habitat attributes at the watershed, pond or microhabitat scale are associated with more and larger individuals of the species evaluated. It tests the hypothesis that specific habitat attributes of restored ponds have a strong influence over the composition

of the aquatic community that occupies those ponds and over the distribution of species and con-specifics of different size classes within those ponds.

Chapter 2: Assessing the Value of the Umbrella Species Concept¹

2.1 Introduction

For more than 25 years conservation planners have suggested that actions to conserve one species might serve to maintain co-occurring species (Wilcox, 1984; Roberge & Angelstam, 2004). Nevertheless, the relatively few empirical tests of this umbrella-species concept, the majority of which have been published since 2000, have produced equivocal results. This has led conservation professionals to question the utility of umbrella species in conservation planning, although the consensus appears to be that this concept has potential and warrants further testing and improvement (e.g., Caro, 2003; Roberge & Angelstam, 2004; Seddon & Leech, 2008). Sufficient empirical data are now available for a quantitative synthesis testing of some of the key assumptions of the umbrella-species concept.

The general criteria used to identify a potential umbrella species include well-known natural history and ecology, spatial overlap with co-occurring species of concern, moderate negative response to disturbance, and relative ease of sampling (e.g., Caro & O'Doherty, 1999; Fleishman, Murphy & Brussard, 2000; Seddon & Leech, 2008). Specific criteria for identifying potential umbrella species area close taxonomic relation to co-occurring species of concern and a large home range or body size. It has also been suggested that species with specialized resource requirements (e.g., dead wood, old-growth forest, riparian areas) (specialists) may be better umbrellas than those without specialized requirements (generalists) (e.g., Ozaki et al., 2006; Roberge, Mikusinski & Svensson, 2008) and that trophic level may affect a species' potential to serve as an umbrella species, although there is

¹ A version of Chapter 2 has been published. Branton, M. and Richardson, J.S. (2011) Assessing the value of the umbrella-species concept for conservation planning with meta-analysis. *Conservation Biology*, **25**, 9 - 20.

no consensus as to what trophic level is best (Caro et al., 2004; Roth & Weber, 2008; Sergio et al., 2008).

Empirical studies of the umbrella-species concept have tended to use paired designs to compare species richness and, in some instances, relative abundance of co-occurring species. These studies have used a wide range of taxonomic groups as putative umbrella species (e.g., birds, mammals) and as co-occurring species (e.g., insects, fungi). The studies have examined empirical data from tropical and temperate ecosystems (e.g., forest, savannah) at extents ranging from individual trees to thousands of square kilometers. Researchers typically used either hypothetical reserves or land-management scenarios designed to meet the area or specific resource needs of the umbrella species, or they used existing reserves not specifically designed to meet the ecological requirements of umbrella species to test the umbrella-species concept. In studies of hypothetical scenarios, the richness and abundance of co-occurring species in locations where the umbrella species was present or abundant were compared with randomly selected areas that were environmentally similar but where the umbrella species was absent or unlikely to persist (e.g., Ozaki et al., 2006; Roberge et al., 2008). In retrospective evaluations of existing reserves, comparisons were made of the richness and abundance of umbrella and co-occurring species inside and outside the reserves (e.g., Caro, 2003; Dunk, Zielinski & Welsh Jr., 2006). Overall, the results of research evaluating umbrella species are variable and appear to be highly context dependent.

We used meta-analyses to examine quantitatively whether key assumptions underlying the concept of umbrella species are met. We explored whether species richness and abundance of individuals (per species or taxonomic group) were greater in areas where putative umbrella species are present than where they are absent. We tested whether species

richness or abundance of co-occurring species varied as a function of the umbrella species' taxonomic class, taxonomic similarity to co-occurring species, or body size. Further, we investigated whether the potential to serve as an umbrella species varied among species with specialized or general resource requirements. We also examined whether the efficacy of putative umbrella species differed among trophic levels.

2.2 Methods

2.2.1 Data Selection and Extraction

We used the electronic database ISI Web of Science (1965 to March 2009) and the search engine Google Scholar to search the literature for the terms umbrella species, which does not have a common synonym in the conservation literature, and surrogate species. We reviewed a paper if, from the abstract, it appeared to include original data. Fifteen articles from an initial pool of 66 reported data that were suitable for this meta-analysis. We included only studies with paired comparisons in our meta-analysis because the response variables measured in reserve design studies differed. Multiple paired comparisons were reported in most studies; therefore, sample sizes for each analysis differed and depended on the number of paired comparisons conducted for each variable (Table 2.1).

We categorized putative umbrella species as being in the same or a different (across) taxonomic group as the co-occurring species. If an umbrella species was identified as having specific resource requirements in the original study, it was categorized as a specialist; otherwise, it was considered a generalist. We determined trophic level following Schoener

Table 2.1. Attributes of studies included in meta-analysis evaluating whether conservation of putative umbrella species also conserves co-occurring species

					No. of pairs of putative umbrella species and group of co- occurring species by response		
				Study	variable*	abundance	
Reference	Vegetation	Putative umbrella species	axonomic group of co-occurring		Species	per	per taxonomic
Bifolchi and Lode, 2005	Riparian (N. America)	Lutra lutra (European otter)	anurans, birds, molluscs	18	3	na*	na
Caro, 2001	Forest (Africa)	Various megafauna (mammals)	small mammals	25	1	8	1
Caro, 2003	Forest (Africa)	Various megafauna (mammals)	large/medium and small mammals	24, 20	2	19	2
Caro et al. 2004	Forest (Central America)	Panthera onca (jaguar), Tapirus bairdii (Baird's	amphibians, birds, mammals	4	20	na	20
		tapir), <i>Dicotyles pecari</i> (white-lipped peccary), <i>Ateles geoffroyi</i> (spider monkey)					
Dunk et al. 2006	Forest (N. America)	Strix occidentalis (Northern Spotted Owl)	amphibians, molluscs	152, 241	2	na	na
Fontaine et al. 2007	Forest (Africa)	Various megafauna (mammals)	molluscs	145	1	na	1
Gardner et al. 2007	Forest (Africa)	Various mégafauna (mammals)	amphibian, bird, insect, mammal, plant	20	6	24	5
Hurme et al. 2008	Forest/agricultural (Europe)	Pteromys volans (Siberian flying squirrel)	fungus, insect, lichen	20	3	36	3
Ozaki et al. 2006	Forest/agricultural	Accipiter gentilis (Northern	bird, insect, plant	80	4	na	4
Pakkalla et al. 2003	Forest/agricultural	Tetrao urogallus (Capercaillie)	bird, insect, plant	82	1	3	1
Ranius, 2002	Forest/agricultural (Europe)	Osmoderma eremita (beetle)	insect	41	1	na	na
Roberge et al. 2008	Forest/agricultural (Europe)	Dendrocopos leucotos (White-backed Woodpecker)	bird, cryptogam, insect	122	3	na	na
Roth and Weber, 2008	Alpine (Europe)	Milvus milvus (Red Kite), M. migrans (Black Kite), A. gentilis (N. Goshawk), A. nisus (Eurasian Sparrowhawk), Buteo buteo (Common Buzzard), Falco tinnunculus (Eurasian Kestrel), S. aluco (Tawny Owl), Parus ater (Coal Tit), P. caeruleus (Blue Tit), P. cristalus (Crested Tit), P. major (Great Tit), P. montanus (Willow Tit), P. palustris (Marsh Tit)	bird, insect, plant	64, 283, 4	5 39	na	na
Sergio et al. 2006	Alpine (Europe)	A. gentilis (N. Goshawk), Glaucidium passerinum (Pygmy Owl), Aegolius funereus (Tengmalms Owl), S. aluco (Tawny Owl), Asio otus (Long-eared Owl), Otus scops (Scops Owl) T. urgoallus (Canercaillia)	bird	50	20	1	6

(1968): herbivores, consume <10% animal matter; omnivores, 10–90% animal matter; and carnivores, >90% animal matter. We also assigned umbrella species to size classes on the basis of body mass: birds, ≤ 0.02 , >0.02–0.1, >0.1–0.25, >0.25–0.5, >0.5–1, and >1–5 kg; mammals, ≤ 0.25 , >0.25–10, >10–20, >20–50, >50–100, >100–500, and >500 kg. We restricted our meta-analysis to studies that reported species richness and relative abundance of individuals (hereafter abundance) of co-occurring species. We did not evaluate vegetation type (e.g., savannah, forest), which may affect the efficacy of umbrella species because small sample sizes for each type precluded robust statistical analyses. In some instances authors reported data in multiple categories (e.g., the same species could be reported in the categories all birds and mountain birds; Suter, Graf & Hess, 2002). In these instances, we used the most general category in our analyses. (See Appendix A, Table A.1 – A.3) for a summary of the data that were included in the data set.)

Species richness is the primary response variable that has been used to assess the success of conservation schemes based on putative umbrella species, although some studies use density or abundance of individuals as an approximation of population viability (Fleishman, Noss & Noon, 2006). Abundance data are reported herein as abundance per species or as abundance per taxonomic group (e.g., bird, amphibian), depending on the level of detail provided in the original study. The response variable abundance per taxonomic group does not provide information on the viability of an individual species, but it provides an estimate of relative productivity of species in different taxonomic groups. We examined both measures of abundance because only a subset of the studies reported abundance by species. When more than one putative umbrella species was evaluated and when species richness or abundance were reported for more than one group of co-occurring species, we

treated each pair of putative umbrella and group of co-occurring species as an independent estimate (e.g., one mammal umbrella species and two groups of co-occurring species was two data sets). Thus, our sample size for each analysis was based on the number of pairs analyzed for each response variable (Table 2.1). We extracted data directly from text and tables in the articles, estimated data from figures (ByteScout Software) in the articles, or obtained data directly from the authors (Dunk et al., 2006; Sergio et al., 2006).

2.2.2 Data Analyses

The effect size calculated in meta-analyses is a standardized metric for comparing and analyzing diverse studies. Effect sizes from individual studies are combined to provide an estimate of the strength of an effect across studies (Rosenberg, Adams & Gurevitch, 2000). Ideally in meta-analyses, effect size is weighted by means, sample sizes, and standard deviations for the control and the experimental group. Studies with larger sample sizes and lower variance have higher weight than studies with smaller sample sizes and greater variance (Rosenberg et al., 2000). Nevertheless, estimates of variability are often not reported in published articles. When this is the case, a study can still be included in the meta-analyses if one weights by sample size alone. Alternatively, studies without estimates of variability can be excluded from the meta-analysis; this option increases the probability of type I error (Shurin et al., 2002; Lajeunesse & Forbes, 2003). To include the maximum number of studies in our meta-analysis, we used weights from sample size alone to calculate effect sizes, which may have increased the probability of type II error (Gurevitch & Hedges, 1999; Shurin et al., 2002). We used Hedges'd, which can be applied to data sets that contain zeros, to calculate the effect size (Rosenberg et al., 2000). Hedges'd calculates effect sizes by subtracting the

mean effect size of the response variable (species richness, abundance per species, or abundance per taxonomic group) in the control (areas in which putative umbrella species were absent) from the experimental mean (areas in which putative umbrella species were present) and multiplying this value by a standardized value that scales the result by sample size (Rosenberg et al., 2000).

We conducted a categorical meta-analysis in which data were grouped according to the hypotheses being tested. Categorical variables were treated as random effects because we expected the true effect may vary among studies (Gurevitch & Hedges, 1999). We included all data in the calculation of grand mean effect sizes; however, when fewer than three data sets were available for a given category (e.g., body size ≤ 0.25 kg), we excluded those data from further statistical analyses in that category. The expected value for the null hypothesis was zero, with values >0 indicating a positive effect (i.e., greater species richness or abundance) of the presence of umbrella species and values <0 indicating a negative effect (Rosenberg et al., 2000). When the confidence interval associated with an effect size overlapped zero, the effect was not statistically significant.

We visually assessed a normal quantile plot to determine whether the data fit a normal distribution. We considered slight violations of normality acceptable and treated data sets with <5% of data points falling outside the 95% confidence intervals of the normal quantile plot as normal. We analyzed data with non-normal distributions with bootstrapping (5000 iterations) and calculated confidence intervals with a bias correction when >50% of the bootstrap values were above or below the original value (Rosenberg et al., 2000). Resampling techniques, such as bootstrapping, can be used when data are not distributed

normally. Moreover resampling uses data, not ranks, and therefore is more powerful than traditional nonparametric tests (Gurevitch & Hedges, 1999).

We used a rank correlation test (Spearman's rho) to determine whether there was a significant correlation between sample size and effect size that suggests a bias toward publication of tests with larger effects. If we detected such publication bias, we used fail-safe numbers (Rosenthal's method) to determine the number of nonsignificant, unpublished, or missing studies necessary to change the results of the meta-analysis from significant to nonsignificant. If the fail-safe number was large relative to the number of original studies (at least 5n+10, where n is the number of original studies), we treated the results as a reliable estimate of the true effect (Rosenberg et al., 2000).

We tested for homogeneity of the cumulative mean effect sizes between categories with a random-effects model of among versus within group heterogeneity that was based on the statistic Q (Rosenberg et al., 2000). We tested the total heterogeneity of each categorical group QT against a chi-square distribution with the null expectation that all effect sizes would be equal. A significant QT indicates the variance among effect sizes is unequal and other variables may explain the structure in the data. When the null expectation was rejected, we used between-group variance (QB) to identify other factors that might explain the structure in the data. For non-normal data, we based our calculation of the p value on resampling. We used MetaWin (version 2.15; Rosenberg et al., 2000) for all analyses, and considered results significant at α = 0.05. We did not adjust for multiple comparisons because the analysis was exploratory. Nevertheless, we provide p values for each test to indicate its associated level of significance.
2.3 Results

All 15 studies we analyzed were published since 2000 (Table 2.1). Species richness was used as a measure of the benefits conferred to co-occurring species by umbrella species more often than abundance per species and more than twice as often as abundance per taxonomic group (n= 106, 90, and 40, respectively). The data set of abundance per taxonomic group had a normal distribution and no publication bias (ρ = 0.28, p= 0.08). The species richness and abundance per species data sets had non-normal distributions and the Spearman rho tests were significant (respectively, ρ = 0.40, p< 0.001 and ρ = 0.40, p= 0.0001), which indicates publication bias. The fail-safe numbers for species richness and abundance per species were large (respectively, 419,479 and 52,016).

Relative to control sites mean species richness (mean = 6, 95% CI 3.4–9.1), abundance per species (mean = 4.0, 95% CI 2.4–5.7), and abundance per taxonomic group (mean = 3.1, 95% CI 1.5–4.6) were higher in sites where putative umbrella species were present. Overall mean effect sizes were significant for species richness (QT= 1077.9, df = 105, p< 0.0001), abundance per species (QT 904.4, df = 89, p< 0.0001), and abundance per taxonomic group (QT 477.1, df = 39, p< 0.0001), which indicates factors in addition to the presence or absence of umbrella species (e.g., taxonomic group, body size) may explain the structure in the data. Birds and mammals were used as umbrella species in all studies with the exception of one in which insects were used (Ranius, 2002). For species richness the effect size for birds as umbrella species (QB= 61.9, df = 1, p= 0.007). For abundance per taxonomic group, the effect size for birds was four times greater than for mammals (QB=13.9, df = 1, p= 0.0002) (Figure 2.1). For abundance per species, birds and mammals did not

differ significantly (QB= 389.1, df = 1, p= 0.21) (Figure 2.1). For consistency in all subsequent analyses, however, we analyzed birds and mammals separately. Mean effect sizes were significantly positive for all response variables except co-occurring species richness and abundance per taxonomic group when the umbrella species was a mammal.



Figure 2.1 Mean effect size with 95% confidence intervals for species richness (SR), abundance per species (SpAb), and abundance per taxonomic group (TaxAb) of co-occurring species in conservation schemes with avian or mammalian umbrella species. Numbers in parentheses in x-axis labels are number of pairs of putative umbrella species and group of co-occurring species, and letters above bars indicate significant differences between means (**p< 0.01; ***p< 0.001). Where confidence intervals overlap the zero line, the effect is not significant.

There were no significant differences between across-taxonomic group and sametaxon umbrella schemes for co-occurring species richness (birds: QB= 1.5, df = 1, p= 0.72; mammals: QB= 2.1, df = 1, p= 0.31) or abundance per species for mammals (QB= 3.12, df = 1, p= 0.44) (Figure 2.2a,b). Data were insufficient to analyze abundance per species across taxa for putative avian umbrella species. Effect sizes for all response variables were higher in across-taxonomic group schemes than in same-taxon schemes, although the effect size was significant only for abundance per taxonomic group (birds: QB= 4.0, df = 1, p= 0.04; mammals: QB= 12.9, df = 1, p= 0.0003). When birds were putative umbrella species, the mean effect size was significantly positive for species richness and abundance per species but was not significant for abundance per taxonomic group (Figure 2.2a). When mammals were the umbrella species, mean effect sizes were significantly positive across taxonomic groups for abundance per species and per taxonomic group and for same-taxon schemes for abundance per species only (Figure 2.2b).

When the putative umbrella species was a bird, the mean effect size for species richness was at least five times higher when the bird was in the smallest size category (<0.02 kg) than when it was in any other size category (Figure 2.3a) There were no significant differences or consistent trends among the other size categories that suggested a relation between effect size and body size. Mean effect sizes were positive for all size categories and response variables, although not significantly so for species richness, when the body size of umbrella species was in the categories >0.50–1.00 kg or >1.00–5.00 kg. We could not make statistical comparisons between size categories for abundance per species (\geq 0.25–0.50 kg: mean = 9.5, 95% CI 3.2–18.2, n= 5) or abundance per taxonomic group (>0.50–1.00 kg: mean = 16.1, 95% CI 6.0–26.2, n= 4) with avian umbrella species because samples sizes were <3 for all other size categories.

For mammals the mean effect sizes for species richness and abundance per species and taxonomic group, some positive and some negative, were similar regardless of size category (Fig. 2.3b–d). The effect sizes for species richness and abundance per taxonomic



Figure 2.2. Mean effect size with 95% confidence intervals for species richness (SR), abundance per species (SpAb), and abundance per taxonomic group (TaxAb) of co-occurring species in conservation schemes with (a) avian and (b) mammalian putative umbrel umbrella species that are in the same (same) and different (across) taxonomic groups as co-occurring species. Numbers in parentheses in x-axis labels are number of pairs of putative umbrella species and groups of co-occurring species. Letters above bars indicate significant differences between means (*p< 0.05; ***p< 0.001). Where confidence intervals overlap the zero line, the effect is not significant.



Figure 2.3. Mean effect size with 95% confidence intervals for (a) species richness (SR) of co-occurring species in conservation schemes with an avian umbrella species and of co-occurring (b) species richness, (c) abundance per species (SpAb), and (d) abundance per taxonomic group (TaxAb) in conservation schemes with mammalian umbrella species. Putative umbrella species are categorized by size (in kilograms). Numbers in parentheses in x-axis labels are number of pairs of putative umbrella species and groups of co-occurring species. Letters above bars indicate significant differences between means (*p<0.05; **p< 0.01). Where confidence intervals overlap the zero line, the effect is not significant.

group of co-occurring species for the smallest (<0.25 kg) and largest (>500 kg) size categories were greater than for all other size classes. Nevertheless, pairwise comparisons were not consistently significant and trends were not apparent for either response variable by size category (Figure 2.3b–d). The mean effect sizes for abundance per species in the two size classes evaluated were similar and both were significantly positive (Figure 2.3c).

There were no significant differences in effect sizes between putative umbrella species classified as resource generalists or specialists for species richness (birds: QB= 25.0, df = 1, p= 0.15; mammals: QB= 0.05, df = 1, p= 0.87), abundance per species (mammals: QB= 0.002, df = 1, p= 0.98), or abundance per taxonomic group (mammals: QB= 3.2, df = 1, p= 0.07) (Figure 2.4a,b). Data were insufficient to support pairwise comparisons of generalists within abundance per species and for specialists within abundance per taxonomic group for avian umbrella species. For birds, mean effect sizes were significantly positive for all response variables except abundance per taxonomic group for generalists (Figure 2.4a). Mean effect sizes were also positive for mammals, but only significantly so for abundance per species (Figure 2.4b).

When putative avian umbrellas were categorized by trophic level, all effect sizes were positive. For omnivorous umbrella species, richness of co-occurring species was more than four times greater than carnivores and eight times greater than herbivores (Figure 2.5a). In pairwise comparisons, only the difference between omnivores and carnivores was significant (QB= 125.0, df = 1, p= 0.001). For mammals the mean effect sizes for carnivores were negative and for herbivores were positive; however, the effect sizes were significantly different than zero only for herbivore abundance per species (Figure 2.5b). For mammalian umbrella species, differences between trophic groups were not significant for species



Figure 2.4. Mean effect size with 95% confidence intervals for species richness (SR), abundance per species (SpAb) and abundance per taxonomic group (TaxAb) of co-occurring species in conservation schemes with (a) avian and (b) mammalian putative umbrella species. Putative umbrella species are categorized as habitat generalists or specialists. Numbers in parentheses in x-axis labels are number of pairs of putative umbrella species and groups of co-occurring species. Where confidence intervals overlap the zero line, the effect is not significant.



Figure 2.5. Mean effect size with 95% confidence intervals for species richness (SR), abundance per species (SpAb), and abundance per taxonomic group (TaxAb) of co-occurring species in conservation schemes with (a) avian and (b) mammalian putative umbrella species. Putative umbrella species are categorized by the trophic levels herbivore (herb), omnivore (omn), or carnivore (carn). Numbers in parentheses in x-axis labels are number of pairs of putative umbrella species and groups of co-occurring species. Letters above bars indicate significant differences between means (**p< 0.01). Where confidence intervals overlap the zero line, the effect is not significant.

richness (QB= 4.1, df = 1, p= 0.15) or abundance per taxonomic group (QB= 1.5, df = 1, p= 0.52). Data were insufficient to support comparisons among trophic levels for abundance per species or abundance per taxonomic group for birds and abundance per species for mammals.

2.4 Discussion

Narrative reviews evaluating the potential of putative umbrella species to confer benefits to co-occurring species have concluded that the umbrella-species concept has potential, but needs to be refined (e.g., Caro, 2003; Roberge & Angelstam, 2004). Having a set of criteria that transcend ecological settings and species would make the selection of putative umbrella species more efficient, although confirmation of an umbrella species would still require site- and species-specific studies (Seddon & Leech, 2008). Results of our metaanalysis did not support the use of the specific criteria we tested (e.g., large body size, specialized resource requirements) to guide the selection of umbrella species, but we found that richness and abundance of co-occurring species tended to be greater (i.e., effect size >0) in areas with than without putative umbrella species.

Our results should be interpreted within the context of the potential limitations and sources of bias of this meta-analysis, which may constrain the transferability of the results. Estimates of variance were often not reported in the literature; therefore, we did not use information on variance to estimate effect sizes. By weighting the effect size by sample size, we were able to include more studies in the analysis. It is unlikely that the studies we examined were independent because several data sets were produced by the same authors or for the same areas. We found a publication bias in data on species richness and abundance per species. There was a strong taxonomic bias in our data set toward birds and mammals as

both umbrella and co-occurring species. Some data from the literature could not be included in our analysis because differences in study design precluded the calculation of a common effect size and because some categories were represented by only one study.

2.4.1 Assessment of Criteria for Selection of Umbrella Species

Originally the umbrella-species concept assumed mammals with large home ranges would be good potential umbrella species because their protection required conservation of a large area and the larger an area conserved, the more co-occurring species could benefit from that conservation (Wilcox, 1984). These assumptions led to the idea that umbrella species should have a large home range or body size (Wilcox, 1984; Seddon & Leech, 2008), assuming there is a positive relation between body size and home range for birds and mammals (Schoener, 1968; Peters & Wassenberg, 1983). We found that large body size in mammals was not associated with relatively high species richness or abundance of cooccurring species and that species richness of co-occurring species was highest in conservation schemes with the smallest bodied putative avian umbrella species. These results are inconsistent with the prevailing assertion that the larger the minimum area requirement of a species the more effective its conservation will be at conferring benefits to co-occurring species.

The original umbrella-species concept also implicitly assumed that umbrella species would function across taxonomic groups; that is, reserves established for one species or a group of species would confer benefits to many co-occurring species (Wilcox, 1984). Studies evaluating the cross-taxonomic effectiveness of umbrella species have reported benefits conferred to co-occurring species under conservation schemes with both across-taxonomic

group (e.g., Hurme et al., 2008) and same-taxon umbrella species (e.g., Fleishman et al., 2001). Often the same study provides evidence of both (e.g., Betrus, Fleishman & Blair, 2005; Roth & Weber, 2008) or shows a putative umbrella species is effective in providing benefits to one across-taxonomic group but not another (e.g., Roberge et al., 2008). We did not find significant differences between across-taxonomic group and same-taxon umbrella species schemes for species richness or abundance per species, however abundance per taxonomic group was higher in across-taxonomic group schemes than in same-taxon schemes. These equivocal results do not suggest taxonomic similarity or difference of umbrella and co-occurring species provides a useful criterion for the selection of umbrella species.

It has been suggested that conservation schemes that use umbrella species may be more successful when umbrella species are selected on the basis of ecological criteria rather than general characteristics (e.g., ubiquity, Fleishman et al., 2001) or statistical chance (e.g., more species in a larger area) (Martikainen, Kaila & Haila, 1998). Species with specialized resource requirements may be effective umbrella species if conservation measures taken to protect them also protect resources for co-occurring species (e.g., dead wood, riparian vegetation) (Berger, 1997; Ozaki et al., 2006; Roberge et al., 2008). Nevertheless, a putative umbrella species' resource requirements may be so specialized that few other species would benefit (Seddon & Leech, 2008) from conservation of those particular resources. Our results indicate that differences in co-occurring species richness and abundance are not consistently related to whether a species is a resource generalist or specialist.

Trophic level may affect a species' potential to serve as an umbrella species (Sergio et al., 2006; Roth & Weber, 2008). Top predators have been proposed as indicators of areas

with high species richness for a number of reasons, including that top predators have large area requirements; may select sites with many prey species or heterogeneous resources; and may attack or deter predators or competitors of prey species, thereby allowing them to persist (e.g., Noss et al., 1996; Sergio et al., 2006). Comparative studies evaluating species richness of birds, butterflies, and trees or plants at sites with raptors or birds on a lower trophic level that are breeding, or present, report both of the following two findings. First, breeding areas for raptors have high species richness relative to areas with breeding birds on lower trophic levels (Sergio et al., 2006). Second, species richness at sites where raptors are present and at sites where birds on lower trophic levels are present (Roth & Weber, 2008) is similar. Results of a comparative study in which mammals were used as putative umbrella species showed that co-occurring species richness and abundance of amphibians, mammals, and birds were similar in sites where the umbrella species was a predator relative to sites where the umbrella species was on a lower trophic level (not predators) (Caro et al., 2004). Our results weakly support the use of trophic level as a criterion for the selection of avian umbrella species. We found higher species richness of co-occurring species in areas with omnivorous avian umbrella species than in areas with carnivorous avian umbrella species. Nevertheless, species richness was also higher in areas with carnivorous avian umbrella species than in areas without them, which suggests that carnivorous birds are effective umbrella species, but not as effective as omnivores. Trophic level was not an effective selection criterion for mammalian umbrella species. Co-occurring species richness and taxonomic group abundance were similar between trophic levels, although mean co-occurring species richness and taxonomic group abundance were higher in areas without carnivorous mammalian umbrella species than with them, which suggests mammalian carnivores may not be effective umbrella species.

Although we found little support, or equivocal support, for the specific umbrella species selection criteria we tested, our results clearly indicated that species richness and abundance of co-occurring species were higher when birds were used as umbrella species than when mammals were used. The reason for this is unclear. Some disparity in the response of co-occurring species in sites with and without putative umbrella species might be anticipated due to differences in species richness (higher for birds than mammals) (Silva, Brown & Downing, 1997; Betrus et al., 2005) and in maximum population densities (lower for birds) (Silva et al., 1997), although those differences should not affect the ability of a species to serve as an umbrella species. Birds tend to disperse farther than mammals of the equivalent size class (Sutherland et al., 2000); therefore, given equivalent body size, birds may be better able than mammals to locate areas with higher-quality resources that would attract co-occurring species.

2.4.2 Abundance and Species Richness

Measures of conservation success are often selected on the basis of the cost or ease of data collection rather than on explicit management goals (Wiens et al., 2008). Initially, it was thought that conservation of umbrella species might maintain viable populations (i.e., population unlikely to go into rapid decline) (Caro, 2003) of the umbrella and many cooccurring species, not just high species richness (e.g., Wilcox, 1984; Caro, 2003; Lindenmayer & Fischer, 2003). Nevertheless, assessing population viability of multiple species is resource intensive, and such assessments are rare in studies of umbrella species. In contrast, it is relatively easy to quantify species richness, but the use of species richness as the primary measure of diversity has been criticized as an information-poor measure that provides little insight into the composition of the community or the potential viability of species that are present (Fleishman et al., 2006). Abundance data provide more information than presence–absence data and sometimes can be used as a proxy for population viability, although they do not necessarily reflect population dynamics in space and time (Simberloff, 1998; Fleishman et al., 2000; Caro et al., 2004). We found that species richness and abundance of co-occurring species were both greater in sites where putative umbrella species were present than in sites where the umbrella species were absent and that the direction of the mean effect (i.e., positive or negative) was the same regardless of the response variable measured. Although this suggests that when abundance data are unavailable species richness alone might be an effective metric for evaluating the success of conservation schemes that use umbrella species, the advantage of having abundance data is that sites with similar species richness can be prioritized for conservation on the basis of likely population viability, although abundance and viability are not always linked, and productivity of species that are present.

2.4.3 Merit of Umbrella Species Concept

Until recently there were too few empirical studies on how conservation strategies designed for putative umbrella species may benefit co-occurring species to support a quantitative analysis. In our meta-analysis, species richness and abundance were consistently higher in sites where umbrella species were present than where they were not. Although we found the selection of putative umbrella species could not be based on body size, taxonomic similarity to co-occurring species, general or specialized resource requirements or trophic level, our results indicated species richness and abundance of co-occurring species were

consistently higher when birds were used as umbrella species than when mammals were. Nevertheless, the majority of the studies evaluating avian umbrella species have used birds, plants, and insects as co-occurring species. Only one study evaluated whether conservation of a bird might serve to protect co-occurring amphibians (Dunk et al., 2006), and there were no studies in which the potential for birds to serve as umbrella species for mammals was evaluated. Abundance was higher in sites with mammalian umbrella species than without them, but species richness did not tend to differ between sites with or without mammalian umbrella species, which suggests that mammals may be less effective umbrella species than birds. The potential for fishes, amphibians, and reptiles to function as umbrella species has been considered conceptually, but not evaluated empirically, and the potential for plants or insects to function as umbrella species has rarely been tested (Hitt & Frissel, 2004; Lawler & White, 2008; Roberge et al., 2008). Our results demonstrate that there is merit to the umbrella-species concept as a conservation tactic but that additional empirical testing, including evaluating potential umbrella species from underrepresented taxonomic classes (e.g., amphibians) and systems (e.g., aquatic) is warranted.

Chapter 3: Beyond Species Presence and Absence: A Test of the Umbrella Species Approach in Restored Floodplain Ponds

3.1 Introduction

The most effective way to preserve biodiversity, including ecosystems, biological assemblages, species and populations, is to set aside protected areas that encompass a representative sample of biodiversity, maintain natural processes and viable populations, and exclude threats (Margules & Pressey, 2000). However, areas available for preservation and protection in conservation reserves are limited and diminishing (Vitousek et al., 1997). Approaches that have been used to design reserves need to be applied more broadly in areas with conservation potential (e.g., agricultural, light residential) including degraded terrestrial and aquatic systems. The umbrella species concept, in which conservation measures designed to benefit one, or a group of, species should confer benefits to populations of co-occurring species, has been evaluated for its use in reserve design and for its potential to determine the size and/or structural characteristics of an area to be protected or managed (Caro & O'Doherty, 1999; Roberge & Angelstam, 2004; Branton & Richardson, 2011). The need to validate the effectiveness of potential umbrella species in providing benefits to co-occurring species with empirical studies has long been recognized (Caro & O'Doherty, 1999). Some researchers have also advocated for the identification of potential mechanisms by which cooccurring species benefit from conservation of an umbrella species such as specific resource requirements or dispersal corridors (e.g., Lambeck, 1997; Ozaki et al., 2006). The application of the umbrella species concept holds potential for restoration planning particularly if presumed umbrella and co-occurring species respond similarly to restoration.

Species richness is the most common measure of the effectiveness of potential umbrella species despite the fact the umbrella species approach was originally focused on population sizes and viability (i.e., population unlikely to go into rapid decline, Caro, 2003) of both umbrella and co-occurring species (e.g., Berger, 1997). This is problematic from a conservation planning perspective because species richness provides no information on species density or demography, and therefore about persistence of populations, or about the composition of ecological communities (Fleishman et al., 2006). Umbrella species may be more valuable for conservation planning if both their presence and abundance vary similarly to co-occurring species in response to disturbance or restoration (Fleishman et al., 2000), although this has rarely been tested (but see Koper & Schmiegelow, 2007). The amount of data required to determine if umbrella and co-occurring species respond similarly to disturbance and/or restoration is substantially greater than the presence and absence data required to determine their spatial overlap. However, the benefits associated with this investment in data collection may be realized if restoration techniques can be modified as a result of the information gathered. When the spatial transferability of one or a group of umbrella species across a region with common ecology and ecological challenges can be established, the design and monitoring of conservation and restoration planning can be facilitated across that region (e.g., Pakkala, Pellikka & Linden, 2003; Betrus et al., 2005).

The potential for the umbrella species approach to be used to inform the design of regional restoration planning in an aquatic system is the focus of this study. In the Pacific Northwest and British Columbia off-channel floodplain habitats, including sloughs, side channels and beaver ponds provide rearing and overwintering habitat for juvenile salmonids including coho salmon (*Oncorhynchus kisutch*, hereafter "coho") (Sandercock, 1991). The

channelization of rivers and isolation of floodplain habitat has simplified and reduced these habitats, the scarcity of which may limit coho production (Beechie, Beamer & Wasserman, 1994). For more than two decades, off-channel floodplain channels and ponds have been restored, created and enhanced ("restored") to increase the available habitat necessary for spawning and rearing salmonids including coho (Lister & Finnigan, 1997). We used data collected from floodplain ponds restored primarily for coho in southwestern British Columbia, Canada to evaluate if other aquatic vertebrate and benthic invertebrate species, including species of conservation concern (listed species), benefited from those restoration projects. As is often the case, coho are being evaluated as an umbrella species retrospectively (Betrus et al., 2005). Given the imperiled status of coho and other Pacific salmon (Pacific Fisheries Resource Conservation Council, 2010), regional conservation programs, including habitat restoration, are likely to continue into the future. In this context, an iterative approach that uses data collected from monitoring and assessment of restoration projects to provide insights for the modification of future projects that may benefit coho and co-occurring species is imperative (Roni, 2005).

We evaluated if floodplain pond habitat restored for coho provides benefits to cooccurring aquatic vertebrates (fish and amphibians) and benthic invertebrates, as measured by species richness, abundance and biomass. Although all of the ponds were restored for coho, pond habitat attributes varied (e.g., elevation, depth, aquatic structure) and coho abundance ranged from 2 - 460 individuals per pond over the study period. With this range of abundance, we were able to test if species richness, abundance and biomass of cooccurring species varied in a pattern similar to the response variables related to the population viability (*sensu* Caro, 2003) of coho (i.e., abundance and biomass per unit effort).

We also evaluated if variation in species' abundance and biomass could be explained by environmental attributes of the restored ponds. We tested the generality of the results by sampling in multiple ponds in three watersheds within the same region. Finally, our analysis allowed us to evaluate the relative sensitivity of species richness compared to abundance and biomass to assess benefits conferred to co-occurring species through habitat restoration for coho.

3.2 Materials and Methods

3.2.1 Study Sites

This study was conducted in the Fraser River Basin of southwestern British Columbia, Canada (Figure 3.1). This area has been heavily impacted and damage to streams in this area includes loss of riparian vegetation, water diversion and stream channelization. The major threats to biodiversity in this region are habitat loss through ecosystem conversion and degradation, and exotic species.



Figure 3.1. Location of study sites in southwestern British Columbia, Canada.

We considered all 100 projects implemented by Fisheries and Oceans Canada (DFO) as of 2004 that restored off-channel pond habitat primarily for juvenile coho in southwestern British Columbia as candidate study sites (Pers. Comm., Matt Foy, DFO). These ponds were restored by improving the connectivity of existing ponds to surface water flow and by creating new ponds using groundwater or water diverted from nearby dams, rivers and creeks to flood bermed or excavated areas. The flooding of bermed areas provide more complex habitat than excavated ponds. Common features of many of the restoration projects were the addition of wood (root wads or large pieces of wood) and the creation of deep channels. Water sources for the projects were classified by DFO as surface water, groundwater or a combination of the two. The restoration technique and habitat features of each pond are summarized in Appendix B (Table B.1).

The criteria we used in screening sites for inclusion in our study included presence of pond habitat (not side-channels or streams), no direct tidal influence, surface or groundwater fed (not glacial), adequate accessibility for field sampling, no stocking of fish (including coho) and a minimum of four restored ponds per watershed. Sites fed primarily by glacial runoff were not included because colder waters temperatures often exclude use by amphibians. If ponds were directly connected to each other (i.e., not connected through the mainstem of the river), only one of the individual ponds in the complex was selected for evaluation based primarily on accessibility for field work. Out of the 100 sites initially reviewed, 17 restored floodplain ponds in three watersheds: Chilliwack (n= 9), Coquitlam (n = 4) and Seymour (n = 4) (Figure 3.1) met our criteria and were included in our study. Most sites were eliminated as candidates in the initial screening because they did not have

primarily pond habitat or there were not at least four ponds in the watershed. Others were eliminated because they were glacier fed or because accessibility for sampling was limited. Land use surrounding the restored floodplain ponds was primarily forested or agricultural with residential areas nearby. Study sites were located at altitudes from 10 to 400 m above sea level and receive an average of between 1500 and 2200 mm of rain annually (http://pacificclimate.org/docs/publications/ GVRD.RainfallUpdate.pdf).

3.2.2 Field Sampling

3.2.2.1 Vertebrate Sampling

We sampled ponds three times, (1) May-June 2006, (2) late July-August 2006, and (3) February-March 2007, prior to freshets that would initiate the outmigration of coho smolts. We selected these study periods to increase the likelihood of detecting species present in ponds only for certain life stages. For instance, some frog and salamander species are primarily present in ponds when they are breeding or as larvae [e.g., northern red-legged frog (*Rana aurora*), northwestern salamander (*Ambystoma gracile*), rough-skinned newt (*Taricha granulose*)] although they may still be present as adult frogs or as neotenic adults (e.g., northwestern salamander). For coho, this sampling period was intended to capture a cohort exposed to similar environmental conditions both in the marine environment for adult spawners and in freshwater for their offspring (the cohort of interest).

Between 30 and 50 minnow traps, depending on each pond's size, baited with salmon roe in perforated film canisters were set in each pond. For sampling purposes we used an initial visual assessment to divide each pond into sections using features including depth, aspect, riparian structure and aquatic structure. This ensured that all habitat types represented in the pond were sampled (Olson, Leonard & Bury, 1997). Approximately the same number of traps was set haphazardly in each section of the pond. Captured juvenile and adult fish and amphibians were counted, identified to species, weighed and fork length (fish) or snoutvent and total length (amphibians) were measured (Barbour et al., 1999; Corkran & Thoms, 2006). We anaesthetized fish using buffered MS222 prior to taking fork length and mass measurements.

3.2.2.2 Benthic Invertebrate Sampling

In May-June 2006, we collected three benthic invertebrate samples from each pond using a standard D-frame. We collected semi-quantitative travelling kick net samples, standardized by time, by sweeping the net over sediment disturbed while shuffling backwards (Wissinger, Greig & McIntosh, 2009). We selected sampling locations using a random number table to select habitat units where possible, or by access combined with aspect if there were limited areas within a pond that could be accessed due to depth, substrate (i.e., deep mud) or other barriers (e.g., dense conglomerations of large wood). Samples were preserved in the field in 10% formalin. They were then sorted in the laboratory and organisms identified to the lowest practical level (family or genus). Large samples were subsampled. Benthic invertebrates from each pond were composited, blotted dry and weighed to the nearest 0.01 gram.

3.2.2.3 Habitat Assessment

We documented each pond's habitat structure in July and August 2006 by surveying wood, macrophytes, algae, benthic organic matter, percent overhead riparian cover and water

depth every metre along the length of four to six equidistant transects of each pond (determined by the size of the pond) starting and ending two metres past water's edge (Anonymous, 1995; Johnston & Slaney, 1997). The proportion of all measurements for each structural component was calculated by dividing the number of times a given component was documented by the total number of measurements from that pond (e.g., 30 readings with large wood out of a total of 100 readings = 0.3). All ponds had predominantly fine (i.e., muddy) substrate except in small areas with gravels where streams entered them. We placed temperature loggers at two depths (approximately 30 cm and 100 cm below the surface of the water) in each of the ponds from May or June 2006 to July 2007. Some data loggers were lost or malfunctioned particularly from August 2006 to February 2007 when minimum water temperatures were most likely to have occurred. As such, we relied exclusively on maximum temperatures calculated as the average temperature of the warmest seven day period. Many ponds had inaccessible shorelines, therefore we estimated pond area using the area estimation function of Google Earth (Version 3.0, Google Inc., Mountain View, CA).

3.2.3 Analyses

In contrast with other evaluations of the umbrella species concept that compare species richness and abundance between areas with and without umbrella species present, we did not compare restored and "control" ponds (e.g., naturally occurring ponds or ponds restored for other purposes) due to the lack of the availability of suitable control ponds. Instead, we were able to evaluate the relationships between the species richness, abundance and biomass of co-occurring species and that of coho abundance and biomass, which varied widely across restored ponds. We categorized species by broad taxonomic groupings as follows: fish excluding coho (n = 13); fish excluding coho and three-spined stickleback

(*Gasterosteus aculeatus*); amphibians (n = 6) and all benthic invertebrates identified to the lowest practical level (n = 60). A summary of species by category and full species lists for vertebrates and benthic invertebrates are provided in Appendix B (Tables B.2 to B.5). Vertebrates were separated by taxonomic class to permit the evaluation of the suitability of coho as an umbrella species within and across taxa. Fish were tested with and without three-spined stickleback as the relationship between coho and other fish species would have been obscured by the relationship between coho and three-spined stickleback alone. Three-spined stickleback were extremely abundant comprising an average of 97% (SD = 3) of the total fish abundance and 69% (SD = 30) of the biomass (excluding coho) in eight of the nine ponds where they occurred. In the ninth pond three-spined stickleback accounted for only 3% of the abundance and 0.1% of biomass of fish, and in the remaining eight ponds no three-spined stickleback were documented.

We used a fourth category for fish and amphibians listed as species at risk (listed) by federal or provincial conservation authorities. The Salish sucker (*Catostomus* sp.) (endangered) and northern red-legged frog are protected in Canada under the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), the Species at Risk Act (SARA) and by the province of British Columbia (BCMOE, 2011). The Salish sucker is listed as endangered based on several criteria including a restricted global population with an estimated total population in Canada of less than 10,000 individuals. Their decline is attributed to loss and degradation of habitat including removal of streamside vegetation, loss and sedimentation of spawning areas and sub-lethal temperature effects and interactions with exotic species (COSEWIC, 2002b; COSEWIC, 2004a; BCCDC, 2011a). The main threats to northern red-legged frogs are from habitat degradation and loss and predation and

competition from bull frog (Lithobates catesbeianus) (COSEWIC, 2002a; COSEWIC,

2004b; BCCDC, 2011c). Cutthroat trout (*O. clarkii*) and Dolly Varden (*Salvelinus malma*) have a provincial conservation status of Special Concern in British Columbia due to habitat degradation and loss including disruption of migration routes and loss of spawning grounds (BCMOF, 1999b; BCMOF, 1999a; BCCDC, 2011d; BCCDC, 2011b). Northern red-legged frog, cutthroat trout and Dolly were all included in the listed category for statistical analyses. The Salish sucker was excluded from the listed category in order to focus on species that have the potential to benefit from the umbrella species approach which is intended to be used to provide conservation benefit for species that are less sensitive than the umbrella species. An endangered species such as the Salish sucker is likely more sensitive than the potential umbrella species coho and any improvement in the status of this species will require a specially tailored management approach (COSEWIC, 2002b).

3.2.3.1 Abundance and Biomass

We calculated abundance and biomass per unit effort (i.e., per trap night). Although abundance and biomass are related, the two measures may reflect real differences, specifically there may be many small individuals in one pond and fewer larger individuals in another. Abundance and biomass were calculated by dividing the total number or biomass of individuals captured in a pond by the total number of traps used in that pond in a sampling period resulting in relative abundance or biomass normalized by trap night. In some sampling periods a large number of individuals of some species (e.g., three-spined stickleback, northwestern salamander) were captured. In those instances after more than 15 individuals of one species were captured, we measured the first five individuals in each subsequent pond sampling section and any additional individuals were assigned to length classes (e.g., 4 - 5 cm). We estimated biomass for unweighed individuals by assigning them the mean biomass for conspecific individuals measured in their length class in that sampling period. We did not use mass–length regressions to estimate biomass because the regression equations calculated negative mass for the numerous small individuals (fry) that could not be accurately weighed and were therefore assigned an estimated mass (0.1 g). Moreover, because length was estimated to length class, not measured, the regression would have been based on the central tendency (i.e., individuals classified as 4 - 5 cm long would enter the regression as 4.5 cm) resulting in similar estimates to those based on mean biomass. In some instances, fish and amphibians escaped as they were being removed from the traps prior to measurement. They were assigned to length categories and their biomass was also estimated, although with greater uncertainty if no other individuals of their size class were measured, in which case the average for that species across all ponds in that sampling season was used to estimate biomass.

3.2.3.2 Species Richness

Estimates of species richness can be influenced by the level of sampling effort or by the relative abundance of organisms in the systems being sampled (Gotelli & Colwell, 2001). Rarefaction methods are used to standardize data and allow for a meaningful comparison among datasets with unequal sampling effort. We used sample-based rarefaction curves with 1000 iterations, without replacement, in a Monte Carlo type analysis, to calculate species richness using the expected richness function (Mau Tau) in EstimateS (Colwell, 2009). The pond with the fewest individuals in a category that was greater than zero was used to determine how many individuals species richness was rarefied to. When this would have resulted in rarefying to an extremely small number of individuals (e.g., three or less for

species of conservation concern) we rarefied to the lowest value greater than 5 (arbitrary cutoff). Ponds with a species richness of zero for a category were retained in the analysis based on the assumption the zero value represented the real absence of species in that category from the pond, although we cannot preclude the possibility that with more sampling some species from that category may have been detected.

3.2.3.3 Regressions and Multivariate Analyses

We evaluated the relationships between coho productivity and the richness and productivity of co-occurring species in restored ponds using the random and repeated functions in mixed models (PROC MIXED) (SAS 9.1, SAS Institute, Cary, NC). Watershed was the random variable, coho abundance and biomass were the fixed explanatory variables, and rarefied species richness, abundance and biomass (normalized to sampling effort) were the dependent response variables. The three sampling sessions were the repeated measures. PROC GLIMMIX was used for listed species only as the data did not meet the assumptions of normality. Both watershed and sampling sessions were treated as random variables in this model. When there was zero variance associated with watershed, as indicated by the error message 'estimated G matrix is not positive definite', there was no watershed effect and therefore no random variable was used. A pseudo R-squared was calculated for analyses conducted used PROC MIXED using sums of squares (1-SSE/SSE). We transformed data to normalize residuals and meet the assumption of normality for general linear models. Tests were considered significant at alpha = 0.1 to reduce the likelihood of a type II error, i.e., rejection of the null hypothesis that there was an effect when a real effect may have existed, which would be more likely with alpha = 0.05 because of large sampling variability or small sample size (Peterman, 1990; Bryant, 2004).

We used redundancy analysis to evaluate the relationship between species abundance and biomass and environmental variables (e.g., proportion of readings with wood, depth, temperature) (ter Braak & Smilauer, 2002) (CANOCO 4.5). Ordinations were used to illustrate the distribution of vertebrate and benthic invertebrate species abundance and biomass along the first two environmental axes. Benthic invertebrate species that were not present in at least three ponds were excluded from the analysis. Data were not transformed to meet the assumptions of normality as the ordination uses a Monte Carlo analysis that does not assume a normal distribution, however the original species data included many zeros so we used a log (x+1) transformation for species data (ter Braak & Smilauer, 2002). We scaled species data by dividing species scores by their standard deviation and standardized the data using species error variance to counteract rare species unduly dominating ordination. The percentage of the total variance (i.e., inertia) in the species data explained by environmental variables is given by the species-environment relation. We used a global Monte Carlo permutation test (499 permutations) to determine the statistical significance of the relationship between the species and environmental variables represented by the first canonical axis alone and for all four axes together. Correlations between each axis and environmental variables were considered significant (P < 0.05) at a critical value of r = 0.48.

3.3 Results

Similar patterns and general levels of significance were observed in tests using abundance and biomass therefore figures illustrating significant results are provided only for coho abundance as the explanatory variable.

3.3.1 Species Richness

There were positive relationships between the species richness of listed species and fish and coho abundance and between the species richness of fish and coho biomass (Table 3.1, Figures 3.2a, b). Benthic invertebrate species richness decreased significantly as coho abundance and biomass increased (Table 3.1, Figure 3.2c). There were no significant relationships between amphibian species richness and coho abundance or biomass (Table

3.1).

Table 3.1. Analysis of the relationships between dependent variables species richness, abundance and biomass of co-occurring species of conservation concern (listed species), fish, amphibians, benthic invertebrates and the abundance and biomass of putative umbrella species coho using watershed as a random variable, as appropriate.

Species richness	Coho abundance§	Pseudo R ²	Coho biomass	Pseudo R ²
Listed species†	F _{1,49} = 3.60, P = 0.06	na	F _{1,47} = 1.20, P = 0.28	na
Fish (no coho)*	F _{1,47} =9.86, P = 0.003	0.26	F _{1,47} =4.86, P = 0.03	0.16
Amphibians	F _{1,33} =0.00, P = 0.98	0.00	F _{1,33} =0.05, P = 0.83	0.00
Invertebrates	F _{1,47} = 8.43, P = 0.006	0.39	F _{1,47} = 8.43, P = 0.006	0.23
Abundance or biomass **	Coho abundance§	Pseudo R ²	Coho biomass	Pseudo R ²
Abundance or biomass ** Listed species¶	Coho abundance§ F _{1,33} =4.03, P = 0.05	Pseudo R ² na	Coho biomass F _{1,33} =85.42, P<0.0001	Pseudo R ² na
Abundance or biomass ** Listed species¶ Fish (no coho)*	Coho abundance§ F _{1,33} =4.03, P = 0.05 F _{1,33} =25.44, P <0.0001	Pseudo R ² na 0.33	Coho biomass F_{1,33} =85.42, P<0.0001 F _{1,33} =2.19, P = 0.15	Pseudo R ² na 0.04
Abundance or biomass ** Listed species¶ Fish (no coho)* Fish (no coho, no stickleback)*	Coho abundance§ $F_{1,33} = 4.03, P = 0.05$ $F_{1,33} = 25.44, P < 0.0001$ $F_{1,33} = 6.96, P = 0.01$	Pseudo R ² na 0.33 0.12	Coho biomass $F_{1,33} = 85.42, P < 0.0001$ $F_{1,33} = 2.19, P = 0.15$ $F_{1,47} = 16.49, P = 0.0002$	Pseudo R ² na 0.04 0.30
Abundance or biomass ** Listed species¶ Fish (no coho)* Fish (no coho, no stickleback)* Amphibians‡	Coho abundance§ $F_{1,33} = 4.03, P = 0.05$ $F_{1,33} = 25.44, P < 0.0001$ $F_{1,33} = 6.96, P = 0.01$ $F_{1,33} = 0.57, P = 0.46$	Pseudo R ² na 0.33 0.12 0.01	Coho biomass $F_{1,33} = 85.42, P < 0.0001$ $F_{1,33} = 2.19, P = 0.15$ $F_{1,47} = 16.49, P = 0.0002$ $F_{1,33} = 0.65, P = 0.43$	Pseudo R ² na 0.04 0.30 0.01

Transformations

* square root dependent and independent variable

† square root - independent variable

 $\pm \log_{e}$ - independent variable

 $\P \log_e$ - dependent and independent variable

§ PROC GLIMMIX used for listed species only. PROC MIXED used for all other analyses. df = 47 with random variable using PROC MIXED, df = 33 without random variable using PROC MIXED, df=49 using PROC GLIMMIX with season as a random variable, df=47 using PROC GLIMMIX with watershed as a random variable, df=33 using PROC GLIMMIX with watershed as a random variable, df=33 using PROC GLIMMIX without random variables

** Response variables abundance and biomass with, respectively, explanatory variables abundance and biomass



Figure 3.2. Relations between the relative abundance (individuals per trap night) of putative umbrella species coho and the species richness of (a) listed species, (b) fish and (c) benthic invertebrates and abundance of (d) listed species, (e) fish, (f) fish excluding three-spined stickleback and (g) benthic invertebrates. Average coho abundance over three sampling sessions used for relations with benthic invertebrates (panels c and g). Watersheds distinguished for each relation (◊Chilliwack, ∘Coquitlam, ΔSeymour) and sampling sessions shaded to distinguish sampling sessions one though three (respectively shaded, open and shaded with white cross).

3.3.2 Abundance and Biomass

The abundance and biomass of listed species increased as those same measures increased for coho (Table 3.1, Figure 3.2d). There was a significantly negative relationship between the abundance of fish and that of coho, however when three-spined stickleback were excluded from the model that relationship became positive (Table 3.1, Figures 3.2e, f). Similarly, there was no significant relationship between the biomass of fish and coho, however when three-spined stickleback were excluded from the model, that relationship was positive (Table 3.1). As coho abundance and biomass increased, benthic invertebrate abundance and biomass decreased (Table 3.1, Figure 3.2g). There were no significant relationships between amphibian abundance or biomass and that of coho (Table 3.1).

3.3.3 Variance in Vertebrate and Benthic Invertebrate Abundance and Biomass Explained by Environmental Gradients

Environmental attributes explained 30.3% of the variance in aquatic vertebrate species (including coho) abundance data using axis 1 alone and the cumulative variance explained by axes 1 and 2 was 48.4%. The relation between species and environment was significant for the first canonical axis (eigenvalue = 0.27, P = 0.01) and for all canonical axes (Trace = 0.88, P = 0.002). Aquatic vegetation, elevation, maximum temperature, and wood were correlated with axis 1 (Figure 3.3a), organic matter was correlated with axis 2, depth at

water's edge was correlated with axis 3 and variation in depth was correlated with axis 4. In the ordination salmonids, including coho, were clustered on the negative side of axis 1 which was characterized by higher elevation, more wood, groundwater inputs, lower maximum temperatures and less aquatic vegetation. The listed species northern red-legged frog was also on the negative portion of axis 1 but, like Chinook salmon (*O. tshawytscha*), the relationship with the environmental variables, as indicated by the length of the arrows in the direction of the significant environmental feature, was not as strong. Because only two axes are shown in the ordinations, it is not possible to determine what the relationship was between species and significant environmental features on axis 3 and axis 4.

Environmental variables explained 28.7% of the variance in aquatic vertebrate species biomass on axis 1 and the cumulative variance explained by axes 1 and 2 was 47.5%. The relation between species and environment was significant for the first (eigenvalue = 0.25, P = 0.04) and for all canonical axes (Trace = 0.88, P = 0.002). Aquatic vegetation, elevation, maximum temperature, water source, and wood were significantly correlated with axis 1. Organic matter and maximum depth were correlated, respectively, with axis 2 and 4. No variables were correlated with axis 3 (Figure 3.3b). Salmonids (including coho), northern red-legged frog and northern Pacific treefrog (*Pseudacris regilla*) clustered on the negative portion of axis 1 which was characterized as higher elevation, more wood, less aquatic vegetation, groundwater inputs and lower maximum temperatures. On axis 2 cyprinid redside shiners (*Richardsonius balteatus*), longnose dace (*Rhinichthys cataractae*) and northwestern salamander clustered where there was more organic matter and away from the remainder of the species.



Figure 3.3. Redundancy analysis ordination of the relative abundance (a) and biomass (b) of vertebrate species and environmental attributes. Significant correlations with axis 1 and axis 2 are marked with, respectively, * and †. Axis 1: elevation, groundwater and wood increase towards -1.0 and maximum temperature and aquatic vegetation increase towards 1.0. Axis 2: organic matter increases towards 1.0 and aquatic vegetation increases towards -0.8.

Environmental variables explained 21.8% of the variance in benthic invertebrate species and coho abundance on axis 1 and the cumulative variance explained by axes 1 and 2 was 41.0%. The relation between species and environment was significant for the first canonical axis (eigenvalue = 0.18, P-value = 0.02) and for all canonical axes combined (Trace = 0.84, P = 0.002). Aquatic vegetation, elevation, maximum temperature, organic matter, variation in depth and wood were correlated with axis 1. Algae, variation in depth and area were correlated, respectively, with axes 2, 3 and 4. In general few benthic invertebrates were clustered near to coho (Figure 3.4a). Relatively more benthic invertebrates were on the positive side of axis 1 which was characterized by lower elevations, warmer maximum water temperatures, more aquatic vegetation, less wood and organic matter and a more uniform depth profile. While algae was strongly positively correlated with axis 2, with more algae present closer to 1.0 on the axis, benthic invertebrates were equally distributed along the axis. Coho was located around the zero mark of axis 2 indicating no relationship with algae.

Environmental variables explained 74.1% of the variance in biomass of benthic invertebrate species and coho on axis 1 and the cumulative variance explained by axes 1 and 2 was 100%. The high variance explained was due to the fact only two independent constraints could be formed with the environmental variables. The relation between species and environment was significant for the first (eigenvalue = 0.71, P = 0.01) and for all canonical axes (Trace = 0.96, P = 0.006). Aquatic vegetation, maximum temperature, variation in depth and wood were correlated with axis 1 and area was correlated with axis 2 (Figure 3.4b). Benthic invertebrates and coho were located on opposite sides of axis 1 with more benthic invertebrate biomass in ponds characterized by more aquatic vegetation, less wood, higher maximum temperatures and less variation in depth. Benthic invertebrates



Figure 3.4. Redundancy analysis ordination of the relative abundance (a) and biomass (b) of coho and benthic invertebrate species and environmental attributes. Significant correlations with axis 1 and axis 2 are marked with, respectively, * and †. Axis 1: variation in depth and wood increase towards -1.0 and maximum temperature and aquatic vegetation increase towards 1.0. Axis 2: area increases towards 1.0.

and coho were at approximately the same level on axis 2 indicating a similar response to area which was positively correlated with axis 2. In addition to significant correlations with environmental axes, several environmental variables were correlated. Wood was negatively correlated with aquatic vegetation (r = -0.63) and positively correlated with organic matter (r = 0.57). Maximum temperature and aquatic vegetation were positively correlated (r = 0.54) as were maximum depth and variation in depth (r = 0.71).

3.4 Discussion

The umbrella species concept was articulated more than 25 years ago, however until recently there has been a lack of empirical studies evaluating the concept (Wilcox, 1984). The vast majority of studies that have been conducted in terrestrial systems in the context of reserve design (Roberge & Angelstam, 2004). It has rarely been evaluated in a restoration context where habitat has been specifically modified or created to benefit a potential umbrella species (but see Suazo et al., 2009). The investigation of the potential use of the umbrella species approach to help guide and streamline restoration work is particularly important for freshwater and riparian ecosystems which have suffered disproportionately from anthropogenic habitat degradation and modification (Sala et al., 2000). Our explicit evaluation of the relative sensitivity of different metrics that may be used to test the viability of the umbrella species approach, together with an assessment of habitat features that may be associated with more desired restoration outcomes, provides support for the use of more labour-intensive metrics, such as abundance and biomass compared to species richness, at least in the validation phase of testing the umbrella species approach.
Our study provides evidence of an umbrella species functioning in a restored aquatic system for sensitive vertebrate species and fish. We found that coho was more effective as an umbrella species for other fish than for amphibians, and that benthic invertebrate species richness and productivity were actually lower in ponds where coho are more productive. However, the strong positive relationships between coho and listed species present at our study sites, which included fish and an amphibian, suggest that taxonomic similarity or dissimilarity may not always be as important to the effectiveness of an umbrella species as association with similar habitat features or as shared resource requirements (e.g., see Seddon & Leech, 2008). The negative relationship between coho and invertebrate richness, abundance and biomass is consistent with the fact that, in general, benthic invertebrates clustered away from coho in ordinations with environmental attributes of ponds. As we did not test potential direct impacts of coho on benthic invertebrates, we cannot preclude the possibility that benthic invertebrate species richness and productivity were depressed through direct relationships (e.g., predation, competition) with coho. Finally, we found that what is measured may influence how successful a conservation treatment is perceived to be as the relative sensitivity of the variables we measured generally increased as follows: species richness < abundance \leq biomass for listed species and fish. There was no such trend for benthic invertebrates and we could not assess the relative sensitivity for amphibians as there were no significant relationships to assess.

The restored ponds we studied were in three watersheds within the Coast Mountain range. The abundance and biomass of coho in floodplain ponds ranged over orders of magnitude indicating inconsistent success of the restoration measures (e.g., excavation of ponds, addition of wood, reconnection to streams and groundwater). For some of the

variables measured, we had to account for watershed as contributing to variance among the ponds (i.e., abundance and biomass of listed species, species richness of fish and invertebrates). For listed species this may be attributable to the fact that only two of the three species were found in the Coquitlam ponds compared with three in the Seymour and Chilliwack ponds. Despite some differences among watersheds, the general trend that higher coho abundance and biomass were associated with higher species richness (abundance only), abundance and biomass of listed species and fish was robust across watersheds suggesting that our results are broadly applicable to this region.

The positive or non-significant relationships between coho abundance and biomass and the species richness, abundance and biomass co-occurring vertebrate species are notable. Unlike reserve selection exercises that aim to maximize species richness of co-occurring species, when habitat is being restored there are concerns that habitat restored for one species may result in unintended detrimental effects for co-occurring species (Roni et al., 2006a; Suazo et al., 2009). For instance, reports that the introduction of upper trophic level fish to mountain lakes may be detrimental to amphibians have raised concerns that increasing habitat for salmonids may have negative impacts on amphibian populations (Finlay & Vredenburg, 2007). In our study for vertebrates we found either a positive (listed species, fish) or neutral (amphibians) relationship with coho which is consistent with Roni (2003) who found few or no negative or positive effects on non-salmonid fish and an amphibian in response to the placement of large wood as a stream restoration treatment. Our results suggest that co-occurring vertebrate species generally benefitted from pond restoration by virtue of their presence in the ponds, but just did not, in the case of amphibians, parallel the response of coho. The species composition of the community that populates the habitat must

also be considered when assessing the success of restoration. We found two exotic amphibians, bull frogs and green frog (*L. clamitans*), in several ponds, specifically in ponds with low coho productivity. This information is useful from a management perspective as those particular ponds were providing little benefit for coho, the target of the restoration and were providing habitat for exotic species that may have a detrimental impact on native species. It is not clear if the low coho productivity in those ponds was due to unfavourable conditions (e.g., extreme water temperatures), increased predation from the exotic species or other unmeasured factors.

Although all of the ponds we studied were restored for coho, the environmental attributes of the ponds varied widely. When engineering off-channel ponds for coho, some of the considerations in design include pond size, water source (surface water or ground water), depth profile (maximum, variation) and placement of aquatic structure, particularly wood (Rosenfeld et al., 2008). Site-specific differences among ponds not generally directly manipulated as part of the restoration include colonization by aquatic vegetation, organic matter inputs and type and extent of riparian cover. The specific site locale for projects is determined by a combination of land (including aquatic habitats) available for conservation and ecological considerations such as access to the main-stem of the river and can range from low elevation ponds surrounded by agriculture or light residential to high elevation forested areas.

Environmental variables explained significant variation in both vertebrate and invertebrate species abundance and biomass. Like coho, the abundance and biomass of the listed species (cutthroat trout, Dolly Varden and northern red-legged frog) were associated with relatively higher elevations, more wood and less vegetation as aquatic structure and

lower maximum temperatures. Increased biomass was also associated with groundwater fed ponds. It is not clear why the abundance and biomass of coho and listed species were associated with higher elevations but elevation may be associated with variables that we did not measure such as surrounding land use. Our higher elevation ponds tended to be located in forests and lower elevation ponds tended to be in proximity of agriculture and low density residential areas. The lack of a significant correlation with pond area (mean = 4116 m^2 , SE 903) is consistent with an assessment of smolt density as a function of pond area that found the optimal pond area threshold to be below $5,000 - 10,000 \text{ m}^3$ with decreases in smolt density in larger ponds (Rosenfeld et al., 2008). The association of coho and listed species with wood is consistent with the literature which reports wood to be important for salmonids in both stream and pond environments (Bustard & Narver, 1975a; Roni & Quinn, 2001; Giannico & Hinch, 2003). It is not clear if the abundance and biomass of coho and the listed species was higher where there was less aquatic vegetation due to the vegetation itself or due to the lack of wood in those ponds. Our results, which indicated higher biomass of coho and listed species in groundwater fed ponds and in ponds with lower maximum temperatures, are consistent with literature that reports higher coho density in groundwater fed side-channels with lower water temperatures in summer and warmer temperatures in winter (Morley et al., 2005). Other factors that we did not directly measure that may influence water temperature include the amount of open water present, pond morphology and the amount and height of riparian vegetation.

The evaluation of habitat as a mechanism by which umbrella species can benefit cooccurring species provides conservation practitioners valuable insights regardless of whether or not the umbrella species is effective (e.g., Suter et al., 2002; Ozaki et al., 2006). While

primary design considerations would remain focused on the species that the restoration was motivated by, if other habitat features could be identified that would augment the restoration to provide benefits to co-occurring species, be neutral at worst for the target species and be feasible from an engineering and cost perspective, those features could be included as part of restoration projects broadening the overall conservation benefits (e.g., see Koper & Schmiegelow, 2007). Equally, if there are habitat features associated with exotic species (such as the association of bull frog and green frog with warmer maximum water temperatures in our study) that are detrimental to native species, restored habitat could be designed to be less hospitable to those species (e.g., designed to have greater groundwater influence to moderate water temperatures).

3.4.1 Endpoints for Evaluating the Efficacy of Umbrella Species

Typically assessments of the umbrella species approach involve comparing species richness, and less often abundance, of species in areas with and without a presumed umbrella species (Branton & Richardson, 2011). Sites are typically classified based on the presence or absence of the umbrella species, though in some instances the documented relative abundance of umbrella species is used as the basis for classifying sites (e.g., Caro et al., 2004). On the basis of presence or absence alone, all of the ponds in this study would have been classified as having the umbrella species present. The resolution we gained by considering the relative abundance of the umbrella and the co-occurring species allowed us to better assess the function of coho as an umbrella species as well as to identify habitat features of the restored ponds that were associated with higher abundance and biomass of both the umbrella and other species of interest.

Researchers who advocate for the status of populations of co-occurring species to be assessed in studies of the umbrella species concept recognize that species richness should not be the sole indicator of how well potential umbrella species function (Caro, 2003; Lindenmayer & Fischer, 2003; Betrus et al., 2005; Seddon & Leech, 2008). Had we restricted our evaluation of the potential benefits conferred by restoration efforts to cooccurring species richness we would have concluded that conservation efforts designed for coho provide little or no benefit to other vertebrates, and that they have a negative impact on benthic invertebrate species richness, abundance and biomass. However by evaluating abundance and biomass, we were able to determine that where coho is most productive, so are several listed vertebrate species. The relative sensitivity of abundance compared to species richness has also been documented in studies using putative avian and mammalian umbrella species (e.g., Pakkala et al., 2003; Ozaki et al., 2006; Gardner et al., 2007; Hurme et al., 2008). A meta-analysis of empirical studies of the umbrella species concept found consistency between the direction (positive or negative) of relationships for species richness and abundance, but generally the magnitude of the effect was greater for abundance suggesting that it may better detect more subtle responses to conservation (Branton & Richardson, 2011).

3.4.2 Management Implications

The first step in habitat restoration has been described as the identification of one or a group of species (i.e., analogous to umbrella species) to guide the restoration process followed by the determination of the biotic and abiotic resources required by this/these species (Miller & Hobbs, 2007). It seems a natural extension to apply the umbrella species

concept which would entail an explicit evaluation of the benefits provided by the habitat restoration for co-occurring species, although we recognize that even post-restoration monitoring of target species is not always done. The most basic application of the umbrella species concept has been to compare species richness between sites with and without umbrella species. The assessment of similarity of response of umbrella and co-occurring species to conservation measures and the evaluation of the habitat features that can be linked to, for instance, increased richness or abundance of co-occurring species provide specific feedback that can be applied to future projects. While this does not initially appear to be the "short cut" promised by the umbrella species concept (Seddon & Leech, 2008), when used as part of a regional conservation plan, the initial investment to fine tune restoration strategies to ensure both the umbrella and co-occurring species are benefitting are efficient in the long run. In this way an initial pilot study could give way to planned monitoring that would be a requirement of any rigorous conservation program (Lambeck, 1997; Lindenmayer et al., 2002).

Chapter 4: An Evaluation of the Relationships Among Ecosystem Function, Species Diversity and Habitat Complexity in Restored Freshwater Ponds

4.1 Introduction

The unprecedented rate of loss of biodiversity globally has raised concerns over possible consequences of the loss of species and changes in community composition for ecosystem function (Schulze and Mooney 1993, Chapin et al 1997, Naeem et al 2002). Research into biodiversity effects on ecosystem function (BEF) represents a shift from the dominant paradigm that focused on how available resources determined what species assemblages would be present (Huston, 1997; Cardinale et al., 2009). In fact the relationship between biodiversity and ecosystem function (e.g., standing stock, nutrient cycling, stability) is likely a reciprocal causal relationship (i.e., reciprocally coupled) (Cardinale et al., 2006b). In other words, variation in resource availability may drive species diversity and species diversity in turn may determine how efficiently resources are converted (rates of nutrient cycling, detritus processing, biomass production) (Hillebrand & Matthiessen, 2009). The relative importance of direct controls (e.g., available resources and temperature) and biodiversity, as well as their interactions, on ecosystem function may be important when considering how BEF research may contribute to applied conservation issues (Hillebrand & Matthiessen, 2009; Srivastava et al., 2009; Tylianakis et al., 2009).

Historically, simple model systems using single trophic levels with one, rarely more, ecosystem functions were used to identify potential mechanisms underlying the relationship between biodiversity and ecosystem function (Reiss et al., 2009). A number of reviews (Duffy, 2009; Hillebrand & Matthiessen, 2009; Reiss et al., 2009; Lecerf & Richardson,

2010) and meta-analyses (Balvanera et al., 2006; Cardinale et al., 2006a) articulate the rapid development, state and early conclusions resulting from BEF research and the place of BEF research in conservation (Srivastava & Vellend, 2005; Thompson & Starzomski, 2007; Duffy, 2009). Although the results of individual studies vary and their interpretation has been controversial, these meta-analyses report positive effects of biodiversity on ecosystem function overall (Balvanera et al., 2006; Cardinale et al., 2006a; Cardinale et al., 2011). However, it is also clear that what is measured, for example the number of species present compared to what organisms do (i.e, functional diversity, Petchey & Gaston, 2006), influences the strength of BEF effects and that specific relationships may differ between aquatic and terrestrial systems (Lecerf & Richardson, 2010). The strength of observed positive relationships has been found to increase with the number of functions evaluated and the duration of the experiment suggesting that positive effects of species diversity on ecosystem function and properties have likely been underestimated in more simplistic scenarios evaluated to date (Duffy, 2009). Calls for future research frequently include the need to determine if relationships reported in relatively simple systems can be scaled up to complex, natural environments (e.g., Loreau et al., 2001; Hooper et al., 2005; Srivastava & Vellend, 2005; Hillebrand & Matthiessen, 2009; Cardinale et al., 2011).

Two primary mechanisms have been identified to explain why more diverse assemblages perform better than those that are less diverse. The sampling (artificial communities) or selection effect (natural communities) posits that where more species are present there is a greater likelihood that a functionally dominant species will be present and have a positive influence on ecosystem function (Huston, 1997). In contrast, where complementarity is in effect, as would be predicted by niche theory, resource partitioning and

facilitative interactions, diverse mixtures perform best because they are better able to exploit available resources (Cardinale, Palmer & Collins, 2002; Duffy et al., 2007). Species richness has been the most common measure of biodiversity used in BEF research (Balvanera et al., 2006), however it is an information-poor measure that, for example, provides no insight into demography or relative abundance (Fleishman et al., 2006). Moreover, it is not sensitive to shifts in community composition such as the replacement of native with non-native species. Functional diversity, which is a measure of diversity based on richness, evenness and divergence of functional traits (Schleuter et al., 2010; Villéger et al., 2010) has been found to be a better predictor of ecosystem function than species number (Grime, 1997; Petchey & Gaston, 2006; Lecerf & Richardson, 2010). It has been argued that more realistic predictions of the consequences of reduced diversity on ecosystem function will result using functional traits (biological, morphological, physiological or phenological features measurable at the individual level, Violle et al., 2007), instead of species number to represent diversity, though this requires an explicit link between the trait and function of interest (Hillebrand & Matthiessen, 2009).

The importance of habitat complexity, measured as heterogeneity or structure, in conjunction with species diversity has been noted in BEF studies in systems ranging from experimental manipulations of detrital-based communities with varying habitat structure in bromeliads (Srivastava, 2006) to non-experimental tests of parasitism and pollination across ecosystems with naturally heterogeneous resources (Tylianakis et al., 2009). Increased habitat complexity can lead to greater partitioning of resources by providing cover and substrate for colonization by more species. It may also mediate intra- or inter-species competitive or predator-prey relationships and can directly or indirectly alter productivity

(Crowder & Cooper, 1982; Srivastava, 2006). However the relationship between ecosystem function and habitat structure is not always positive. Diversity tends to increase with rising resource availability allowing less competitive species to exploit relatively more abundant resources, however the increase in competition in more enriched environments may also have a negative effect on diversity resulting in the "paradox of enrichment" (Duffy, 2009). In an evaluation of the effect of habitat and trophic structure on ecosystem function in a bromeliad system, increased habitat structure was found to decrease both predation and detrital processing efficiency (Srivastava, 2006). However, while there was less predation on detritivores where habitat complexity was higher, detritivores were also less efficient.

Research into the relationship between levels and kinds of biodiversity and ecosystem function is relevant to ecological restoration as conservation efforts globally must turn to improving the ecological integrity of degraded systems. Evaluating the relationship between biodiversity and ecosystem function in ecosystems where species are being "added" (albeit not experimentally), instead of removed, provides a unique opportunity to evaluate some of the findings of BEF research in the context of habitat restoration. While historically restoration projects have often been motivated by single species, the mounting evidence that ecosystem function increases over time with higher biodiversity and greater heterogeneity of resources suggests that restoration, as conservation more generally, should prioritize providing benefits for as many species as possible (Hillebrand & Matthiessen, 2009; Tylianakis et al., 2009). Moreover, because of our limited understanding of complex natural systems, it has been argued that biodiversity may well act as a proxy of a system that provides multiple ecosystem functions (Palumbi et al., 2009). Therefore, managing for the maximization of diversity (however it is measured) may prove to maintain the ecosystem

functions of value where we do not fully understand the mechanism behind the ecosystem functions (Duffy, 2009).

The case for the utility of BEF research for restoration has been made in instances when high levels of ecosystem function (e.g., production, nutrient retention) are the goal of the restoration and plant diversity has been found to be positively related to that increased productivity or to increased stability in the face of perturbation (Hughes & Stachowicz, 2004; Srivastava & Vellend, 2005). However, we are not aware of any studies that have evaluated BEF in restored systems using vertebrates as the target species of the restoration.

We used several measures of vertebrate and benthic invertebrate diversity (i.e., species and functional trait richness and evenness – hereafter called diversity when referring to these measures generally), habitat complexity and interactions between diversity and habitat complexity to evaluate their relative importance for ecosystem function in off-channel ponds restored for juvenile coho salmon (Oncorhynchus kisutch) (hereafter "coho). We used relative standing biomass of vertebrates, benthic invertebrates and algae (measured as chlorophyll a) as proxies for ecosystem function. Although standing biomass is a simple measure of ecosystem function it has a long history in BEF literature and is amenable to use in an observational study of this type. We expected positive relationships between standing biomass and diversity, with stronger effects for diversity measures of functional traits than for species richness alone. We expected a positive relationship between standing biomass and habitat complexity assuming that more complex habitat would have more resources that could be translated to biomass. We anticipated that diversity and habitat complexity would have more explanatory power together than alone with stronger positive relationships where habitat complexity is higher. However, we also expected to find some exceptions to these

positive relationships as increased habitat structure can reduce efficiency ultimately impacting ecosystem function negatively. Finally, we evaluated the relationship between standing biomass and time since restoration. We expected that the strength of relationships between biodiversity, habitat complexity and ecosystem function to be stronger in ponds that had been restored for a longer time.

4.2 Materials and Methods

4.2.1 Study Sites

This study was conducted in the Fraser River Basin of southwestern British Columbia, Canada (Figure 3.1). Like river systems globally, river and floodplain habitat in this area have been simplified, habitat has been lost through ecosystem conversion and degradation, and water quality has been diminished through diversion and inputs of nutrients and pollutants (Levings & Nishimura, 1996; Sala et al., 2000; Beechie et al., 2010). For more than two decades, off-channel floodplain ponds and channels have been restored, created and enhanced (all categories referred to herein as restored) in British Columbia to increase the available habitat necessary for spawning and rearing coho (Lister & Finnigan, 1997). We considered all 100 projects implemented by Fisheries and Oceans Canada (DFO) before 2004 that restored floodplain pond habitat primarily for coho in southwestern British Columbia as candidate study sites. These ponds were restored by improving the connectivity of existing ponds to surface water flow and by creating new ponds using groundwater or water diverted from nearby dams, rivers and creeks to flood bermed or excavated areas. The flooding of bermed areas provide more complex habitat than excavated ponds. Common features of many of the restoration projects were the addition of wood (root wads or large pieces of wood) and the creation of deep channels (2 - 3 m deep). Water sources for the projects were

classified by DFO as surface water, groundwater or a combination of the two. The restoration technique and habitat features of each pond are summarized in (Appendix C, Table C.1).

The criteria we used in screening sites for inclusion in our study included presence of pond habitat (not side-channels or streams), no direct tidal influence, surface or groundwater fed (not glacial), adequate accessibility for field sampling, no stocking of fish (including coho) and a minimum of four restored ponds per watershed. Sites fed primarily by glacial runoff were not included because colder waters temperatures often exclude use by amphibians. If ponds were directly connected to each other (i.e., not connected through the mainstem of the river), only one of the individual ponds in the complex was selected for evaluation based primarily on accessibility for field work. Out of the 100 sites initally reviewed, 17 restored floodplain ponds in three watersheds: Chilliwack (n= 9), Coquitlam (n = 4) and Seymour (n = 4) (Figure 3.1) met our criteria and were included in our study. Most sites were eliminated as candidates in the initial screening because they did not have primarily pond habitat or there were not at least four ponds in the watershed. Others were eliminated because they were glacier fed or because accessibility for sampling was limited.

Land use surrounding the restored floodplain ponds is primarily forested or agricultural with residential areas nearby. The study sites were located at altitudes ranging from 10 to almost 400 m above sea level and receive between an average of 1500 and 2200 mm of rain annually. <u>http://pacificclimate.org/docs/publications/GVRD.RainfallUpdate.pdf</u>.

4.2.2 Field Sampling

4.2.2.1 Sampling Periods

We sampled ponds three times, (1) May-June 2006, (2) late July-August 2006, and (3) February-March 2007, prior to freshets that would initiate the outmigration of coho smolts. We selected these study periods to increase the likelihood of detecting species that are present in ponds only for certain life stages (Roberge & Angelstam, 2004). For instance, some frog and salamander species are primarily present in ponds when they are breeding or as larvae [e.g., northern red-legged frog (*Rana aurora*), northwestern salamander (*Ambystoma gracile*), rough-skinned newt (*Taricha granulosa*)], although they may still be present as adult frogs or as neotenic adults (e.g., northwestern salamander).

4.2.2.2 Vertebrate Sampling

We set between 30 and 50 minnow traps baited with salmon roe in perforated film canisters in each pond. The total number of traps used was determined based on the ponds' size and complexity. We used an initial visual assessment to divide each pond into sections using features including depth, aspect, riparian structure and aquatic structure to ensure that all habitat types represented in the pond were sampled (Olson et al., 1997). Approximately the same number of traps was set haphazardly in each section of the pond. We identified, counted, weighed and measured all captured juvenile and adult fish (fork length for salmonids or total) and amphibians (snout vent and total length) (Barbour et al., 1999; Corkran & Thoms, 2006). In some sampling periods a large number of individuals of some species (e.g., three-spined stickleback, northwestern salamander) were captured. In those instances after more than 15 individuals of one species were captured, we measured the first five individuals in each subsequent sampling section and any additional individuals were

assigned to length classes (e.g., 4 - 5 cm). We estimated biomass for unweighed individuals by assigning them the mean biomass for conspecific individuals measured in their length class in that sampling period. Fish were anesthetized using buffered MS222 prior to being measured and weighed. We received approval by the University of British Columbia Animal Care Committee and obtained all necessary federal and provincial trapping permits.

4.2.2.3 Benthic Invertebrate Sampling

In May-June 2006, we collected three benthic invertebrate samples from each pond using a standard D-frame net. We used semi-quantitative travelling kick net samples, standardized by time, by sweeping a standard D-frame net over sediment disturbed while shuffling backwards (Wissinger et al., 2009). We selected sampling locations using a random number table to select habitat units where possible, or by access combined with aspect if there were limited areas within a pond that could be accessed due to depth, substrate (i.e., deep mud) or other barriers (e.g., dense conglomerations of large wood). Samples were preserved in the field in 10% formalin. Samples were sorted in the laboratory and organisms identified to the lowest practical level (family or genus). Sub-sampling was used for large samples. After they were identified, samples were composited, blotted dry and weighed to the nearest 0.01 gram. One invertebrate biomass sample appeared to be an outlier (three times higher than other samples from the same pond and more than 10 times higher than the rest of samples). This may be due to a large-bodied individual being included in the sample, however individual masses were not recorded so this could not be confirmed. We removed that data point from subsequent analysis, and therefore for that pond (Chilliwack 1) the mean value for biomass was based upon two instead of three samples.

4.2.2.4 Habitat Assessment

We documented each ponds' habitat structure in July and August 2006 using standard techniques of Anonymous (1995) and Johnston and Slaney (Johnston & Slaney, 1997). The amount of (e.g., per cent cover) aquatic (e.g., large wood, root wads, overhanging banks, aquatic vegetation) and riparian structure and water depth were recorded every metre along the length of four to six equidistant transects of each pond (number of transects determined by the size of the pond).

4.2.2.5 Algae

We collected algae as a measure of primary productivity. Unglazed ceramic tiles (7.5 cm^{2}) were fixed to L-brackets that were then attached to rebar. There were two tiles, placed 30 cm apart, per piece of rebar. Three pieces of rebar (six tiles in total) were deployed several metres from each other (dependent upon the pond configuration) on the southern shore of each pond for six weeks. The rebar was set so that the top tile was approximately 30 cm below the surface of the water. This depth was selected to ensure that tiles would remain under water as water depth tends to decline as the summer progresses. However, water levels dropped below the level of the tiles in one pond, Chilliwack 5, reducing our sample size to 16 ponds for algal biomass. We analyzed chlorophyll a using EPA method 455 for fluorescence detection (Arar & Collins, 1997). Algae was removed from the tiles using a small brush and rinsed with distilled water into a holding vessel. The known volume of sample water was filtered using glass fiber filter. The pigment was extracted in 90% acetone for a minimum of 2 and a maximum of 24 hours. All samples were refrigerated during extraction. After filtering samples were centrifuged and fluorescence was measured on an aliquot of the supernatant. If the readings were too high, the sample was diluted and

fluorescence was measured again. Concentrations were reported in $\mu g/L$ and converted to $\mu g/cm^2$.

4.3 Data Analysis

4.3.1 Metric Calculation

We calculated richness and evenness of species, functional traits and habitat. Body size, which is thought to be a consistently important functional trait in animals (Petchey & Gaston, 2006; Reiss et al., 2009) was used as a functional trait for vertebrates, based on the assumption that size would affect both habitat use and predator-prey relationships. Feeding group was used to define functional traits for benthic invertebrates, but not vertebrates as they were not differentiated by feeding strategies to the same extent as benthic invertebrates.

As sampling effort goes up, typically more species are found or, in the case of traits, individuals with particular traits (Gotelli & Colwell, 2001). Rarefaction methods are used to account for differences in sampling intensity by standardizing data to the sampling site with the fewest individuals reported. In other words, if 50 individuals were recorded in one pond and 150 in another, richness would be calculated for 50 randomly selected individuals from the second pond. The Shannon diversity index, which incorporates richness and relative abundance, was used as a measure indicating the relative evenness of species, functional trait or habitat features (Petchey & Gaston, 2006). We used sample-based rarefaction curves with 1000 iterations, without replacement, in the Monte Carlo type analysis, to calculate richness using the expected richness function (Mau Tau) and the Shannon diversity index in EstimateS (Colwell, 2009). For vertebrate species richness and diversity, data from all three seasons were pooled for rarefaction to reflect total species richness for the pond. Vertebrate functional richness and diversity (body size class) were rarefied for each sampling event

separately because we anticipated that shifts in body size over the seasons were more important than an aggregate measure over the whole year. For habitat richness, the number of transect points (instead of individuals for species richness) was used to determine to what number habitat richness was rarefied. Structural components algae, aquatic vegetation, wood (including large wood, branches, rootwads and snags), organic matter (twigs and leaves) and boulders were the elements of habitat included in the analysis.

We developed a metric for habitat complexity to integrate rarefied habitat richness and the coefficient of variation for water depth. We used the coefficient of variation of depth to represent how variable the depth profile was with the assumption that more variable profiles provide more complex habitat. Both rarefied habitat richness values and the coefficient of variation for depth were standardized such that the maximum value recorded for each variable was equal to 1. Habitat complexity was calculated using the average of habitat richness and the coefficient of variation of depth. In order to aid in the interpretation of significant statistical tests that included an interaction with habitat complexity, we classified sites as low (mean \pm S.D.: 0.52 ± 0.03 , n = 3), medium (0.63 ± 0.03 , n = 8) and high (0.76 ± 0.07 , n = 6) habitat complexity. The distinction was somewhat arbitrary; however, there is a clear break between the categories of low and high. Medium represents a transition between the two levels of complexity.

4.3.2 Statistical Analyses

We tested correlations between species richness and Shannon diversity and between functional richness and functional Shannon diversity for both vertebrates and benthic invertebrates. Vertebrate species richness and evenness were strongly correlated (r = 0.89, p < 0.0007) as were functional richness (biomass categories) and evenness (r = 0.96. p <

0.0001). Benthic invertebrate species richness and Shannon diversity were also correlated (r = 0.55, p = 0.02) but functional richness (based on feeding strategies) and Shannon diversity were not (r = 0.36, p = 0.16). Based on these correlations, we evaluated both vertebrate and invertebrate species richness and functional richness as well as invertebrate functional evenness in subsequent statistical analyses.

We used a mixed model (PROC MIXED, SAS version 9.1, SAS Inc., Cary, NC) with a random variable (watershed) to test the relationships between standing biomass as the response variable and diversity and habitat complexity as predictor variables. For tests with vertebrate standing biomass as the response variable, a repeated measures term (ponds in each sampling session) was also included in the model as vertebrates were sampled three times over the course of a year. As benthic invertebrates and algae were sampled only once in May-June, only the data from the first (i.e., spring) sampling period were used as predictor variables. We also tested the effect of time since restoration on standing biomass.

We calculated a pseudo R^2 (1-SSE/SSY) as a measure of the improvement of the tested models compared to the null models (random variable only). A pseudo R-squared can be used to evaluate how well multiple models predict the same outcome using the same data (Long, 1997; Freese & Long, 2006). Negative values for the R-squared indicate that the tested model is worse than the null model. Tests were considered significant at alpha = 0.1 to reduce the likelihood of a type II error, i.e., rejection of the null hypothesis that there was an effect when a real effect may have existed, which would be more likely with alpha = 0.05 because of large sampling variability or small sample size (Peterman, 1990; Bryant, 2004). In applied research that may influence resource management decisions, the cost associated with the finding of no effect when in fact an effect exists can be costly (Peterman, 1990). No

corrections were made for multiple comparisons; however, we did consider the strength of the statistical relationships to be more meaningful where there was consistency in the results of the different tests (Moran, 2003). A summary of all biological and habitat data used in statistical analyses is provided in supplementary tables (Appendix C, Table C.1).

4.4 Results

In preliminary mixed models, watershed was included as a random term, however it explained no variance for benthic invertebrate biomass or chlorophyll *a* standing stock and therefore was left out of the final models for those variables. Vertebrates were sampled three times so pond was included as a repeated variable for vertebrate biomass only.

4.4.1 Vertebrate Biomass

Vertebrate biomass was significantly higher in ponds with more habitat complexity (Table 4.1, Figure 4.1a). There was a significant (P = 0.03) quadratic relationship between vertebrate biomass and benthic invertebrate species richness (Table 4.1). Vertebrate biomass increased from low to mid-levels of benthic invertebrate species richness and then decreased as benthic invertebrate species richness continued to rise (Figure 4.2a).

Vertebrate biomass was highest in ponds with medium habitat complexity and where functional trait richness was higher (Table 4.1, Figure 4.3a). The model that tested the interaction between habitat complexity and functional trait richness ($R^2 = 0.11$) was not an improvement upon the fit of models with those variables tested alone (Table 4.1). There were no other significant relationships between vertebrate biomass and other measures of diversity or the length of time a pond had been restored (Appendix C, Table C.2).

Table 4.1. Significant results from mixed models testing the relationships between response variables standing biomass of vertebrates, benthic invertebrates and chlorophyll *a*, and explanatory variables of species and functional trait richness and Shannon diversity, habitat complexity and their interactions. Vertebrates were sampled three times so pond was included as a repeated variable for vertebrate biomass only. In preliminary mixed models watershed was included as a random term, however it explained no variance for benthic invertebrate biomass or chlorophyll *a* production and therefore was left out of the final model for those variables.

Response variable	Explanatory variables	Sample size F ratio		P value	Model Pseudo R ²
vertebrate biomass*	complexity	51	F _{1,47} = 6.94	0.01	0.1
	BI_SR	51	F _{1,46} = 3.82	0.06	0.17
	BI_SR†	51	F _{1,46} = 4.79	0.03	
	a a manufa with st	54	F - 2.4F	0.40	0.4
		51	$F_{1,45} = 2.43$	0.12	0.1
	vert_FR"	51	$F_{1,45} = 5.40$	0.02	
	complexity X vert_FR*	51	$F_{1,45} = 4.49$	0.4	
benthic invertebrate biomass complexity		17	$F_{445} = 4.96$	0.04	0.23
		.,	1,15 1.00	0.01	0.20
	BI_SR	17	F _{1,15} = 4.45	0.05	0.31
	vert_SR	17	F _{1,15} = 4.88	0.05	0.2
	oomnlovity	17	E - 240	0.00	0.45
	complexity	17	$F_{1,13} = 3.49$	0.09	0.45
	vert_SR	17	$F_{1,13} = 4.73$	0.04	
	complexity X vert_SR	17	$F_{1,13} = 5.19$	0.05	
	complexity	17	F _{1 13} = 1.82	0.2	0.42
	vert FE	17	$F_{1,13} = 5.34$	0.04	
	_ complexity* X vert FR	17	$F_{1,13} = 4.89$	0.05	
			.,		
chlorophyll <i>a</i> biomass	complexity	16	F _{1,12} = 5.22	0.05	0.26
	BI_FG_SD	16	F _{1,12} = 4.14	0.08	
	complexity X BI_FG_SD	16	F _{1,12} = 3.98	0.08	
	complexityt	16	F = 4.92	0 12	0.36
	vort SD+	16	F = 3.00	0.12	0.00
		10	$F_{1,12} = 3.90$	0.07	
	complexity X vert_SR‡	16	F _{1,12} = 3.73	0.06	

Benthic invertebrate = BI Vertebrate = vert Species richness = SR Functional richness = FR Shannon diversity index = SD habitat complexity = complexity

* square root transformed

† squared

‡ log₁₀ transformed



Figure 4.1. Linear regression relationships between (a) vertebrate biomass and (b) benthic invertebrate biomass and habitat complexity in restored floodplain ponds. Vertebrates were sampled three times (FS1, FS2 and FS3) and benthic invertebrates were sampled only once (FS1). Data are untransformed.



Figure 4.2. Linear regression relationships between (a) vertebrate biomass and benthic invertebrate species richness and benthic invertebrate biomass (b) vertebrate species richness and (c) benthic invertebrate species richness in restored floodplain ponds. Vertebrates were sampled three times (FS1, FS2 and FS3) and benthic invertebrates were sampled only once (FS1). Data are untransformed.

4.4.2 Benthic Invertebrate Biomass

There was a negative relationship between benthic invertebrate biomass and habitat complexity (Table 1, Figure 4.1b). Benthic invertebrate biomass was higher in ponds with greater vertebrate (Figure 4.2b) and benthic invertebrate species richness (Table 4.1) (Figure 4.2c). The model including the interaction between habitat complexity and vertebrate species richness on benthic invertebrate biomass ($R^2 = 0.45$) was a substantial improvement upon the null model compared to models using habitat complexity ($R^2 = 0.23$) and vertebrate species richness ($R^2 = 0.20$) alone (Figure 4.3b). Ponds with lower habitat complexity had greater benthic invertebrate biomass where there was also higher vertebrate species richness (Table 4.1, Figure 4.3b).

Benthic invertebrate biomass was highest in ponds with the greatest vertebrate functional trait richness and low or medium habitat complexity (Figure 4.3c). This model testing the interaction between habitat complexity and vertebrate functional trait richness was a marked improvement on the null model ($R^2 = 0.42$) compared to models testing habitat complexity ($R^2 = 0.23$) or vertebrate functional trait richness ($R^2 = 0.02$) alone (Table 4.1). There were no other significant relationships between benthic invertebrate biomass and other measures of diversity or time since restoration (Appendix C, Table C.2).

4.4.3 Chlorophyll *a* Biomass

Models testing the relationship between chlorophyll *a* biomass and habitat complexity or diversity were only significant when interaction terms were tested. Chlorophyll *a* biomass was higher in ponds with lower habitat complexity and higher vertebrate species richness compared to ponds with higher habitat complexity (Figure 4.3d). This resulted in a better model fit ($R^2 = 0.36$) compared to models testing habitat complexity ($R^2 = 0.07$) or vertebrate



Benthic invertebrate functional trait Shannon diveristy index

Figure 4.3. Linear regression relationships between ecosystem function and diversity plus habitat complexity. Habitat complexity was estimated from standardized measures of habitat richness and coefficient of variation of depth and grouped into categories of low, medium and high complexity. Relationships shown are between (a) vertebrate biomass and vertebrate functional trait richness, (b) benthic invertebrate biomass and vertebrate species richness, (c) benthic invertebrate biomass and vertebrate functional trait richness (FS1 only) and algal biomass, measured as chlorophyll *a*, and (d) vertebrate species richness and (e) benthic invertebrate functional trait Shannon diversity index in restored floodplain ponds. Vertebrates were sampled three times (FS1, FS2 and FS3) and benthic invertebrates were sampled only once (FS1). Data are untransformed.

species richness ($R^2 = 0.01$) alone (Tables 4.1). In the relationship between chlorophyll *a* and explanatory variables habitat complexity and benthic invertebrate functional trait richness, the most productive ponds had low or medium habitat complexity but also tended to have low benthic invertebrate functional trait Shannon diversity indices (Table 4.1, Fig. 4.3e). There were no other significant relationships between chlorophyll *a* and other measures of diversity or the length of time a pond had been restored (Appendix C, Table C.2).

4.5 Discussion

Given the complex interactions that characterize natural ecological systems, it is not surprising that we found different patterns among measurements of ecosystem function for different taxonomic classes and biotic diversity, habitat complexity and their interactions in restored floodplain ponds. Despite this variability, the most common pattern we found was that standing biomass (a measure of ecosystem function) was positively related with species diversity. Moreover, vertebrate species diversity and habitat complexity accounted for more of the variance in standing biomass together than individually, although the direction of the relationship was not consistent. The majority of significant relationships we observed, with or without considering interactions with habitat complexity, had species richness as the explanatory variable. Notably ponds that had been restored for a longer period of time did not demonstrate increased ecosystem function.

For each measure of ecosystem function, we tested five relationships with diversity alone, one with habitat complexity alone and five with interactions between diversity and habitat complexity. We wanted to test the relative sensitivity of different measures of diversity with a range of response and explanatory variables. We used a weight of evidence type approach in which relationships observed repeatedly, regardless of "how significant" the p-value was, provide more support that those relationships are meaningful (Moran, 2003).

4.5.1 Habitat Complexity

Habitat complexity can influence ecosystem function by altering the density or diversity of species present (Schwartz et al., 2000; Srivastava, 2006). This may be due to a more complete exploitation of niches present or because of the greater likelihood of higher functioning species being present (Srivastava & Vellend, 2005). In our study we found that habitat complexity interacted with diversity to influence ecosystem function. This was consistent across all three taxonomic groups tested but the direction of the relationship varied by taxonomic group and was stronger for functional richness. Consistent with our prediction that increased habitat complexity should enhance ecosystem function, vertebrate biomass was higher where habitat complexity was higher. However, the negative relationship we found between benthic invertebrate and chlorophyll *a* biomass and habitat complexity in interactions with species diversity are contrary to studies that have shown a positive relationship between measures of ecosystem function and increasing habitat heterogeneity or structure (Cardinale, Nelson & Palmer, 2000; Srivastava, 2006; Tylianakis et al., 2009). Reduced habitat structure may have provided less cover for vertebrate predators and

consumers of benthic invertebrates and algae resulting in increased benthic invertebrate and chlorophyll *a* production in simpler habitat (Power, 1984; Devries, 1990).

4.5.2 Vertebrate Biomass

Contrary to our expectations, we found no relationship between vertebrate biomass and vertebrate species richness. However, vertebrate biomass was higher in sites with higher vertebrate functional trait richness (i.e., body size classes) and higher habitat complexity. These results are consistent with biological or functional characteristics of species, rather than their number, having a stronger influence on ecosystem function (Grime, 1997; Petchey & Gaston, 2006; Villéger et al., 2010). For aquatic vertebrates size class may be a more important determinant of complementarity of resource use, as assumed by niche theory (Hutchinson, 1957; Hooper et al., 2005), than species richness if animals of a similar size utilize similar habitat regardless of species. Ponds with more habitat complexity tended to have deeper areas. These deeper areas likely provide cover for the larger individuals (e.g., Dolly Varden, cutthroat trout, see Figure 5.10) which may have then been able to exploit resources that were not accessed by smaller animals that were found predominantly in shallower water (e.g., green frog, northwestern salamander, northern red-legged frog, Figure 5.10). Species traits are presumed to have the strongest effect in areas with greater habitat heterogeneity where there is the least overlap in those traits (Petchey & Gaston, 2006).

Vertebrate biomass was highest at a mid-range of benthic invertebrate species richness. This is consistent with the theory that there is a saturating relationship whereby each additional species contributes positively to ecosystem function only to a point (Hooper et al., 2005). A negative relationship between diversity and ecosystem productivity could then result if there are more species than limiting resources can support (Hillebrand &

Matthiessen, 2009). Alternatively, if inferior competitors are able to colonize due to good dispersal capabilities, or if they are resistant to predation rather than being competitive in terms of growth and reproduction thereby taking resources from more efficient species, ecosystem function could be depressed (Mouquet, Moore & Loreau, 2002). If food resources in this system, i.e., benthic invertebrates and their basal food sources, limit productivity, then a more species-rich, but less productive, benthic invertebrate community could slow the flux of energy contributing to vertebrate biomass (Smokorowski & Pratt, 2007).

4.5.3 Benthic Invertebrate and Chlorophyll a Biomass

The positive relationships between benthic invertebrate biomass and both vertebrate and benthic invertebrate species richness are supportive of the theory that ecosystem function is enhanced where diversity is greater (Cardinale et al., 2006a; Cardinale et al., 2009). The relationship with vertebrate species richness may be consistent with either the increased invertebrate prey base for vertebrates supporting higher vertebrate species richness or the top-down predation pressure of vertebrates on benthic invertebrates being moderated by inter-species relationships making vertebrates less efficient at competing with or preying upon benthic invertebrates. Alternatively resources may not have been a limiting factor and the positive relationship may simply reflect a more resource rich environment. The positive relationship between benthic invertebrate biomass and benthic invertebrate species richness is consistent with niche theory, that the more species present the better able they are to exploit the available resources (Cardinale et al., 2002).

4.5.4 Summary

The patterns we observed are generally consistent with mechanisms reported in the underlying BEF literature that report a positive relationship between diversity and ecosystem function. Though we used very simple measures of traits, our results are supportive of the importance of considering functional traits and functional diversity (Petchey & Gaston, 2006). Our results differed from the literature insofar as increased habitat complexity was not necessarily associated with higher functionality. This highlights the importance of considering habitat structure in studies of BEF and the fact that we should not expect different taxonomic classes, or likely taxonomic groups at finer scales of resolution, to respond similarly to habitat complexity.

Chapter 5: Evaluation of the Relationship Between Habitat Features at Three Spatial Scales and the Abundance and Biomass of Coho Salmon and other Aquatic Vertebrates in Restored Floodplain Ponds

5.1 Introduction

Approximately 10% of known animal species are found in fresh waters which cover just 0.8% of the earth's surface area, making freshwaters a hotspot for biodiversity (Strayer & Dudgeon, 2010). Habitat loss, degradation and fragmentation are among the foremost drivers of the loss of biodiversity globally and freshwaters are particularly susceptible to these impacts because humans live in disproportionate numbers near water (Vitousek et al., 1997; Sala et al., 2000; Vorosmarty et al., 2010). As many as one third of freshwater species are extinct or imperiled in North America and Europe and this imperilment tends to be greater for freshwater biota than their terrestrial and marine counterparts (Ricciardi & Rasmussen, 1999; Strayer & Dudgeon, 2010). The ramifications of the decline of freshwater ecosystems include the immediate consequences to biota, the loss of ecosystem services, and associated economic impacts and social losses (Daily, 1997; Lake et al., 2007).

Despite the substantial resources that have been spent to conserve and restore freshwater systems using both small- and large-scale restoration projects, river systems continue to degrade (Bernhardt et al., 2005; Palmer, 2009). While this degradation reflects continued anthropogenic pressure on river systems, the lack of success of many restoration projects has been attributed to the inadequate consideration of watershed-scale influences (e.g., floods, sedimentation) that overwhelm local restoration projects (Minns, Kelso &

Randall, 1996; Lake et al., 2007; Palmer, 2009). This is an important omission as habitat represents a set of nested physical and chemical characteristics that can act as a filter constraining the movement and response of biota to habitat at more local scales (Poff, 1997). Biotic interactions and habitat conditions at lower hierarchical scales in turn influence local community composition (Poff, 1997). If relationships between specific habitat features at the relevant scales and project success are known, that information can be used to improve the design of future restoration projects. However, one of the challenges with improving the practices of ecological restoration in river systems is that stream and floodplain restoration projects tend to be implemented opportunistically rather than strategically (e.g., considering watershed scale influences) and experimental frameworks are rarely employed (Holl et al., 2003; Lake et al., 2007). Post-restoration monitoring has been rare and has tended to focus on the integrity of physical structures rather than the response of biota to restoration (Bernhardt et al., 2005; Roni, 2005; Palmer et al., 2007). Nonetheless, a post hoc study of restored systems can be used to reveal patterns that may inform the practice of restoration. Using quantitative comparisons amongst sites that have undergone similar kinds of restoration, but that vary along environmental gradients or in terms of management practices, it may be possible to identify the relative importance of specific factors (e.g., hydrology, cover) that may limit or promote restoration (Holl et al., 2003).

Historically, the driver for freshwater habitat restoration has been concern for a single species or group of species, with the majority of those conducted to restore fisheries resources (Roni, Hanson & Beechie, 2008). However, it is inevitable that other species will be affected, positively or negatively, by alterations (including restoration) to habitat and changes to the aquatic community (Boon, 1998; Pess et al., 2005). Habitat alterations

resulting from restoration may provide valuable habitat to species within the floodplain, however, changing habitat may also have unintended consequences such as leading to shifts in species composition favoring exotic species. An evaluation of the biological response of an assemblage of species provides information regarding different components of ecosystem structure and function and is important for advanced stages of management such as restoration (Rosenfeld, 2003; Pess et al., 2005). Moreover, if the habitat needs of multiple species can be met simultaneously it is a more efficient use of resources, rather than to focus on the habitat needs of just one species.

An estimated 90% of fish habitat has been lost in the lower Fraser River of southwestern British Columbia, Canada since the beginning of the twentieth century (Levings & Nishimura, 1996). Anthropogenic activities such as agriculture, forestry, road building and urban development have resulted in the simplification or reduction in floodplain habitat in large coastal rivers in British Columbia, and throughout the Pacific Northwest (Beechie et al., 2010). The loss of highly productive, complex floodplain habitat that provides nursery, rearing and overwintering habitat has been identified as an important factor that limits the production of coho salmon (Oncorhynchus kisutch, hereafter "coho") (Beechie et al., 1994; Solazzi et al., 2000) but also has a negative impact on benthic invertebrates, other fish species and amphibians that also rely upon floodplain habitat at some, or all, stages in their life cycles (Ward et al., 1999; Welsh et al., 2001; Stevens, Paszkowski & Foote, 2007). The response of coho to restoration of floodplain ponds has been less studied than their response to restoration in stream and side-channel habitat despite the recognition that the availability of pond habitat may be an important factor limiting overwintering survival (Nickelson et al., 1992; Cederholm et al., 1997). Studies of both streams and floodplain side-

channels have reported that large wood, pools and temperature are determinants of coho abundances (Bustard & Narver, 1975a; Giannico & Hinch, 2003; Morley et al., 2005).

For more than two decades, off-channel floodplain ponds and channels have been restored, created and enhanced (e.g., reconnected hydrologically, instream habitat improvements) in British Columbia and the Pacific Northwest specifically to increase the available habitat necessary for coho rearing and spawning (Lister & Finnigan, 1997; Pess et al., 2005). Post-restoration monitoring of these restored floodplain ponds in southwestern British Columbia has been limited to trapping of outmigrating coho smolts and has not included the broader aquatic community. Post-restoration monitoring of floodplain ponds in the interior of British Columbia indicates that the production of coho varies widely amongst projects (Cooperman et al., 2006). While some variability in the abundance of coho may be explained by escapement, it may also be affected by site-specific habitat features which also vary widely amongst projects. We explicitly evaluated the relationship between relative abundance and biomass of coho (young of year) and habitat features that were manipulated in the restoration (e.g., depth, cover, area) as well as watershed-scale features that were not manipulated (e.g., land use, elevation). We conducted the same analysis to determine the impact of floodplain pond restoration projects and specific habitat features on adults and juveniles of all other vertebrate species in the ponds. We also evaluated the relative influence of habitat features at different scales (watershed, pond and micro-habitat) on the abundance and biomass of coho and other aquatic vertebrates.

5.2 Methods

5.2.1 Study Site Selection

This study was conducted in the Fraser River Basin of southwestern British Columbia, Canada (Figure 2.1). We considered all 100 projects implemented by Fisheries and Oceans Canada (DFO) as of 2004 that restored off-channel pond habitat primarily for coho as candidate study sites (Pers. Comm., Matt Foy, DFO). These ponds were restored by improving the connectivity of existing ponds to surface water flow and by creating new ponds using groundwater or water diverted from nearby dams, rivers and creeks to flood bermed or excavated areas. The flooding of bermed areas provide more complex habitat than excavated ponds. Common features of many of the restoration projects were the addition of wood (root wads or large pieces of wood) and the creation of deep channels (2 - 3 m deep). Water sources for the projects were classified by DFO as surface water, groundwater or a combination of the two. The restoration technique and habitat features of each pond are summarized in Table 5.1.

The criteria we used in screening sites for inclusion in our study included presence of pond habitat (not side-channels or streams), no direct tidal influence, surface or groundwater fed (not glacial), adequate accessibility for field sampling, no stocking of fish and a minimum of four restored ponds per watershed. Ponds fed primarily by glacial runoff were excluded because colder waters temperatures often exclude use by amphibians. If ponds were part of a complex (i.e., multiple ponds connected directly to each other, not through the mainstem river), only one of the individual ponds was selected for evaluation based primarily on facilitating access for field work. Out of the 100 sites initially considered, 17 restored floodplain ponds in three watersheds [Chilliwack (n = 9 ponds), Coquitlam (n = 4) and
						Maximum			
Watershed_		Project age	Elevation		Water	temperature			
pond#	Restoration type	(years)	(m)	Area (m²)	source	(°C)*	Forested [†]	Non-forested†	River†
Chilliwack_1	reconnected, flooded	11	158	1 34 19	surface	18.3	0.96	0.01	0.03
Chilliwack_2	reconnected, flooded	10	381	4211	combined	15.5	0.97	0.01	0.02
Chilliwack_3	excavated	2	11	1280	surface	22.1	0.40	0.51	0.07
Chilliwack_4	excavated	8	18	5525	surface	15.8	0.09	0.85	0.07
Chilliwack_5	reconnected	20	15	3000	ground	21.5	0.13	0.80	0.07
Chilliwack_6	excavated	2	38	825	surface	15.9	0.32	0.60	0.06
Chilliwack_7	excavated	8	19	519	surface	16.4	0.10	0.77	0.13
Chilliwack_8	reconnected, flooded	8	422	7231	surface	11.1	0.97	0.01	0.02
Chilliwack_9	excavated	8	19	1717	surface	16.6	0.15	0.70	0.15
Coquitlam_1	excavated	23	90	4308	surface	20.4	0.70	0.30	0.00
Coquitlam _2	excavated	23	124	4045	surface	18.8	0.98	0.01	0.01
Coquitlam_3	excavated	5	84	1462	ground	12.8	0.73	0.27	0.00
Coquitlam _4	excavated	13	28	3566	surface	19.4	0.63	0.36	0.01
Seymour_1	flooded	7	152	3667	surface	14.8	0.93	0.04	0.03
Seymour_2	flooded	8	104	532	ground	9.1	0.90	0.06	0.03
Seymour_3	flooded	14	167	2679	ground	10.6	0.97	0.00	0.03
Seymour_4	flooded	7	168	12000	combined	15.9	0.97	0.00	0.03

Table 5.1. Restoration type, age and habitat attributes of ponds restored for juvenile coho salmon.

* Average for warmest consecutive 7-day period

† Proportion of land cover or survey points

Watershed_ pond #	Wetland/lake†	Roads†	% slope	Chlorophyll a µg/cm2	Algae†	Aquatic vegetation†	Boulder (>25 cm)†	Organic matter†
Chilliwack_1	0.00	0.02	1.64	171.02	0.00	0.80	0.00	0.02
Chilliwack_2	0.00	0.02	1.80	94.16	0.01	0.40	0.01	0.04
Chilliwack_3	0.02	0.02	1.25	133.38	0.00	1.05	0.00	0.02
Chilliwack_4	0.00	0.02	1.29	117.73	0.74	1.09	0.00	0.00
Chilliwack_5	0.00	0.02	1.31	na	0.19	1.15	0.00	0.00
Chilliwack_6	0.02	0.03	1.21	82.27	0.37	0.53	0.00	0.00
Chilliwack_7	0.00	0.03	1.33	81.42	0.11	0.64	0.00	0.09
Chilliwack_8	0.01	0.02	1.92	123.11	0.10	0.27	0.06	0.10
Chilliwack_9	0.00	0.04	1.34	122.11	0.87	0.04	0.06	0.00
Coquitlam _1	0.00	0.02	3.29	47.17	0.00	0.83	0.04	0.03
Coquitlam 2	0.00	0.01	5.41	98.13	0.00	0.10	0.05	0.35
Coquitlam 3	0.00	0.02	2.95	97.63	0.00	0.00	0.18	0.02
Coquitlam _4	0.00	0.08	2.17	237.36	0.00	0.28	0.00	0.03
Seymour_1	0.00	0.01	0.85	95.38	0.00	0.09	0.00	0.17
Seymour_2	0.01	0.01	0.95	129.35	0.00	0.38	0.00	0.09
Seymour_3	0.00	0.01	4.49	66.99	0.00	0.27	0.02	0.20
Seymour_4	0.00	0.02	0.76	49.09	0.00	0.31	0.00	0.32

* Average for warmest consecutive 7-day period † Proportion of survey points

Table 5.1 cont.

Watershed pend #	Dingrian aquart	Woodt	Coefficient of	Maximum dapth (am)	Depth at water's
watersneu_ponu #	Ripanan cover j	woou	variation in depth	Maximum depth (cm)	edge (cm)
Chilliwack_1	0.03	0.17	0.48	235	5.70
Chilliwack_2	0.01	0.57	0.67	179	1.83
Chilliwack_3	0.00	0.05	0.53	177	28.10
Chilliwack_4	0.00	0.35	0.76	390	1.67
Chilliwack_5	0.04	0.17	0.51	156	1.38
Chilliwack_6	0.17	0.32	0.52	171	0.86
Chilliwack_7	0.20	0.42	0.56	261	9.00
Chilliwack_8	0.00	0.65	0.78	241	4.17
Chilliwack_9	0.15	0.25	0.54	185	9.17
Coquitlam _1	0.12	0.69	0.57	218	0.00
Coquitlam _2	0.12	0.70	0.5	248	5.10
Coquitlam _3	0.01	0.98	0.95	351	4.50
Coquitlam _4	0.00	1.00	0.62	174	4.75
Seymour_1	0.01	1.43	0.72	224	24.60
Seymour_2	0.04	0.91	0.43	87	0.00
Seymour_3	0.01	0.68	0.68	227	11.17
Seymour_4	0.08	1.38	0.51	152	0.75

* Average for warmest consecutive 7-day period † Proportion of survey points

Seymour (n = 4)] met our criteria and were used in this study (Figure 3.1). Land use surrounding the restored floodplain ponds is primarily forested or agricultural with residential areas nearby. The study sites were located at altitudes ranging from 10 to almost 400 m above sea level and receive an average of between 1500 and 2200 mm of rain annually (http://pacificclimate.org/docs/publications/GVRD.RainfallUpdate.pdf).

5.2.2 Vertebrate Sampling

We sampled ponds three times, (1) May-June 2006, (2) late July-August 2006, and (3) February-March 2007, prior to freshets that would initiate the outmigration of coho smolts. We selected these study periods to increase the likelihood of detecting species that are present in ponds only for certain life stages (Roberge & Angelstam, 2004). For instance, some frog and salamander species are primarily present in ponds when they are breeding or as larvae [e.g., northern red-legged frog (*Rana aurora*), northwestern salamander (*Ambystoma gracile*), rough-skinned newt (*Taricha granulosa*)], although they may still be present as adult frogs or as neotenic adults (e.g., northwestern salamander).

We set between 30 and 50 minnow traps baited with salmon roe in perforated film canisters in each pond in each of the three sampling periods. The total number of traps used was determined based on the ponds' size and complexity and normalized to trap night. We used a visual assessment of pond features, including depth, aspect, riparian structure and aquatic structure, to divide each pond into sections for sampling purposes. This ensured coverage of all habitat types in the pond (Olson et al., 1997). Approximately the same numbers of traps were set haphazardly in each sampling area. We identified, counted, weighed and measured all captured fish (fork length for salmonids or total) and amphibians (snout vent and total length) (Barbour et al., 1999; Corkran & Thoms, 2006). Fish were anesthetized using buffered MS222 prior to being measured and weighed. We received approval by the University of British Columbia Animal Care Committee and obtained all necessary federal and provincial trapping permits.

For watershed and pond level analyses, average abundance and biomass were calculated by dividing the total number or biomass of individuals captured in a pond by the total number of traps used in that pond in a sampling period resulting in relative abundance or biomass normalized by trap night. The results for the three sampling periods were then averaged. For estimates of relative abundance and biomass by microhabitat type, the number or biomass of individuals associated with a particular microhabitat type was divided by the total number of traps set in that habitat type in that sampling period resulting in relative abundance or biomass in each habitat type normalized to trap night.

In some sampling periods a large number of individuals of some species [e.g., threespined stickleback (*Gasterosteus aculeatus*) and northwestern salamanders] were captured. In those instances after more than 15 individuals of one species were captured, we measured the first five individuals in each subsequent habitat unit and any additional individuals were assigned to length classes (e.g., 4 - 5 cm). We estimated biomass for unweighed individuals by assigning them the mean biomass for conspecific individuals measured in their length class in that sampling period. We did not use mass–length regressions to estimate biomass because the regression equations calculated negative masses for the numerous small individuals (fry) that could not be accurately weighed and were therefore assigned an estimated mass (0.1 g). Moreover, because length was estimated to length class, not

measured, the regression would have been based on the central tendency (i.e., individuals classified as 4 - 5 cm long would enter the regression as 4.5 cm) resulting in similar estimates to those based on mean biomass. In some instances, fish and amphibians escaped prior to measurement. They were assigned to length categories and their biomass was also estimated, although with greater uncertainty if no other individuals of their size class were measured, in which case the average for that species across all ponds in that sampling season was used to estimate biomass.

5.2.3 Watershed, Pond and Trap-scale Habitat Characteristics

We used seven parameters to characterize study ponds at the watershed scale: watershed area, elevation at the highest point in the catchment, slope from the highest point in the catchment to each pond, and percent land coverage of forests, river, wetland/lake and roads within 1 km. Percent forests, river, wetland/lake and roads within 1 km of each pond were generated using GIS. We used landcover data from an ArcGIS file geodatabase called veg_comp_lyr_r1_poly.gdb (Vegetation Resources Inventory (VRI) - Forest Vegetation Composite Polygons and Rank 1 Layer) acquired from the British Columbia Land and Resource Data Warehouse (LRDW). This file-based geodatabase contains vegetation cover from the BC Ministry of Forests. All "treed" and "shrub" categories were summed to create the forested category. Roads, streams and waterbodies (lakes and ponds) were from the Corporate Watershed Base (CWB), formerly known as TRIM Watershed Atlas (TWA) (scale 1:20,000). Buffers were added to linear features to estimate area for small streams and roads, represented only as lines in the GIS. Specifically, a 2 m buffer was added to each side of the lines representing streams and a 4 m buffer was added to each side of lines representing

roads. These features were then clipped to measure only the sections in 1 km pond buffers and the area of each resulting polygon was recalculated and the associated data exported to tables for further analysis. ArcGIS was used for all the GIS operations. Slope was calculated by subtracting the elevation of each pond from the elevation at the top of the catchment and dividing by the distance between the two points. The distance between the points was estimated by approximately following the path of the river using the path tool in Google Earth (Version 3.0, Google Inc., Mountain View, CA). Catchment area was reported in government reports (GVRD, 1999; FVRD, 2005).

We documented pond-scale habitat structure in July and August 2006 using standard techniques of Anonymous (1995) and Johnston and Slaney (1997). The presence of aquatic (e.g., large wood - diameter >10 cm, algae, overhanging banks, aquatic vegetation) and riparian cover and water depth were recorded every metre along the length of four to six equidistant transects of each pond (number of transects determined by the size of the pond). The proportion of all measurements for each structural component per pond was calculated by dividing the number of times a given component was documented by the total number of measurements from that pond (e.g., 30 readings with large wood out of a total of 100 readings = 0.3). All ponds had predominantly fine (i.e., muddy) substrate except at stream inlets where substrate tended to be gravels and small rocks. We placed temperature loggers at two depths (approximately 30 cm and 100 cm below the surface of the water) in each of the ponds from May or June 2006 to July 2007. Some data loggers were lost or malfunctioned, particularly from August 2006 to February 2007 when minimum water temperatures were most likely to have occurred. As such, we relied exclusively on maximum temperatures calculated as the average temperature of the warmest consecutive seven-day period. Many

ponds had inaccessible shorelines, therefore we estimated pond area using the area estimation function of Google Earth (Version 3.0, Google Inc., Mountain View, CA).

Microhabitat structure (i.e., trap scale), including algae, aquatic vegetation, boulders (i.e., rocks >25 cm in diameter), wood (large wood, rootwads/snags), undercut banks, riparian cover and other cover (e.g., bridges, culverts), within 2 m of the trap in any direction was recorded when each trap was set. If any of those elements were visible, they were counted as present. The substrate below and the depth of each trap were also recorded. Only microhabitat features present at >10% of the traps (i.e., algae, aquatic vegetation, boulders, wood and riparian cover) were used in statistical analyses.

5.2.4 Statistical Analysis

We evaluated environmental variables at three habitat scales, watershed, pond and microhabitat (trap) and two biological attributes of aquatic vertebrates, abundance and biomass. The degrees of freedom varied depending on the scale of the analysis. The unit of replication for the watershed and pond scale habitat variables was pond with a sample size of 17 and for microhabitat scale analyses trap was the unit of replication with a maximum sample size of 1259. The sample size (and degrees of freedom) was less for some analyses depending on what habitat features or species were present. The variation in average abundance and biomass of all species explained by environmental variables at the watershed and pond scale were tested jointly (all environmental variables together) using canonical correspondence analysis (CCA) and independently (environmental variables individually) using general additive models (ter Braak & Smilauer, 2002) and general linear mixed models (PROC GLIMMIX). We also used CCA to compare the amount of variation explained at

different scales. To do this we paired habitat variables at the watershed, pond and microhabitat level with abundance and biomass associated with each trap and compared the percent of variation explained by each habitat scale.

Detrended correspondence analysis (DCA) indicated that the gradient length for species abundance and biomass aggregated by pond ranged from 0.9 to 2.7 and 0.9 to 2.6 respectively at the and at the trap level they ranged from 3.6 to 5.5 for abundance and 3.5 to 4.6 for biomass. In order to enable comparisons amongst the three scales, we used canonical correspondence analysis (CCA), recommended for unimodal data (DCA gradients >3), to evaluate the relationship between species abundance and biomass and habitat variables (ter Braak & Smilauer, 2002) (CANOCO 4.5). Data were not transformed to meet the assumptions of normality as the ordination uses a Monte Carlo analysis that does not assume a normal distribution, however, the original species data included many zeros so we used a log (x+1) transformation for species data (ter Braak & Smilauer, 2002). We used Hill's scaling, suitable for unimodal response, based on the distance rule which extends the centroid principle and takes a species' point as the optimum of its unimodal response (ter Braak & Smilauer, 2002). We used a global Monte Carlo permutation test (499 permutations) to calculate the percentage of the total variance (i.e., inertia) of species data explained by habitat variables, and to determine the statistical significance for the first canonical axis alone and for all four axes together. Watershed was treated as a covariable.

General linear mixed models and ordinations were considered significant at alpha = 0.1 to reduce the likelihood of a type II error, i.e., rejection of the null hypothesis that there was an effect when a real effect may have existed, which would be more likely with alpha = 0.05 because of large sampling variability or small sample size (Peterman, 1990; Bryant,

2004). Correlations between each axis and habitat variables were considered significant (P < 0.05) at a critical value of r = 0.48 for watershed and pond level data (n = 17) and r = 0.08 for trap level data (n = 1259). The level of significance was lower for correlations in order to facilitate the interpretation of the large number of significant correlations, particularly for trap level data which had a large sample size. Ordination diagrams were used to illustrate the relationship of original species data with environmental variables. Arrow length corresponds to the importance of each habitat variable and direction indicates its correlation with the axes.

For each canonical axis, we determined which, if any, species had >25% of their variation in abundance explained by the joint habitat variables on one of the canonical axes. Species response curves were then generated between each of those species and the individual habitat variables correlated with that axis (ter Braak & Smilauer, 2002). We used a generalized additive model with a Poisson distribution to determine the additional variance explained by the fitted model (i.e., the model with one habitat variable) compared to the null model, based on Akaike Information Criterion (AIC) values (ter Braak & Smilauer, 2002). This provides a basis for comparing what habitat feature best explained the variation in abundance or habitat of each species evaluated (ter Braak & Smilauer, 2002).

Species response curves were not used for trap scale habitat data because there were insufficient predictor values for habitat in the model as, with the exception of depth, the range of values for habitat were limited to absent (0) or present (1). Therefore, to evaluate the relationship between species abundance and biomass and habitat at the trap level we use PROC GLIMMIX, for nonlinear data. For each habitat feature, the abundance or biomass of each species was normalized to habitat-specific trap night (e.g., number of traps with or without wood) and summed by pond for each sampling period. We first tested the full model

including watershed and sampling event (pond) as random variables. If either random variable did not have an influence, the model was run without it. The degrees of freedom for each species and habitat type reflect the variability in the random terms included in the model as well as the number of individuals of each species and the number of traps in associated with each habitat type.

5.3 Results

5.3.1 Habitat and Species Overview

Ponds in Chilliwack had among the most and least forested area surrounding them (9 to 97%), Coquitlam had an intermediate to high percentage of forested watershed (63 to 98%) and Seymour had consistently highly forested land cover (90 to 97%) (Table 5.1). Chilliwack was the largest watershed (123,000 ha) (FVRD, 2005) followed by Coquitlam (20,461 ha)(GVRD, 1999) and Seymour (12,374 ha)(GVRD, 1999). Chilliwack had the highest percentage of river and wetland/lake coverage within 1 km of ponds and the lowest percent slope (Table 5.1). The pond with the most roads as adjacent landcover was in Coquitlam (8%), the least road coverage was in Seymour (1%), and Chilliwack had a consistently 2 to 3% of roadcover (Table 5.1). The steepest watershed was Coquitlam although there was a steep slope from the head of the watershed to one pond in Seymour (Table 5.1). Ponds in all watersheds ranged in elevation from low (11 m to 28 m) to mid (Coquitlam 124 m and Seymour 167 m) and high (Chilliwack 422 m). The ponds ranged in size from approximately 500 to 13000 m² and maximum temperatures ranged from 9 to 22°C based on the mean of the seven warmest consecutive days from June 2006 to June 2007 (Table 5.1). When classified by water source, average maximum temperatures were highest

for surface water fed (17.22 +/- 3.00° C), lowest for groundwater fed (13.48 +/- 5.53° C) and in between for combined watersource (15.73 +/- 0.30° C). The specific habitat in ponds was variable (Table 5.1). Two habitat categories were comprised of more than one element (wood = large wood and rootwads/snags, aquatic vegetation = submerged and emergent vegetation) therefore the proportion of that habitat type could exceed 1.

A total of 20 vertebrate species were trapped in a total of 1259 traps. A number of species had very low abundance and/or distribution among ponds (Appendix D, Tables D.1 and D.2). To be included in statistical analyses, a species had to represent at least 1% of the total number of individuals collected and be present in at least three ponds. The resulting species list included four salmonids [coho, cutthroat trout (*O. clarki*), Dolly Varden (*Salvelinus malma*) and rainbow trout (*O. mykiss*)], sculpin (*Cottus* sp.), three-spined stickleback and three amphibians [green frog (*Lithobates clamitans*), northwestern salamander and northern red-legged frog]. Three-spined stickleback was the most abundant species (Figure 5.1). In contrast, coho, Dolly Varden, three-spined stickleback and northwestern salamanders all contributed fairly evenly to biomass (Figure 5.1).

5.3.2 Comparison of Variance Explained by Watershed, Pond and Microhabitat Data

Using CCA, pond-scale environmental variables accounted for more variance in average species abundance (68%) and biomass (79%) than watershed variables (44% and 58%, respectively), however, this was only significant for the first axis of the biomassenvironmental relations at the pond level (Table 5.2). Though the amount of variance



Figure 5.1. Percent of total abundance or biomass of species trapped in restored off-channel ponds.

explained was much lower using trap level data, pond level environmental variables again accounted for more variation in average abundance and biomass (each at 13%) than did either paired watershed (8% for both) or trap level (respectively 2% and 1%) environmental variables and the species environment relation was significant at all scales (Table 5.2). The covariable watershed accounted for between 7 and 22% of the variance in species abundance and 5 to 13% for biomass.

5.3.3 Watershed Scale

The first environmental axis was significant at the watershed scale for average abundance (i.e., catch per unit effort) (F = 4.288, P = 0.05) and biomass (F = 4.256, P = 0.06), and all four axes were significant for average biomass (F = 2.328, P = 0.01) but not for abundance (F = 1.466, P = 0.144) (Table 5.2). The amount of forested area and elevation were correlated with axis 1 for abundance (r = 0.73 and r = 0.90) and biomass (r = 0.70 and r = 0.79) and the amount of wetland lakes within 1 km was negatively correlated with axis 1 for average biomass only (r = -0.49) (Figs 5.2 and 5.4). Watershed area was correlated with axis 2 for average abundance (r = 0.71) and on axes 2 and 3 for biomass (r = 0.62 and r = -0.51, respectively). Percent road as land cover (r = 0.51) and percent slope (r = -0.55) were correlated with axes 3 and 4 for abundance. The percent of forested landcover within 1 km of a pond was negatively correlated with percent river land cover (r = -0.70) and positively correlated with elevation (r = 0.70). Watershed area was positively correlated with percent river cover (r = 0.54) and negatively correlated with percent slope (r = -0.63). No other variables were correlated at the watershed scale.

Five of the nine species we evaluated had more than 25% of the variance in their average abundance or biomass explained by axis 1 and no species had more than 25% of the variability in their abundance explained by the other canonical axes (Table 5.2). The abundance and/or biomass of coho, Dolly Varden and sculpin had generally positive relationships with percentage of forested landcover (Table 5.3, Figs 5.3a and 5.5a). Three-

Table 5.2. Percentage of total variance of species abundance (individuals per trap night) and biomass (g per trap night) explained by environmental variables using canonical correspondence analysis (CCA). The significance of the relationship between species data and the first and all four canonical ordination axes is reported. Total variance is the sum of variance explained by the four axes, watershed (covariable) and unexplained variance. For (1) watershed and (2) pond level analyses average abundance and biomass were calculated by dividing the total number or biomass of individuals captured in a pond by the total number of traps used in that pond in a sampling period resulting in relative abundance or biomass normalized by trap night. In (3) watershed, (4) pond and (5) microhabitat analyses the total abundance and biomass for each trap was the untransformed number or biomass of individuals in each trap.

Variance	Eigenvalues	% of total variance	Eigenvalues	% of total variance					
A	verage abundance (ind	ividuals per trap night)	Average biomass (g per trap night)					
(1) Landscape so	(1) Landscape scale environmental variables								
1st axis	0.32	27*	0.32	30*					
sum 4 axes	0.51	44	0.65	58**					
watershed	0.26	22	0.11	13					
unexplained	0.40	34	0.12	14					
total inertia	1.16	100	0.88	100					
(2) Pond level er	vironmental variables								
1st axis	0.37	31	0.34	38**					
sum 4 axes	0.79	68	0.69	79					
watershed	0.26	22	0.11	13					
unexplained	0.12	10	0.07	8					
total inertia	1.16	100	0.88	100					
	Individual	Biomass (g) per trap							
(3) Landscape s	numuuu sale environmental vari	ahlas	Diomass						
(5) Lanuscape so		6***	0.27	۲***					
sum 4 aves	0.30	8***	0.27	8***					
watershed	0.42	7	0.40	5					
unevolained	4 37	85	4 84	87					
total inertia	5 14	100	5 54	100					
(4) Pond level er		100	0.04	100					
1st axis	0 345	7***	0.35	6***					
sum 4 aves	0.64	, 13***	0.00	13***					
watershed	0.352	7	0.28	5					
unexplained	4 12	, 80	4 53	82					
total inertia	5 136	100	5 54	100					
(5) Microhabitat	(trap) level environmen	tal variables	0.01	100					
1st axis	0.081	2***	0.03	1***					
sum 4 axes	0.128	-2***	0.08	1***					
watershed	0.352	- 7	0.28	5					
unexplained	4.656	91	5.18	93					
total inertia	5.136	100	5.55	100					
* 0.4 *** 0.4									

* p=0.1, ** p =0.05, ***p=0.01, **** p <0.001



Figure 5.2. Canonical correspondence analysis ordination of average species abundance and watershed scale environmental variables. Species with >25% of their variation explained and environmental variables significantly correlated with either axis are marked with * for axis 1 and † for axis 2. Species are italicized and environmental features are bolded.



Figure 5.3. Fitted regression models using a generalized additive model with a Poisson distribution for species abundance and (a) % forested landcover within 1 km of restored pond and (b) elevation.



Figure 5.4. Canonical correspondence analysis ordination of average species biomass and watershed scale environmental variables. Species with >25% of their variation explained and environmental variables significantly correlated with either axis are marked with * for axis 1 and † for axis 2. Green frog, which was located in the top of the top left close to -2 horizontal and 5 vertical, was excluded from the figure, but not the analysis, as it compressed the centre of the figure. Species are italicized and environmental features are bolded.

spined stickleback increased in abundance as forested landcover approached 25% and then decreased sharply with additional forested land cover (Tale 5.3, Fig 5.3a) and biomass declined steadily as the amount of forested landcover increased (Table 5.3, Fig 5.5a). Dolly Varden abundance and biomass increased as elevation increased (Figs 5.3b and 5.5b). Northern red-legged frog abundance and sculpin biomass also had positive relationships with



Figure 5.5. Fitted regression models using a generalized additive model with a Poisson distribution for species biomass and (a) % forested landcover within 1 km of restored pond, (b) elevation and (c) % wetland /lake landcover within 1 km.

Table 5.3. Fitted regression models for individual species with greater than 25% of their variation in abundance or biomass explained by an environmental axis and habitat features that were significantly correlated with an environmental axis. Separate analyses were conducted for watershed and pond scale habitat variables. A generalized additive model with a Poisson distribution was used to determine the additional variance explained by the fitted model (i.e., the model with one habitat variable) compared to the null model, based on Akaike Information Criterion (AIC) values (ter Braak & Smilauer, 2002).

				% improvement
Variable	Species	Null model	Fitted model	over null
	Landscape scale	abundance		
forested land cover	coho salmon	23.53	16.01	32*
	Dolly Varden	4.28	1.29	70*
	three-spined stickleback	108.48	29.93	72****
elevation	Dolly Varden	4.28	2.95	31*
	three-spined stickleback	108.48	72.38	33**
	red-legged frog	0.95	0.44	54***
	Landscape scal	e biomass		
forested landcover	coho salmon	59.81	36.06	40**
	sculpin	61.63	43.97	29*
	three-spined stickleback	115.15	90.91	21*
elevation	Dolly Varden	150.63	81.22	46**
	sculpin	61.63	41.02	33**
wetland	Dolly Varden	150.63	103.52	31*
	three-spined stickleback	115.15	87.17	24**
	Pond scale ab	undance		
coefficient of variation	coho salmon	23.53	13.24	44***
or depth				
maximum temperature	coho salmon	23.53	12.09	49***
	Dolly Varden	4.28	2.27	47**
	sculpin	1.76	0.86	51****
	three-spined stickleback	108.48	68.49	37**
	Pond scale b	iomass		
coefficient of variation	coho salmon	59.81	35.73	40**
of depth	sculpin	61.63	40.8	34**
	three-spined stickleback	115.15	57.62	50***
area	Dolly Varden	150.63	65.67	56***
	three-spined stickleback	115.15	38.04	67****
wood	coho salmon	59.81	31.9	47***
* p=0.1, ** p =0.05, ***p	=0.01, **** p <0.001			

elevation initially followed by declines (Table 5.3, Figs 5.3b and 5.5b). Three-spined stickleback biomass had a positive relationship and Dolly Varden had a positive, then negative relationship with the amount of wetland/lake land cover (Table 5.3, Fig 5.5c).

5.3.4 Pond Scale

Neither the first (F = 1.348, P = 0.26) nor any of the other environmental axes (F = 1.009, P = 0.47) explained significant variation in species abundance at the pond scale (Fig 5.6). The first environmental axis explained 38% of total variance in biomass (F = 1.577, P = 0.05) but together all environmental axis did not explain a significant amount of variation (F = 1.456, P = 0.23) (Table 5.2) (Fig 5.8). Axis 1 explained more than 25% of the variance in species abundance and biomass for coho, Dolly Varden, sculpin and three-spined stickleback. Axis 3 also explained more than 25% of the variance biomass of rainbow trout and northwestern salamander. At the pond scale algal production (measured as chlorophyll *a*) was lower in groundwater-fed ponds (r = -0.53), boulders were negatively correlated with aquatic vegetation (r = 0.64). Maximum depth was also negatively correlated with riparian cover (r = 0.48) and positively correlated with variation in depth (r = 0.53).

Coho abundance and biomass increased and three-spined stickleback and sculpin biomass decreased as depth became more varied in the ponds (Table 5.3, Figs 5.7a and 5.9a). The relative abundance of coho and Dolly Varden had a hump-shaped relation with temperature that peaked at about 10°C whereas the abundance of three-spined stickleback and sculpin had a positive relationship with temperature (Table 5.3, Fig 5.7b). The biomass of three-spined stickleback declined as pond area increased whereas Dolly Varden biomass increased to ponds of approximately 12,000 m² then began to decline (Table 5.3, Fig 5.9b). Wood had a significant negative relationship with three-spined stickleback biomass and a positive relationship with the biomass of coho until the average number of wood features increased to more than one wood element per transect point (i.e., >1.0, Table 5.1) (Table 5.3, Fig 5.9c).



Figure 5.6. Canonical correspondence analysis ordination of average species abundance and pond scale environmental variables. Species with >25% of their variation explained and environmental variables significantly correlated with either axis are marked with * for axis 1 and † for axis 2. Species are italicized and environmental features are bolded.



Figure 5.7. Fitted regression models using a generalized additive model with a Poisson distribution for species abundance and (a) co-efficient of variation of depth and (b) maximum temperature.



Figure 5.8. Ordination of average species biomass and pond scale environmental variables. Species with >25% of their variation explained and environmental variables significantly correlated with either axis are marked with * for axis 1 and † for axis 2. Species are italicized and environmental features are bolded.



Figure 5.9. Fitted regression models for species biomass and (a) co-efficient of variation of depth (b) area (m³), (b) and (c) proportion of wood.

5.3.5 Trap Scale

The first environmental axis explained significant variation for trap level abundance and biomass using watershed (F = 0.299, P = 0.01; F = 0.269, P = 0.01, respectively), pond (F = 0.345, P = 0.01; F = 0.347, P = 0.01, respectively) and trap (F = 0.081, P = 0.01; F = 0.031, P = 0.01, respectively) level environmental variables. All four environmental axes also explained significant variation in species abundance and biomass using watershed (F = 0.415, P = 0.01; F = 0.428, P = 0.01, respectively), pond (F = 0.664, P = 0.01; F = 0.737, P = 0.01, respectively) and trap (F = 0.128, P = 0.01; F = 0.081, P = 0.01, respectively) level environmental variables. The amount of unexplained variation in abundance and biomass, however, ranged from 80 to 93% (Table 5.2). Species response curves were not used to further evaluate relationships between species and habitat features because there were insufficient predictor values for habitat in the model as, with the exception of depth, the range of values for habitat were limited to absent (0) or present (1).

Using a general linear mixed model to evaluate the relationships between trap level abundance and biomass species data and trap level habitat data there were more significant relationships between species biomass and habitat type than between species abundance and habitat type. However in all instances, if the relationship between a species and a habitat variable was significant for abundance, it was also significant for biomass (Table 5.4). Coho, cutthroat trout, Dolly Varden and northwestern salamander biomass had significant relationships with four or five of the variables we evaluated, rainbow trout and three-spined stickleback had significant relationships with three variables followed by northern red-legged frog and sculpin with two and green frog with one significant relationship. In contrast there were zero to a maximum of two significant relationships between these species abundance and habitat variables (Table 5.4).

There were two to fifteen times more coho, Dolly Varden and rainbow trout where there was algae near traps than where there was no algae. Similarly there was a 2 to 15-fold increase in biomass of all salmonids in the presence of algae compared to no algae. Threespined stickleback biomass was also higher in the presence of algae but the increase in biomass over traps with no algae was modest (1.5x). Species' responses to aquatic vegetation

Table 5.4. Analysis of relationships between abundance and biomass and microhabitat with season and watershed as repeated measures as appropriate (i.e., if there was an effect associated with season or watershed). Mean and standard deviation (in parentheses) of abundance and biomass is shown for all traps that captured each species with and without a given habitat features (i.e., algae, aquatic vegetation, boulder, wood and riparian cover). Degrees of freedom vary according to how many traps were occupied by each species and whether or not season or watershed were used as repeated measures in the analysis.

Species	Abund	ance (individuals per trap	o night)	Biomass (g per trap night)			
		no algae	algae		no algae	algae	
coho salmon	F1,37 = 7.62†‡	3.35 (4.21)	7.57 (7.86)***	F1,35 = 31.47†	11.57(11.9)	23.58 (26.94)****	
cutthroat trout	F1,15 = 0.19	0.1 (0.08)	0.2	F1,7 = 11.11†‡	5.9 (5.28)	11.72***	
Dolly Varden	F1,10 = 15.66†	0.62 (0.5)	4.55 (0.78)***	F1,10 = 343.50†‡	25.11 (15.79)	184.12 (40.17)****	
rainbow trout	F1,19 = 4.36†	0.15 (0.15)	2.37**	F1,9 = 36.37†	4.29 (7.28)	88.71****	
sculpin	F1,22 = 0.02†	3.74 (0.28)	0.13 (0.09)	F1,14 = 0.56†	12.32 (8.75)	4.27 (2.31)	
three-spined							
stickleback	F1,22 = 1.33†‡	16.59 (14.99)	14.75 (11.96)	F1,22 = 6.25†‡	17.21 (13.48)	25.83 (23.16)**	
green frog	na	na	na	na	na	na	
nw salamander	F1,31 = 0.09†	0.7 (0.85)	0.13	F1,19 = 0.18†	11.02 (15.29)	4.56	
red-legged frog	F1,20 = 0.04†	0.25 (0.28)	0.2	F1,9 = 0†	0.55 (0.7)	0.34	
		no aquatic vegetation	aquatic vegetation		no aquatic vegetation	aquatic vegetation	
coho salmon	F1,62 = 3.28†‡	2.53 (0.72)	2.31 (0.6)*	F1,62 = 25.63†‡	13.84 (18.36)	8.01 (9.56)****	
cutthroat trout	F1,17 = 0.01	1.5 (0.76)	1 (0)	F1,9 = 28.09†	5.16 (5.23)	9.46 (13.22)****	
Dolly Varden	F1,16 = 0.17	2.33 (1.03)	1.33 (0.58)	F1,11 = 15.32†	32.72 (33.31)	5.67 (5.29)***	
rainbow trout	F1,20 = 0.00	1.75 (0.71)	1 (0)	F1,10 = 1.65†	5.12 (8.8)	2.73 (2.27)	
sculpin	F1,27 = 0.87	1.78 (0.97)	1.86 (0.69)	F1,20 = 1.63†	9.17 (9.77)	7 (6.11)	
three-spined							
stickleback	F1,37 = 2.04†	2.6 (0.84)	2.75 (0.46)	F1,37 = 0†‡	14.3 (12.83)	14.31 (11.74)	
green frog	F1,11 = 0.25	1.67 (0.58)	2.67 (0.58)	F1,9 = 2.12†	0.54 (0.58)	2.83 (2.97)	
nw salamander	F 1,48 = 0.01	1.93 (0.73)	2.09 (0.7)	F1,34 = 17.53†	8.25 (13.82)	15.3 (24.71)****	
red-legged frog	F1,27 = 0.74	1.5 (0.71)	1.56 (0.53)	F1,16 = 0.56†	0.61 (1.02)	0.66 (0.84)	

Species	Abundance (individuals per trap night)			Biomass (g per trap night)			
		no boulder	boulder		no boulder	boulder	
coho salmon	F1,46 = 17.96†‡	3.3 (4.16)	4.95 (6.57)****	F1,46 = 41.74†‡	11.05 (12.21)	15.65 (18.05)****	
cutthroat trout	F1,15 = 0.12	0.13 (0.09)	0.14 (0.01)	F1,7 = 9.71†‡	6.87 (5.83)	8.28 (3.91)**	
Dolly Varden	F1,15 = 9.72	0.68 (0.57)	6.33 (na) ***	F1,10 = 98.82†	24.21 (21.46)	241.77 (na)****	
rainbow trout	F1,21 = 3.44	0.15 (0.13)	0.94 (0.75)*	F1,11 = 27.64†	3.11 (4.96)	19.13 (18.45)****	
sculpin	F1,21 = 0.13	0.28 (0.28)	0.32 (0.09)	F1,13 = 0.08†	9.84 (8.92)	12.16 (7.84)	
three-spined							
stickleback	F1,27 = 16.06†‡	17.41 (14.79)	6.12 (6.46)****	F1,27 = 15.11†‡	16.12 (11.31)	5.48 (4.22)****	
green frog	na	na	na	na	na	na	
nw salamander	F1,22 = 14.97	0.61 (0.64)	2.81 (3.22)****	F1,22 = 158.49†	9.21 (9.83)	46.3 (63.97)****	
red-legged frog	F1,20 = 3.05	0.21 (0.27)	1 (na)	F1,9 = 10.79†	0.55 (0.74)	3.07 (na)***	
		no riparian cover	riparian cover		no riparian cover	riparian cover	
coho salmon	F1,62 = 0.04†‡	2.65 (0.7)	2.33 (0.72)	F1,78 = 475.88†‡	11.83 (13.61)	10.84 (13.28)****	
cutthroat trout	F1,18= 0.1	1.88 (0.64)	1 (0)	F1,12 = 21.71†	9.07 (7.76)	4.41 (3.23)****	
Dolly Varden	F1,16 = 0.48	2.33 (1.03)	1.33 (0.58)	F1,15 = 570.03†	33.07 (33.83)	9.17 (3.98)****	
rainbow trout	F1,20 = 0.71	1.5 (0.71)	1.4 (0.55)	F1,15 = 11.9†	4.85 (9.19)	5.49 (6.71)***	
sculpin	F1,24 = 0.28	2.38 (0.74)	1.4 (0.55)	F1,20 = 328.95†‡	8.89 (8.06)	11.66 (6.1)****	
three-spined							
stickleback	F1,30 = 6.26†‡	2.78 (0.67)	1.78 (0.83)**	F1,39 = 165.67†‡	17.02 (11.5)	10.42 (6.82)****	
green frog	na	na	na	F1,12 = 7.93	4.65 (3.66)	2.1 (na)**	
nw salamander	F1,47 = 0.34	2.29 (0.73)	1.7 (0.82)	F1,44 = 527.14†	11.11 (14.84)	5.63 (6.44)****	
red-legged frog	F1,26 = 0.78	1.5 (0.67)	1.25 (0.46)	F1,19 = 26.81†	0.47 (0.72)	1.1 (1.18)****	
		no wood	wood		no wood	wood	
coho salmon	F1,69 = 0.46†‡	3.16 (3.74)	3.75 (4.82)	F1,71 = 5.47†‡	9.63 (10.3)	12.78 (14.64)**	
cutthroat trout	F1,17 = 0.03	0.09 (0.05)	0.18 (0.09)	F1,9 = 1.56†‡	8.56 (10.06)	8.88 (5.17)	
Dolly Varden	F1,19 = 0.29†	0.61 (0.43)	1.2 (1.23)	F1,14 = 34.83‡	17.9 (13.38)	44.72 (49.51)****	
rainbow trout	F1,24 = 0.02†	0.21 (0.22)	0.24 (0.16)	F1,13 = 0.49‡	4.53 (7.23)	5.9 (8.34)	
sculpin	F1,27 = 0.70†	0.26 (0.22)	0.51 (0.38)	F1,20 = 18.75†‡	8.73 (8.29)	15.63 (11.69)****	
three-spined							
stickleback	F1,39 = 0.09†‡	20.8 (14.48)	16.46 (14.59)	F1,39 = 0.01†	18.79 (10.88)	14.16 (11.45)	
green frog	F1,12 = 0.02†	0.6 (0.22)	0.59 (0.44)	F1,10 = 1.11‡	3.92 (2.82)	5.13 (0.27)	
nw salamander	F1,34 = 0.00†	0.86 (1.14)	0.74 (0.76)	F1,34 = 8.32‡	13.58 (20)	11.59 (13.54)***	
red-legged frog	F1,28 = 1.10†	0.5 (0.78)	0.16 (0.2)	F1,18 = 2.37†‡	1.17 (1.44)	0.49 (0.7)	

† repeated season ‡ repeated watershed

na not applicable, insufficient data * p=0.1, ** p =0.05, ***p=0.01, **** p=0.001

were variable. There was a significant decrease in coho abundance where there was aquatic vegetation but no other significant relationships for other species. Coho and Dolly Varden biomass were lower (respectively 1.7x and 5.8x) while cutthroat trout and northwestern salamander biomass was almost doubled in the presence of aquatic vegetation. There were no significant relationships between the amount of wood present and species abundance, however, coho, Dolly Varden and sculpin all had greater biomass (1.3x to 2.5x) in the presence of wood, and three-spined stickleback biomass was slightly lower in the presence of wood than where wood was absent. Three-spined stickleback was the only species whose abundance was affected by riparian cover, specifically it was almost half as abundant in areas with riparian cover compared to areas without. There was a significant relationship between biomass and riparian cover for every species. Rainbow trout, sculpin and northern red-legged frog had greater biomass under riparian cover and the remainder of the species had more biomass in areas without riparian influence. For cutthroat trout, Dolly Varden, green frog, northwestern salamander and northern red-legged frog there was at least a two-fold difference in biomass between traps with and without riparian cover. The presence of boulders had the most influence of all habitat variables measured. Coho, Dolly Varden, Rainbow trout and northwestern salamander were all more abundant in the vicinity of rocks of this size and three-spined stickleback were less abundant. There was no significant relationships between sculpin and rocks >25 cm and there were insufficient data to test this variable for green frog. All other species were heavier in the presence of rocks >25 cm, in some cases substantially so such for as Dolly Varden (10x more biomass).

5.3.6 Depth

Amphibian abundance and biomass were highest in waters ranging from 0 - 60 cm in depth (Fig 5.10). Coho, cutthroat trout and rainbow trout had the greatest abundance and biomass in traps set from 30 - 120 cm deep, though biomass was higher in traps at 60- 120 cm. Dolly Varden were most abundant and the highest biomass in traps set from 60 - 120 cm followed by deeper water (>120 cm) (Fig 5.10). Sculpin were most abundant in water 60-120 cm deep though there was an increase in biomass compared to abundance from 1 - 30 cm and from 120 - 240 cm compared to the between 30 and 120 cm in depth (Fig 5.10). Three-spined stickleback were most abundant and had the highest biomass at intermediate depths (30 - 120 cm) but biomass of three-spined stickleback in deeper waters >120 cm in depth was higher relative to the percent of abundance in deeper waters (12% of abundance >120 cm compared to 20% of biomass at those depths (Fig 5.10).

5.4 Discussion

The variable success and longevity of river restoration projects has been attributed at least in part to the insufficient consideration of limiting factors that operate at the watershed scale (Minns et al., 1996; Palmer, 2009; Beechie et al., 2010). There has also been a chronic lack of post-restoration monitoring or the use of experimental methods that would ideally provide information that would increase the success of restoration in the future (Bernhardt et al., 2005). In our study we were able to detect significant influences on the abundance and biomass of coho and other vertebrate species by watershed, pond and micro-habitat scale environmental features with our *post hoc* study of 17 off-channel



Figure 5.10. Percent of total (a) abundance and (b) biomass for each species by trap depth for all sampling seasons.

floodplain ponds restored primarily, if not exclusively, to provide overwintering and rearing habitat for coho. The abundance of coho varied widely among restored ponds indicating variable success of the restoration projects, at least for coho. The presence of 19 other vertebrate species in the ponds indicates that if habitat is restored, it will be occupied although the patterns of abundance and biomass varied by species.

5.4.1 Associations Between Species Abundance and Biomass and Habitat at the Watershed Scale

The importance of percent forested land (i.e., land not under agricultural, urban or residential use) found in our study, may be related to direct (e.g., sediment loads, water quality and quantity, urban and agricultural runoff) impacts on waterbodies within the watershed but may also represent a lack of development and a more intact and connected floodplain (Pess et al., 2002; Stephenson & Morin, 2009). Elevation, which was positively correlated with percent of forested area, may also represent a lack of development as well as somewhat lower water temperatures. Isolation of floodplains from rivers as well as isolation of habitats within floodplains can limit habitat available for salmon spawning and rearing (Beechie et al., 1994; Pess et al., 2002). Upland habitat is also important for amphibians that use ponds for only a portion of their lifecycle and contiguous upland habitat is important for the movement of amphibians which may vary breeding sites from year to year within a floodplain (Semlitsch, 2008; Ficetola et al., 2011). Like coho, Dolly Varden were more abundant in ponds in forested watershed and in general Dolly Varden abundance and biomass tended to parallel that of coho (Bryant & Woodsmith, 2009). Similarly three-spined stickleback and sculpin tended to have similar responses to watershed and pond scale habitat. Three-spined stickleback had unique relationships with several watershed scale variables. It had a negative association with forested land use, and had a positive relationship between biomass and watershed area and with the amount of wetland/lake landcover. It is not clear if three-spined stickleback distribution tended to be opposite that of coho at the watershed scale due to habitat, trophic interactions between three-spined stickleback and coho or other species, or other unmeasured variables.

5.4.2 Relationships Between Species Abundance and Biomass and Habitat at the Pond Scale

Groundwater fed side-channels and ponds have less variable temperature regimes and tend to stay cooler in summer and warmer in winter compared to surface-fed water channels (Morley et al., 2005). Warm temperatures in summer are associated with an increase in food requirements due to higher metabolic rates (Rimmer, Saunders & Paim, 1985; Welsh et al., 2001). In winter as temperature decreases, fish become slower increasing their vulnerability to predation in daylight and they reduce the amount of time they spend foraging in optimal day-time conditions (Peterson, 1982b; Metcalfe, Fraser & Burns, 1999; Giannico & Hinch, 2003). Increased size has been reported for coho in groundwater fed side-channels with warmer winter temperatures than in surface water fed channels (Giannico & Hinch, 2003) and increased density in ponds with lower minimum summer temperatures (Morley et al., 2005). Problems with temperature loggers in wintertime in our study precluded the analysis of abundance and biomass in colder temperatures. However, we found that coho and Dolly Varden both were more abundant, and three-spined stickleback and sculpin less abundant in ponds with lower maximum summer temperatures.

Increased coho smolt production and density have been associated with shallow, near shore areas (Swales & Levings, 1989; Irvine & Johnston, 1992). Roni et al. (2006b) did not find a significant relationship between coho length or density and depth, however, the maximum depths in that study were just over 1 m and may not have been sufficient to detect a depth effect. We found that coho were more abundant and had greater biomass in ponds with a greater variety of depths, however, the majority of abundance and biomass was

between 30 and 120 cm deep. In our study variation in depth was negatively correlated with maximum temperature, therefore it is not clear if the increased coho abundance and biomass and the decreased three-spined stickleback and sculpin biomass in ponds with more variation in depth was related to increased habitat complexity and cover associated with greater variety in depth or if it was associated with lower summer temperatures.

5.4.3 Relationships Between Species Abundance and Biomass and Habitat at the Microhabitat Scale

We found only one study that evaluated the relationship between coho and specific habitat features in restored floodplain ponds (Roni et al., 2006b). Historic coho smolt trapping data from constructed and natural side-channels and floodplain ponds (e.g., reconnected relict channels, excavated borrow pits) were used to test correlations between coho productivity, density and smolt length and distance to salt water, escapement, habitat area, shoreline irregularity, depth and percent cover (Roni et al., 2006b). Variation in smolt length was explained by distance to salt water, shoreline irregularity and percent cover and abundance was positively correlated with wetted area. While the kind and extent of cover were documented, relationships between biological parameters and particular kinds of cover (e.g., aquatic vegetation, wood, undercut banks), which may be important in restoration design, were not evaluated. In our study the microhabitat variables we evaluated were all associated with food and cover, with the exception of depth. Algae, aquatic vegetation, boulders, wood and riparian vegetation all provide food resources, directly in the instance of algae and aquatic vegetation, and indirectly for the others by providing substrate for invertebrates and biofilm. Both the abundance and biomass of salmonids were higher in the

presence of algae. This is consistent with studies in stream environments showing increased rates of coho growth in streams with higher autochthonous resources (i.e., primary productivity) and green algae that supported grazing insects (Bilby & Bisson, 1987). Autochthonous materials such as algae and algal detritus, are generally more nutritious and digestible than terrestrial plant material (Bilby & Bisson, 1992). A stomach contents analysis of coho in summer found taxa that rely heavily on algae or algae-derived detritus, whereas terrestrial insects were not found to be an important component of the juvenile coho diet (Bilby & Bisson, 1992; but see Allan et al., 2003). Three-spined stickleback were not more abundant but did have higher biomass where there was algae.

A positive relationship between primary productivity and invertebrate productivity would explain an increase of biomass in areas without a riparian influence as we observed for six of the nine species we evaluated. However, the biomass of rainbow trout, sculpin and northern red-legged frog were significantly higher under riparian cover. For northern redlegged frogs this may be due to the fact that adults, which have higher biomass than aquatic larval stages, tended to occur near the shoreline. It is not clear why sculpin and rainbow trout biomass was high under riparian cover as for rainbow trout we would anticipate a similar response to food resources as other salmonids and there is evidence that sculpin also respond similarly to food resources as coho (Bilby & Bisson, 1992).

Wood provides a source of cover for fish (Bustard & Narver, 1975a; Bustard & Narver, 1975b) and may mediate inter- and intra-species interactions such as competition and predation. Wood also provides structure for retaining organic matter that is incorporated into detrital food pathways though this may be less important in lentic than lotic environments (Bryant, Edwards & Woodsmith, 2005). Wood can be colonized by invertebrates and algae

providing a food resource (Johnson, Breneman & Richards, 2003; Bond et al., 2006). The positive influence of wood on coho and other salmonid abundance, length and growth rates is reported throughout the literature for stream environments (e.g., Bilby & Bisson, 1987; Giannico & Hinch, 2003). However, in a study of constructed side-channels there was no correlation between coho density and wood density (Morley et al., 2005). Our results were consistent with the majority of these studies as we found the biomass of coho and Dolly Varden, as well as sculpin, were higher in the presence of wood suggesting that wood provided benefits associated with cover and food to salmonids. It is not clear why northwestern salamanders had higher biomass where wood was not present, but the response of salmonids and non-salmonids [e.g., sculpins, lamprey, giant salamanders (*Dicamptodon* spp.)] to wood has been reported to be variable (Roni, 2003).

Boulders are used to create structures in streams to increase habitat heterogeneity including variability in depth, substrate, cover and water velocity. The effect of boulder placement on the productivity of fish and invertebrates has been reported to be variable (Negishi & Richardson, 2003; Roni et al., 2006a). We found a positive relationship between the proximity to boulders and biomass for all salmonids as well as northwestern salamanders and northern red-legged frog. Of these species there were no significant relationships between abundance and boulders for cutthroat and northern red-legged frog. Three-spined stickleback alone had higher abundance and biomass where there were no boulders. Although we did not study inter-specific interactions, this may be associated with competition or predation by other species that were present near boulders. Boulders may provide cover for fish and benthic invertebrates and a substrate for algae or biofilm. Though we did not measure benthic invertebrates associated with or algae or biofilm on boulders, it is

plausible that the positive relationship between boulders and vertebrate biomass was associated with an increased food source.

Aquatic vegetation provides both cover and food primarily as substrate for epiphytic algae and invertebrates (Smokorowski & Pratt, 2007). The value of aquatic vegetation as habitat is highest at intermediate densities where it provides cover but does not impede movement or efficiency in predation or grazing (Smokorowski & Pratt, 2007). Unlike wood or boulders aquatic vegetation does not provide a temporally (i.e., seasonally) stable substrate. The response to aquatic vegetation of species we evaluated was equivocal. Coho were less abundant and coho and Dolly Varden had lower biomass in vegetated microhabitat. In contrast cutthroat trout and northwestern salamander had almost twice the biomass near vegetation compared to those near unvegetated habitat.

5.4.4 What Measures Should be Used to Assess Restoration

Our results were consistent with a number of studies that have reported stronger relationships between fish biomass or length and habitat than between abundance and habitat change (Roni et al., 2006b; Smokorowski & Pratt, 2007). This suggests assessments of species' responses to changes in habitat (restoration or otherwise) should not rely upon abundance counts alone. Using measures related to size or condition to evaluate the benefit of restoration projects can also be used to address the criticism that increased abundance or density may not mean that the restoration is successful and overall productivity is increasing but that individuals are simply redistributing themselves (Gowan & Fausch, 1996; Roni et al., 2005). If individuals are larger, and size has a positive relationship with survival, reproduction and, for coho, ocean survival (Bilton, Alderdice & Schnute, 1982; Peterson,

1982a), the improved condition of individuals would be evidence of a benefit of restoration or would indicate what habitat features are most effective.

5.4.5 Summary

Consideration of multiple scales of habitat provides insight into optimum conditions for restoration (Palmer, 2009; Beechie et al., 2010) and the identification of habitat features associated with a positive biological response of species of interest can facilitate the prioritization of sites for protection or restoration (Pess et al., 2002). The positive relationship between coho abundance and biomass and percent forested landcover in our study provides evidence of the importance of watershed scale variables in the placement of restoration projects. The similarity in patterns of abundance and biomass we observed across species with respect to microhabitat features suggests that watershed-scale factors act as coarse filters for community composition (Poff, 1997). In other words, if an individual species can get to a pond, it is likely to respond similarly as other species to habitat features, but watershed scale factors may determine if it can reach the pond. More generally, if local site and micro-habitat conditions are appropriate but land use or other watershed-scale variables are not, the restoration may not be successful (Frissell et al., 1986). Our study also provides specific input relevant to the design of restored ponds for coho such as the importance of moderating maximum summer temperatures through, for example, the use of groundwater (Giannico & Hinch, 2003) and/or riparian cover. It also indicates that the practice of creating a varied depth profile and placing wood (e.g., root wads, single logs, aggregates of logs) in ponds should continue to be implemented in future projects. Perhaps
most importantly this study demonstrates that valuable insight into restoration can be gained by studying patterns emerging from a broad study of restored systems (Holl et al., 2003).

Chapter 6: Conclusion

Restoration ecology has been called the "science of habitat and biodiversity recovery" (Young, 2000). It is ideally placed to utilize real world situations to test ecological theory pertinent to the recovery of biodiversity and in turn to use that theory to advance the practice of restoration. That the nexus between ecological theory and restoration practice is underdeveloped is likely due to the relative newness of this academic field and the growing urgency to reverse the degradation of natural systems and the loss of biodiversity that motivates restoration. Ouite simply, the practice of ecological restoration has not waited for theory to chart its course, and in many cases has not taken advantage of currently available theory (Palmer, 2009; Beechie et al., 2010). As a result there are untold numbers of restoration projects in ecosystems around the world for which post restoration monitoring and assessment is rare and the use of experimental manipulations to test the efficacy of restoration practices even rarer (Bernhardt et al., 2005). The need to strengthen the links between ecological theory and ecological restoration has been recognized and will ideally result in an increase in experimental tests of ecological theory using restored systems (Palmer, 2009). Testing theory in complex, natural systems will serve to benefit restoration if it contributes knowledge that increases the predictability of restoration practice and would potentially advance ecological theory, which is often tested in relatively simple controlled systems. While experimental manipulations may be an ideal way to do this, we must also find ways to utilize data that can be garnered from restoration projects that have already been conducted without an experimental framework.

6.1 Integration of Research

I used meta-analysis and a case study with a set of ponds restored for juvenile coho salmon (hereafter "coho") to test approaches and theories from the conservation and ecological literature that have relevance for how we plan, structure and assess restoration projects. Using meta-analysis to assess the efficacy of the umbrella species approach, I found that conservation strategies designed for an umbrella species generally benefit co-occurring species but that the endpoint that is typically measured, species richness, may not be as sensitive as abundance or density for detecting effects. This conclusion differs from those reported in qualitative reviews that conservation efforts designed for a single or small group of species does not reliably benefit co-occurring species (Caro, 2003; Roberge & Angelstam, 2004). The meta-analysis also indicated that commonly accepted criteria (e.g., body size, taxonomic similarity) (Fleishman et al., 2000; Seddon & Leech, 2008) used for the selection of umbrella species are not associated with greater benefits to co-occurring species and may not be useful for selecting candidate umbrella species in the future.

This was the first empirical study of the umbrella species approach that explicitly evaluated the relative magnitude of response of umbrella and co-occurring species in systems, restored or otherwise, along a gradient of environmental conditions. The case study evaluating the effectiveness of juvenile coho as an umbrella species indicated that species of conservation concern (cutthroat trout, Dolly Varden and northern red-legged frog) and fish generally benefitted from the restoration of ponds designed for coho, providing evidence that restoring habitat for one species may benefit other species (Lindenmayer et al., 2002; Roberge & Angelstam, 2004). Coho was more effective as an umbrella species for other fish

than for amphibians, and benthic invertebrate species richness and biomass were actually lower in ponds where coho were more abundant and had greater biomass. I used the congruence of patterns of abundance and biomass of coho and co-occurring species across ponds to assess the efficacy of coho as an umbrella species rather than using presence and absence of coho alone as is typically done in umbrella species studies. This allowed for the assessment of a gradient of response to a gradient of conditions and the identification of habitat features that were associated with greater abundance and biomass of coho and categories of co-occurring species. Testing for congruence of response of umbrella species and co-occurring species to specific aspects of a restoration or conservation design, such as habitat features or dispersal corridors, provides conservation practitioners an indication of what should be included in future restoration projects (Suter et al., 2002; Ozaki et al., 2006). In addition, the identification of habitat features associated with exotic species, bull frogs and green frogs, which were present in some ponds, provided some indication of habitat features that might be altered to make the restoration less hospitable to those species. This study provides support for using umbrella species in planning ecological restoration and further tests of this application of the umbrella species concept in other aquatic and non-aquatic systems is necessary to validate the approach. It is critical, however, that sufficient information on species responses (i.e., not just species richness) and potential mechanisms by which umbrella species confer benefits to co-occurring species should be explicitly evaluated.

The existence of a positive relationship between biodiversity and ecosystem function, though somewhat controversial, has been reported in a number of meta-analyses (Balvanera et al., 2006; Cardinale et al., 2006a; Cardinale et al., 2011). The strength of positive effects

increases with the number of ecosystem functions evaluated and the duration of experiments (Duffy, 2009). The majority of studies used in these meta-analyses use relatively simple experimental systems (e.g., few species, one or two trophic levels) and the need to test these relationships in natural, more complex environments has been identified for more than a decade (Loreau et al., 2001; Hooper et al., 2005; Cardinale et al., 2011). There has also been growing recognition of the need to evaluate the effects of species diversity on ecosystem function considering the role of habitat (Srivastava, 2006; Tylianakis et al., 2009).

This was the first test of the relationship between biodiversity and ecosystem function in a restored ecosystem and one of the few studies that have explicitly considered the role of habitat complexity in mediating that relationship (Srivastava, 2006; Tylianakis et al., 2009). I found evidence of a positive relationship between species diversity and standing biomass (a measure of ecosystem function), although that relationship was not consistent across taxonomic groups or with respect to the role of habitat complexity. Vertebrate biomass was higher where habitat complexity was higher, but benthic invertebrate and chlorophyll *a* biomass were lower where habitat was more complex. The divergent relationships with habitat complexity for different taxonomic groups illustrate the need to consider the role of habitat in future studies of biodiversity-ecosystem function and caution against assuming that increased habitat complexity will automatically confer higher function.

The restoration of physical structure is one of the most fundamental functions of ecological restoration. However, it cannot simply be assumed that biota will recover and benefit when habitat structure is restored (Hilderbrand et al., 2005). This is particularly an issue, for instance, for aquatic systems when restoration projects are implemented *ad hoc* rather than using a watershed approach that clearly defines degrading influences that have led

to the need for the restoration (Palmer, 2009; Beechie et al., 2010). Watershed-scale factors, such as those related to land cover and land use are important determinants of processes that may lead to stream degradation or recovery (Bernhardt et al., 2005; Lake et al., 2007). The particular attributes and configuration of the restored habitat at a local scale will also contribute to the biotic response of restoration. Despite the recognized importance of off-channel habitat for juvenile coho (Beechie et al., 1994; Solazzi et al., 2000), there has been little assessment of the efficacy of restoration projects in that environment (Morley et al., 2005).

This was the first study of the relationship between habitat features at different spatial scales and the biotic response of coho and other vertebrates in restored floodplain ponds. In this study watershed-scale habitat features (percent forested land) explained more variation in the abundance and biomass of vertebrates than pond level (e.g., average depth, groundwater influence) or microhabitat level (algae, riparian cover, wood) habitat attributes. The importance of watershed context is consistent with a number of studies that recommend prioritizing restoration sites based on watershed context and with a watershed perspective (Pess et al., 2002; Bryant, 2004; Stephenson & Morin, 2009).

The positive relationships between coho and algae, wood and temperature are consistent with the literature (Bilby & Bisson, 1987; Giannico & Hinch, 2003; Morley et al., 2005). However, structural components typically used in stream restoration such as the placement of large wood and boulders do not play the same kind of role in influencing morphology in ponds as they do in streams (Bryant et al., 2005; Roni et al., 2006a). This would suggest that the positive relationship I observed between wood and boulders and vertebrate biomass, and to a lesser degree abundance, may be associated with another

function such as providing substrate for algae or as structure for cover (Johnson et al., 2003; Bond et al., 2006). The positive relationships between vertebrate biomass and habitat features used in the restoration design are relevant to the criticism that restoration projects may simply aggregate individuals that would be using other available habitat otherwise rather than creating conditions that lead to a net increase in biota (Gowan & Fausch, 1996; Palmer, 2009). Regardless of whether or not the restoring habitat leads to a net increase in abundance, the fact that individuals have greater biomass in the presence of some habitat features may have implications for the population as there is generally a positive relationship between size, survival and reproduction (Bilton et al., 1982; Peterson, 1982b).

6.2 Management Implications and Applications

Large sums of money are spent on the restoration of freshwater systems with relatively little assessment of the effectiveness of those projects based on physical or biological responses (Bernhardt et al., 2005; Roni, 2005). Pacific salmon are the focus of much habitat restoration in the Pacific Northwest. Despite the fact that floodplain ponds in this region have been restored (primarily for juvenile coho) for more than two decades (Lister & Finnigan, 1997), studies into the effectiveness of those projects are far less common than their counterpart projects in flowing stream environments and rarely include species that were not the target of the habitat restoration (Roni, 2002). This study shows that slowmoving habitat can effectively be restored and occupied by coho and that the relative effectiveness of habitat restoration is associated with specific habitat characteristics within the pond or placement of the pond within the watershed. This study also demonstrates that a range of species may benefit from restoration projects designed primarily for the benefit of

one species. However, the ponds where coho were least abundant had exotic species in them [green frog (Lithobates clamitans), bullfrog (L. catesbiana)] that may have a deleterious effect on native fauna. Resource managers should consider the potential for unintended results of restoration projects, including shifts in community composition, to favor exotic species. The ponds with bull frogs and green frogs present tended to have less forested landscape around them, were at lower elevation and had higher maximum summer water temperatures than ponds that were effective for coho (i.e., higher coho abundance and biomass). Where restoration is being conducted primarily for juvenile coho, ponds should be designed to include substantial amounts of wood and have groundwater either as the primary water source or in combination with surface water to moderate temperature. Resource managers should consider the potential for such unintended effects and ensure that postrestoration monitoring includes at a minimum an assessment of the ecological community and associated habitat. Multiple endpoints (e.g., species richness, abundance and biomass) should be used in the effectiveness assessment of river (or any) restoration projects as different patterns may be revealed depending on the measurement endpoints utilized.

This study shows that a retrospective evaluation of non-experimental restoration projects can be used to validate restoration approaches and test theory. This is critical given the number of restoration projects that have been, and continue to be, conducted using nonsystematic or experimental approaches. Moreover, ecological restoration is all too often required in ecosystems that have been subject to unplanned impacts such as oil spills such as those in Prince William Sound, Alaska (Exxon Valdez) (Peterson et al., 2003) and in the Gulf of Mexico (Deepwater Horizon) (Mitsch, 2010) that require massive restoration with no control or opportunity for before and after studies. The use of a non-experimental approach

to evaluate the efficacy of restoration projects retrospectively and to test the application of ecological theory should be used more widely and would address the chronic lack of study of restoration projects (Bernhardt et al., 2005).

Conservation approaches and theories need to be empirically validated in the systems they are to be applied in. When this is done in the context of regional approaches to restoration, the investment in studying the response to restoration in a subset of sites may result in improvements to restoration design for other projects in the same region, to the extent similar biota and ecological constraints are present. For example, based on the results of the empirical umbrella species study and the assessment of biotic response to environmental features at several spatial scales, future floodplain pond restoration projects for coho should be located in forested areas with measures taken to moderate maximum temperatures (e.g., use of groundwater or riparian vegetation cover). This would serve to provide conditions associated with higher abundance and biomass of coho in this study and less amenable to exotic species such as bull frogs and green frogs that may have deleterious effects on native fauna such as coho and northern red-legged frogs.

6.3 Future Research

I have identified a number of specific approaches that would be beneficial to implement in future studies of ecological restoration. Specifically, testing questions along a gradient of environmental conditions can be sufficiently sensitive to detect biotic responses to restoration and to test questions related to ecological theory. A benefit to this study design is that it used a complex natural system instead of experimental manipulations that tend to minimize the degree of complexity in order to identify causal relationships. This addresses

concerns in the literature about a lack of empirical testing of the umbrella species approach (Roberge & Angelstam, 2004) and concerns that simplified experimental systems do not adequately reflect ecosystem function in real world environments (Duffy, 2009). The lack of a classic experimental framework should not prevent rigorous analysis, though conclusions regarding cause and effect may need to be tempered. Using multiple taxonomic groups, several complementary measurement endpoints as well as explicitly evaluating mechanisms (e.g., habitat) that may mediate the response to restoration can be used to reveal patterns that may not otherwise be apparent. Although the data required to conduct these more in depth analyses may be somewhat onerous, validation of the approaches used in ecological restoration now and in the future are imperative if restoration is to be successful.

In addition to these general recommendations for future work in this area, there are several specific areas for future research that emerged from this study. The umbrella species meta-analysis indicates there is potential for the umbrella species approach to be an effective conservation tool, but that the concept has been insufficiently tested, specifically with respect to what taxonomic groups have been evaluated. Future tests of the umbrella species concept should assess congruence of responses and not rely solely on species richness to assess the efficacy of the umbrella species approach and broaden taxonomic representation beyond the current focus on birds and mammals. The empirical evaluation of the potential for coho to act as an umbrella species was conducted in an aquatic system and all results will require validation in other habitats, as well as further testing in aquatic systems, to test the generality of the results. Aquatic systems are distinct from terrestrial systems in that they are more closed with relatively finite boundaries where the water ends, though those borders may shift seasonally, particularly in floodplain environments. Standing biomass is a simple measure of

ecosystem function and future assessments of biodiversity and ecosystem function in restored systems should include the evaluation of other, and multiple, functions including nutrient processing, system stability and resilience. Similarly, the use of measures such as functional diversity, a measure of diversity based on richness, evenness and divergence of functional traits to predict the consequences of species loss for ecosystem function (Schleuter et al., 2010; Villéger et al., 2010) should also be applied to restored systems where, ideally, diversity is being enhanced rather than eroded. Percent forested landcover within 1 km of a restored pond and elevation were both predictors of species abundance and biomass. Given the importance of watershed-scale habitat features, future studies may benefit from more detailed discrimination of habitat cover types and consideration of other factors such as habitat fragmentation and connectivity (Strayer & Dudgeon, 2010).

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Appendices

Appendix A Summary of Studies Used in Meta-analysis

					ing species								
					rich	ness							
											Umbrella		
				Co-							species		
		Umbrella		occurring	umbrella	umbrella				Across or	generalist		
		species		species	species	species	Sample			same	or	Size class	Trophic
Reference	Source	class	Umbrella species	class	present	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
Bifolchi and			European otter						(North				
Lode 2005	text	mammal	(Lutra lutra)	bird	59.00	62.00	18	1	America) riparian	cross	specialist	>10 - 20	carnivore
Bifolchi and			European otter						(North				
Lode 2005	text	mammal	(Lutra lutra)	amphibian	7.00	6.00	18	1	America) riparian	cross	specialist	>10 - 20	carnivore
Bifolchi and			European otter						(North				
Lode 2005	text	mammal	(<i>Lutra lutra</i>) Various	molluscs	23.00	24.00	18	1	America)	cross	specialist	>10 - 20	carnivore
			megafauna						forest				
Caro 2001	Table 1	mammal	(mammals) Various	mammal	5.00	6.00	25	1	(Africa)	same	generalist	>500	herbivore
Caro et al.			megafauna						forest				
2003	Table 6	mammal	(mammals) Various	mammal	0.57	1.73	24	1	(Africa)	same	generalist	>500	herbivore
Caro et al.			megafauna						forest				
2003	Table 5	mammal	(mammals)	mammal	11.00	6.00	20	1	(Africa) forest	same	generalist	>500	herbivore
Caro et al.			jaguar (<i>Panthera</i>						(Central				
2004	Table 2	mammal	onca)	amphibian	0.24	0.80	4	1	America) forest	cross	generalist	>50 - 100	carnivore
Caro et al.			jaguar (<i>Panthera</i>						(Central				
2004	Table 2	mammal	onca)	mammal	0.33	1.08	4	1	America) forest	same	generalist	>50 - 100	carnivore
Caro et al.			jaguar (<i>Panthera</i>						(Central				
2004	Table 2	mammal	onca)	mammal	0.78	0.74	4	1	America) forest	same	generalist	>50 - 100	carnivore
Caro et al.			jaguar (<i>Panthera</i>						(Central				
2004	Table 2	mammal	onca)	mammal	0.00	0.84	4	1	America)	same	generalist	>50 - 100	carnivore

					Co-occurr	ing species							
					rich	ness							
											Umbrella		
		المعامية		CO-	unabualla	unahualla				A	species		
		Umbrella		occurring	umbrella	umbrella	Sampla			Across or	generalist	Sizo class	Trophic
Reference	Source	class	I Imbrella species	class	species	species	sizo	Variance	Habitat	tava	u specialist	(kg)	lovol
Reference	Jource	01035	ombrena species	01035	present	absent	3120	variance	forest	taxa	specialist	(\\6/	level
Caro et al.			jaguar (<i>Panthera</i>						(Central				
2004	Table 2	mammal	onca)	bird	9.17	11.30	4	1	America) forest	cross	generalist	>50 - 100	carnivore
Caro et al.			Baird's tapir						(Central				
2004	Table 2	mammal	(Tapirus bairdii)	amphibian	2.00	0.21	4	1	America) forest	cross	specialist	>100 - 500	herbivore
Caro et al.			Baird's tapir						(Central				
2004	Table 2	mammal	(Tapirus bairdii)	mammal	1.50	0.69	4	1	America) forest	same	specialist	>100 - 500	herbivore
Caro et al.			Baird's tapir						(Central				
2004	Table 2	mammal	(Tapirus bairdii)	mammal	0.55	2.46	4	1	America) forest	same	specialist	>100 - 500	herbivore
Caro et al.			Baird's tapir						(Central				
2004	Table 2	mammal	(Tapirus bairdii)	mammal	0.17	0.28	4	1	America) forest	same	specialist	>100 - 500	herbivore
Caro et al.			Baird's tapir						(Central				
2004	Table 2	mammal	(<i>Tapirus bairdii</i>) White-lipped	bird	12.16	10.31	4	1	America) forest	cross	specialist	>100 - 500	herbivore
Caro et al.			peccary						(Central				
2004	Table 2	mammal	(<i>Dicotyles pecari</i>) White-lipped	amphibian	0.24	0.80	4	1	America) forest	cross	generalist	>20 - 50	herbivore
Caro et al.			peccary						(Central				
2004	Table 2	mammal	(<i>Dicotyles pecari</i>) White-lipped	mammal	1.50	0.69	4	1	America) forest	same	generalist	>20 - 50	herbivore
Caro et al.			peccary						(Central				
2004	Table 2	mammal	(<i>Dicotyles pecari</i>) White-lipped	mammal	0.90	0.70	4	1	America) forest	same	generalist	>20 - 50	herbivore
Caro et al.			peccary						(Central				
2004	Table 2	mammal	(Dicotyles pecari)	mammal	0.51	0.17	4	1	America)	same	generalist	>20 - 50	herbivore

					Co-occurr	ing species							
					rich	ness							
		Umbrollo		Co-	umbralla	umbralla				A	Umbrella species		
		species		species	species	species	Sample			ACTOSS OF	generalist	Sizo class	Trophic
Reference	Source	class	Umbrella species	class	nresent	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
hererenee	oource	61455	White-lipped	61435	present	ubserre	5120	Variance	forest	tunu	opecianoe	(*8/	lever
Caro et al.			peccary						(Central				
2004	Table 2	mammal	(Dicotyles pecari)	bird	11.75	10.44	4	1	America) forest	cross	generalist	>20 - 50	herbivore
Caro et al.			Spider monkey						(Central				
2004	Table 2	mammal	(Ateles geoffroyi)	amphibian	0.16	0.83	4	1	America) forest	cross	generalist	>0.25 - 10	herbivore
Caro et al.			Spider monkey						(Central				
2004	Table 2	mammal	(Ateles geoffroyi)	mammal	0.25	1.11	4	1	America) forest	same	generalist	>0.25 - 10	herbivore
Caro et al.			Spider monkey						(Central				
2004	Table 2	mammal	(Ateles geoffroyi)	mammal	0.78	2.23	4	1	America) forest	same	generalist	>0.25 - 10	herbivore
Caro et al.			Spider monkey						(Central				
2004	Table 2	mammal	(Ateles geoffroyi)	mammal	0.33	0.23	4	1	America) forest	same	generalist	>0.25 - 10	herbivore
Caro et al.			Spider monkey						(Central				
2004	Table 2	mammal	(Ateles geoffroyi) Northern Spotted	bird	10.00	11.03	4	1	America) forest	cross	generalist	>0.25 - 10	herbivore
Dunk et al.	pers.		Owl (Strix						(North				
2006	comm.	bird	<i>occidentalis</i>) Northern Spotted	molluscs	1.45	0.91	241	1	America) forest	cross	specialist	>0.5 - 1	carnivore
Dunk et al.	pers.		Owl <i>(Strix</i>						(North				
2006	comm.	bird	<i>occidentalis</i>) Various	amphibian	0.60	0.40	152	1	America)	cross	specialist	>0.5 - 1	carnivore
Fontaine et			megafauna						forest				
al. 2007	Table 1	mammal	(mammals) Various	molluscs	1.40	1.90	145	1	(Africa)	cross	generalist	>500	herbivore
Gardner et			megafauna						forest				
al. 2007	Figure 2	mammal	(mammals)	mammal	10.00	12.00	20	1	(Africa)	same	generalist	>500	herbivore

					Co-occurr	ing species							
					rich	ness							
											Umbrella		
				Co-							species		
		Umbrella		occurring	umbrella	umbrella				Across or	generalist		
		species		species	species	species	Sample			same	or	Size class	Trophic
Reference	Source	class	Umbrella species	class	present	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
			Various						c .				
Gardner et			megafauna		40.00	40.00	•••		forest				
al. 2007	Figure 2	mammal	(mammals) Various	amphibian	13.00	10.00	20	1	(Africa)	cross	generalist	>500	herbivore
Gardner et			megafauna						forest				
al. 2007	Figure 2	mammal	(mammals) Various	insect	125.00	115.00	20	1	(Africa)	cross	generalist	>500	herbivore
Gardner et			megafauna						forest				
al. 2007	Figure 2	mammal	(mammals) Various	bird	95.00	64.00	20	1	(Africa)	cross	generalist	>500	herbivore
Gardner et			megafauna						forest				
al. 2007	Figure 2	mammal	(mammals)	plant	60.00	64.00	20	1	(Africa)	cross	generalist	>500	herbivore
			Siberian flying						forest/				
Hurme et al.			squirrel						agricultural				
2008	Table 2	mammal	(Pteromys volans) Siberian flying	fungus	6.40	3.10	20	1	(Europe)	cross	specialist	≤0.25	herbivore
Hurme et al.			squirrel						agricultural				
2008	Table 2	mammal	(Pteromys volans)	lichen	1.90	1.60	20	1	(Europe)	cross	specialist	≤0.25	herbivore
			Siberian flying		2.00	2.00		-	forest/	0.000	opeoianee		
Hurme et al.			squirrel						agricultural				
2008	Table 2	mammal	(Pteromys volans)	insect	3.00	2.90	20	1	(Europe)	cross	specialist	≤0.25	herbivore
	Table 1		Goshawk						forest/				
Ozaki et al.	(home		(Accipiter						agricultural				
2006	, range)	bird	gentilis)	bird	11.80	11.70	80	1	(Europe)	same	generalist	>0.5 - 1	carnivore
	Table 1		Northern						forest/		-		
Ozaki et al.	(home		Goshawk						agricultural				
2006	range)	bird	(Accipiter	insect	14.20	12.70	80	1	(Europe)	cross	generalist	>0.5 - 1	carnivore

					Co-occurr	ing species							
					rich	ness							
		Umbrella		Co-	umbrella	umbrella				Across or	Umbrella species generalist		
		species		species	species	species	Sample			same	or	Size class	Trophic
Reference	Source	class	Umbrella species	class	present	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
	Table 1		Goshawk						forest/				
Ozaki et al.	(home		(Accipiter						agricultural				
2006	range)	bird	gentilis)	plant	25.10	24.20	80	1	(Europe)	cross	generalist	>0.5 - 1	carnivore
	Table 1		Northern						forest/				
Ozaki et al.	(home		Goshawk						agricultural				
2006	range)	bird	(Accipiter	insect	19.90	22.00	80	1	(Europe)	cross	generalist	>0.5 - 1	carnivore
Deliliele et			Comoranillia						forest/				
	toyt	bird	(Tetrae urogallus)	hird	41 20	26.20	07	1	agricultural	como	coocialist	NO 25 0 5	harbiyara
al. 2005	lext	biru	beetle	biru	41.20	50.20	02	T	(Lutope)	Same	specialist	20.25 - 0.5	nerbivore
			(Osmoderma						agricultural				
Ranius 2002	Table 2	insect	<i>eremita</i>) White-backed	insect	6.30	2.20	41	1	(Europe)	same	specialist	≤0.02	herbivore
			Woodpecker						forest/				
Roberge et			(Dendrocopos						agricultural				
al. 2008	Table 1	bird	<i>leucotos</i>) White-backed	insect	0.10	0.10	122	1	(Europe)	cross	specialist	>0.02 - 0.1	herbivore
			Woodpecker						forest/				
Roberge et			(Dendrocopos						agricultural				
al. 2008	Table 1	bird	<i>leucotos</i>) White-backed	bird	54.80	51.40	122	1	(Europe)	same	specialist	>0.02 - 0.1	herbivore
			Woodpecker						forest/				
Roberge et			(Dendrocopos						agricultural				
al. 2008 Roth and	Table 1	bird	<i>leucotos</i>) Red Kite(<i>Milvus</i>	Cryptogams	2.60	1.80	122	1	(Europe)	cross	specialist	>0.02 - 0.1	herbivore
Weber 2008 Roth and	Figure 1	bird	<i>milvus</i>) Black Kite (<i>Milvus</i>	bird	42.40	30.95	464	1	alpine	same	generalist	>1 - 5	carnivore
Weber 2008	Figure 1	bird	<i>migrans</i>) Northern	bird	41.45	30.25	464	1	alpine	same	generalist	>0.5 - 1	carnivore
Roth and			Goshawk										
Weber 2008	Figure 1	bird	(Accipiter	bird	41.55	33.35	464	1	alpine	same	generalist	>1 - 5	carnivore

					Co-occurri	ng species							
					rich	ness							
											Umbrella		
		Line have the		Co-						A	species		
		Umbrella		occurring	umbrella	umbrella	Sampla			Across or	generalist	Sizo class	Trophic
Poforonco	Sourco	species	Limbrolla spacios	class	species	species	sample	Varianco	Habitat	tava	onocialist		lovel
Reference	Jource	Class	Eurasian	Class	present	absent	512E	Variatice	Παυπαι	ιαχα	specialist	(Kg)	level
Roth and			Sparrowhawk										
Weber 2008 Roth and	Figure 1	bird	(Accipter nisus) Common Buzzard	bird	38.70	32.90	464	1	alpine	same	generalist	>0.1 - 0.25	carnivore
Weber 2008	Figure 1	bird	(<i>Buteo buteo</i>) Eurasian Kestrel	bird	39.45	21.10	464	1	alpine	same	generalist	>0.5 - 1	carnivore
Roth and			(Falco										
Weber 2008 Roth and	Figure 1	bird	<i>tinnunculus</i>) Tawny Owl (<i>Strix</i>	bird	36.10	33.10	464	1	alpine	same	generalist	>0.1 - 0.25	carnivore
Weber 2008 Roth and	Figure 1	bird	<i>aluco</i>) Red Kite(<i>Milvus</i>	bird	40.00	33.40	464	1	alpine	same	generalist	>0.25 - 0.5	carnivore
Weber 2008 Roth and	Figure 1	bird	<i>milvus</i>) Black Kite (<i>Milvus</i>	insect	22.13	37.69	283	1	alpine	cross	generalist	>1 - 5	carnivore
Weber 2008	Figure 1	bird	<i>migrans</i>) Northern	insect	22.15	38.83	283	1	alpine	cross	generalist	>0.5 - 1	carnivore
Roth and			Goshawk										
Weber 2008	Figure 1	bird	<i>(Accipiter</i> Eurasian	insect	28.21	34.70	283	1	alpine	cross	generalist	>1 - 5	carnivore
Roth and			Sparrowhawk										
Weber 2008 Roth and	Figure 1	bird	(<i>Accipter nisus</i>) Common Buzzard	insect	35.40	34.01	283	1	alpine	cross	generalist	>0.1 - 0.25	carnivore
Weber 2008	Figure 1	bird	(<i>Buteo buteo</i>) Eurasian Kestrel	insect	30.90	37.90	283	1	alpine	cross	generalist	>0.5 - 1	carnivore
Roth and			(Falco										
Weber 2008 Roth and	Figure 1	bird	<i>tinnunculus</i>) Tawny Owl (<i>Strix</i>	insect	35.90	34.00	283	1	alpine	cross	generalist	>0.1 - 0.25	carnivore
Weber 2008 Roth and	Figure 1	bird	<i>aluco</i>) Red Kite(<i>Milvus</i>	insect	32.50	35.00	283	1	alpine	cross	generalist	>0.25 - 0.5	carnivore
Weber 2008 Roth and	Figure 1	bird	<i>milvus</i>) Black Kite (<i>Milvus</i>	plant	242.80	242.90	459	1	alpine	cross	generalist	>1 - 5	carnivore
Weber 2008	Figure 1	bird	migrans)	plant	248.00	243.70	459	1	alpine	cross	generalist	>0.5 - 1	carnivore

					Co-occurri	ng species							
					rich	ness							
		Umbrella		Co- occurring	umbrella	umbrella				Across or	Umbrella species generalist		- 1.
Poforonco	Sourco	species	Limbrolla species	species	species	species	Sample	Varianco	Habitat	same	0r cnocialist	Size class	Irophic
Reference	Source	CIdSS	Northern	CIdSS	present	absent	size	variance	Habilal	ldXd	specialist	(Kg)	level
Roth and			Goshawk										
Weber 2008	Figure 1	bird	<i>(Accipiter</i> Eurasian	plant	270.30	244.35	459	1	alpine	cross	generalist	>1 - 5	carnivore
Roth and			Sparrowhawk										
Weber 2008 Roth and	Figure 1	bird	(<i>Accipter nisus</i>) Common Buzzard	plant	259.90	243.00	459	1	alpine	cross	generalist	>0.1 - 0.25	carnivore
Weber 2008	Figure 1	bird	(<i>Buteo buteo</i>) Eurasian Kestrel	plant	256.90	214.60	459	1	alpine	cross	generalist	>0.5 - 1	carnivore
Roth and			(Falco										
Weber 2008 Roth and	Figure 1	bird	<i>tinnunculus</i>) Tawny Owl (<i>Strix</i>	plant	248.60	244.30	459	1	alpine	cross	generalist	>0.1 - 0.25	carnivore
Weber 2008 Roth and	Figure 1	bird	<i>aluco</i>) Coal Tit (<i>Parus</i>	plant	267.30	245.05	459	1	alpine	cross	generalist	>0.25 - 0.5	carnivore
Weber 2008 Roth and	Figure 1	bird	<i>ate</i> r) Blue Tit (<i>Parus</i>	bird	36.70	13.70	464	1	alpine	same	generalist	≤0.02	omnivore
Weber 2008 Roth and	Figure 1	bird	<i>caeruleus</i>) Crested Tit (<i>Parus</i>	bird	39.20	22.40	464	1	alpine	same	generalist	≤0.02	omnivore
Weber 2008 Roth and	Figure 1	bird	<i>cristalus</i>) Great Tit (<i>Parus</i>	bird	37.40	23.50	464	1	alpine	same	generalist	≤0.02	omnivore
Weber 2008 Roth and	Figure 1	bird	<i>major</i>) Willow Tit (<i>Parus</i>	bird	38.10	17.16	464	1	alpine	same	generalist	≤0.02	omnivore
Weber 2008 Roth and	Figure 1	bird	<i>montanus</i>) Marsh Tit (<i>Parus</i>	bird	33.50	33.30	464	1	alpine	same	generalist	≤0.02	omnivore
Weber 2008 Roth and	Figure 1	bird	<i>palustris</i>) Coal Tit (<i>Parus</i>	bird	40.10	22.30	464	1	alpine	same	generalist	≤0.02	omnivore
Weber 2008 Roth and	Figure 1	bird	<i>ate</i> r) Blue Tit (<i>Parus</i>	insect	37.30	21.80	283	1	alpine	cross	generalist	≤0.02	omnivore
Weber 2008 Roth and	Figure 1	bird	<i>caeruleus</i>) Crested Tit (<i>Parus</i>	insect	27.80	41.02	283	1	alpine	cross	generalist	≤0.02	omnivore
Weber 2008	Figure 1	bird	cristalus)	insect	38.60	28.50	283	1	alpine	cross	generalist	≤0.02	omnivore

					Co-occurr	ng species							
					rich	ness							
											Umbrella		
				Co-							species		
		Umbrella		occurring	umbrella	umbrella				Across or	generalist		
		species		species	species	species	Sample			same	or	Size class	Trophic
Reference	Source	class	Umbrella species	class	present	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
Roth and			Great Lit (Parus				• • •						
Weber 2008 Roth and	Figure 1	bird	major) Willow Tit (Parus	insect	32.00	38.30	283	1	alpine	cross	generalist	≤0.02	omnivore
Weber 2008 Roth and	Figure 1	bird	<i>montanus</i>) Marsh Tit (<i>Parus</i>	insect	47.40	27.00	283	1	alpine	cross	generalist	≤0.02	omnivore
Weber 2008 Roth and	Figure 1	bird	<i>palustris</i>) Coal Tit (<i>Parus</i>	insect	30.40	38.90	283	1	alpine	cross	generalist	≤0.02	omnivore
Weber 2008 Roth and	Figure 1	bird	<i>ate</i> r) Blue Tit (<i>Parus</i>	plant	256.10	158.60	459	1	alpine	cross	generalist	≤0.02	omnivore
Weber 2008 Roth and	Figure 1	bird	<i>caeruleus</i>) Crested Tit (<i>Parus</i>	plant	254.50	212.80	459	1	alpine	cross	generalist	≤0.02	omnivore
Weber 2008 Roth and	Figure 1	bird	cristalus) Great Tit (Parus	plant	261.10	208.20	459	1	alpine	cross	generalist	≤0.02	omnivore
Weber 2008 Roth and	Figure 1	bird	major) Willow Tit (Parus	plant	257.20	183.40	459	1	alpine	cross	generalist	≤0.02	omnivore
Weber 2008 Roth and	Figure 1	bird	<i>montanus</i>) Marsh Tit (<i>Parus</i>	plant	264.50	237.00	459	1	alpine	cross	generalist	≤0.02	omnivore
Weber 2008	Figure 1	bird	<i>palustris</i>) Northern	plant	259.20	215.90	459	1	alpine	cross	generalist	≤0.02	omnivore
Sergio et al.			Goshawk										
2006	Figure 1	bird	(Accipter gentilis) Pygmy Owl	bird	8.10	4.70	50	1	alpine	same	generalist	>1 - 5	carnivore
Sergio et al.			(Glaucidium										
2006	Figure 1	bird	<i>passerinum</i>) Tengmalms Owl	bird	8.50	4.50	50	1	alpine	same	generalist	>0.02 - 0.1	carnivore
Sergio et al.			(Aegolius										
2006 Sergio et al.	Figure 1	bird	<i>funereus</i>) Tawny Owl (<i>Strix</i>	bird	8.50	4.60	50	1	alpine	same	generalist	>0.1 - 0.25	carnivore
2006 Sergio et al.	Figure 1	bird	<i>aluco</i>) Long-Eared Owl	bird	8.30	5.10	50	1	alpine	same	generalist	>0.25 - 0.5	carnivore
2006	Figure 1	bird	(Asio otus)	bird	9.90	6.50	50	1	alpine	same	generalist	>0.25 - 0.5	carnivore

					Co-occurr	ing species							
					rich	ness							
				Co-							Umbrella species		
		Umbrella		occurring	umbrella	umbrella				Across or	generalist		
		species		species	species	species	Sample			same	or	Size class	Trophic
Reference	Source	class	Umbrella species	class	present	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
Sergio et al.			Scops Owl (Otus										
2006	Figure 1	bird	scops)	bird	8.10	4.30	50	1	alpine	same	generalist	>0.02 - 0.1	carnivore
			Robin										
			(Erithaculus										
			rubecula),										
			Blackbird (Turdus										
			<i>merula</i>), Blackcap										
			(Sylvia										
			atricapilla),										
			crested tit (Parus										
			cristatus),										
			Chaffinch										
			(Fringilla										
			coelebs),										
			European										
Sergio et al.			Goldfinch										
2006	Figure 1	bird	(Carduelis	bird	4.70	5.00	50	1	alpine	same	generalist	>0.02 - 0.1	omnivore

					Co-occurr	ing species							
					rich	ness							
				Co-							Umbrella species		
		Umbrella		occurring	umbrella	umbrella				Across or	generalist		
	_	species		species	species	species	Sample			same	or	Size class	Trophic
Reference	Source	class	Umbrella species	class	present	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
			(Bongsg bongsig)										
			(Buranaan Nightiar										
			eurongeus)										
			Green										
			Woodnecker										
			(Picus viridis)										
			Grev-headed										
			Woodpecker										
			(Picus canus).										
			Gmelin and										
			Eurasian										
			Treecreeper										
Sergio et al.			(Certhia										
2006	Figure 1	bird	<i>familiaris</i>) Northern	bird	5.50	5.10	50	1	alpine	same	specialist	>0.02 - 0.1	omnivore
Sergio et al.			Goshawk										
2006	Figure 1	bird	(Accipter gentilis) Pygmy Owl	plant	4.20	3.00	50	1	alpine	cross	generalist	>1 - 5	carnivore
Sergio et al.			(Glaucidium										
2006	Figure 1	bird	<i>passerinum</i>) Tengmalms Owl	plant	4.60	3.20	50	1	alpine	cross	generalist	>0.02 - 0.1	carnivore
Sergio et al.			(Aegolius										
2006 Sergio et al.	Figure 1	bird	<i>funereus</i>) Tawny Owl (<i>Strix</i>	plant	4.60	3.20	50	1	alpine	cross	generalist	>0.1 - 0.25	carnivore
2006 Sergio et al.	Figure 1	bird	<i>aluco</i>) Long-Eared Owl	plant	4.40	3.00	50	1	alpine	cross	generalist	>0.25 - 0.5	carnivore
2006	Figure 1	bird	(Asio otus)	plant	4.30	3.50	50	1	alpine	cross	generalist	>0.25 - 0.5	carnivore

					Co-occurr	ing species							
					rich	ness							
											Umbrella		
				Co-							species		
		Umbrella		occurring	umbrella	umbrella				Across or	generalist		
		species		species	species	species	Sample			same	or	Size class	Trophic
Reference	Source	class	Umbrella species	class	present	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
Sergio et al.			Scops Owl (Otus										
2006	Figure 1	bird	scops)	plant	3.30	2.10	50	1	alpine	cross	generalist	>0.02 - 0.1	carnivore
			Robin										
			(Erithaculus										
			rubecula),										
			Blackbird (Turdus										
			<i>merula</i>), Blackcap										
			(Sylvia										
			atricapilla),										
			crested tit (Parus										
			cristatus),										
			Chaffinch										
			(Fringilla										
			coelebs),										
			European										
Sergio et al.			Goldfinch										
2006	Figure 1	bird	(Carduelis	plant	3.10	3.00	50	1	alpine	cross	generalist	>0.02 - 0.1	omnivore
					Co-occurr	ing species							
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					rich	ness	-						
											Umbrella		
				Co-							species		
		Umbrella	3	occurring	umbrella	umbrella				Across or	generalist		
		species		species	species	species	Sample			same	or	Size class	Trophic
Reference	Source	class	Umbrella species	class	present	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
			Hazel Grouse										
			(Bonasa bonasia),										
			European Nightjar										
			(Caprimulgus										
			europaeus),										
			Green										
			Woodpecker										
			(Picus viridis),										
			Grey-headed										
			Woodpecker										
			(Picus canus),										
			Gmelin and										
			Eurasian										
			Treecreeper										
Sergio et al.			(Certhia										
2006	Figure 1	bird	familiaris)	plant	3.20	3.10	50	1	alpine	cross	specialist	>0.02 - 0.1	omnivore
Sergio et al.	pers.		Scops Owl (<i>Otus</i>										
2006	comm.	bird	scops)	insect	6.90	3.00	50	1	alpine	cross	generalist	>0.02 - 0.1	carnivore
Sergio et al.	pers.		Long-Eared Owl										
2006	comm.	bird	(Asio otus)	insect	1.80	0.65	50	1	alpine	cross	generalist	>0.25 - 0.5	carnivore

					Co-occurr	ing species							
					rich	ness					Umbrollo		
Reference	Source	Umbrella species class	I Umbrella species	Co- occurring species class	umbrella species present	umbrella species absent	Sample	Variance	Habitat	Across or same taxa	species generalist or specialist	Size class	Trophic
	000100	61455	Robin	01000	present	absent	5120	Variance	Habitat	taxa	opecialise	(18)	level
			(Erithaculus										
			rubecula),										
			Blackbird (Turdus										
			<i>merula</i>), Blackcap										
			(Sylvia										
			atricapilla),										
			crested tit (Parus										
			cristatus),										
			Chaffinch										
			(Fringilla										
			coelebs),										
			European										
Sergio et al.	pers.		Goldfinch										
2006	comm.	bird	(Carduelis	insect	1.80	1.90	50	1	alpine	cross	generalist	>0.02 - 0.1	carnivore

					Co-occurr	ing species							
					rich	ness							
											Umbrella		
				Co-							species		
		Umbrella	3	occurring	umbrella	umbrella				Across or	generalist		
		species		species	species	species	Sample			same	or	Size class	Trophic
Reference	Source	class	Umbrella species	class	present	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
			Hazel Grouse										
			(Bonasa bonasia),										
			European Nightjar										
			(Caprimuigus										
			europaeus),										
			Green										
			Woodpecker										
			(Picus viridis),										
			Grey-headed										
			Woodpecker										
			(Picus canus),										
			Gmelin and										
			Eurasian										
			Treecreeper										
Sergio et al.	pers.		(Certhia										
2006	comm.	bird	familiaris)	insect	1.90	2.00	50	1	alpine	cross	specialist	>0.02 - 0.1	carnivore
Suter et al.			Capercaillie										
2002	Figure 1	bird	(Tetrao urogallus)	bird	16.50	13.40	21	1	alpine	same	specialist	>0.25 - 0.5	herbivore

						Co-oo	ccurring							
						species a	abundance							
												Umbrella		
				Co-								species		
		Umbrella		occurring		umbrella	a umbrella				Across or	generalist		
		species		species	Co-occurring	species	species	Sample			same	or	Size class	Trophic
Reference	Source	class	Umbrella species	class	species	present	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
					multimammate					. .				
			Various megafauna		mouse (Mastomys					forest				
Caro 2001	Table 1	mammal	(mammals)	mammal	natalensis) striped mouse	0.27	7.34	20	1	(Africa)	same	generalist	>500	herbivore
			Various megafauna		(Lemniscomys					forest				
Caro 2001	Table 1	mammal	(mammals)	mammal	<i>striatus</i>) bushveld gerbil	0	0.04	20	1	(Africa)	same	generalist	>500	herbivore
			Various megafauna		(Tatera					forest				
Caro 2001	Table 1	mammal	(mammals) Various megafauna	mammal	<i>leucogaster</i>) meadow rat	0.3	0.35	20	1	(Africa) forest	same	generalist	>500	herbivore
Caro 2001	Table 1	mammal	(mammals)	mammal	(<i>Myomys fumatus</i>) pouched mouse	0	0.02	20	1	(Africa)	same	generalist	>500	herbivore
			Various megafauna		(Saccostomyus					forest				
Caro 2001	Table 1	mammal	(mammals)	mammal	<i>campestris</i>) lesser red musk	0.04	0	20	1	(Africa)	same	generalist	>500	herbivore
			Various megafauna		shrew (Crocidura					forest				
Caro 2001	Table 1	mammal	(mammals)	mammal	<i>hirta</i>) African doormouse	0.04	0.39	20	1	(Africa)	same	generalist	>500	herbivore
			Various megafauna		(Graphiurus					forest				
Caro 2001	Table 1	mammal	(mammals)	mammal	murinus)	0.19	0	20	1	(Africa)	same	generalist	>500	herbivore
			Various megafauna		pigmy mouse (Mus					forest		0		
Caro 2001 Caro et al.	Table 1	mammal	(mammals) Various megafauna	mammal	minutoides)	0	0.14	20	1	(Africa) forest	same	generalist	>500	herbivore
2003	Table 5	mammal	(mammals)	mammal	baboon (<i>Papio sp.</i>) bushpig	0.01	0.07	20	1	(Africa)	same	generalist	>500	herbivore
Caro et al.			Various megafauna		(Potamochoerus					forest				
2003	Table 5	mammal	(mammals)	mammal	larvatus)	0.07	0	20	1	(Africa)	same	generalist	>500	herbivore
Caro et al.			Various megafauna		giraffe (Giraffa					forest		0		
2003	Table 5	mammal	(mammals)	mammal	<i>camelopardalis</i>) hippopotamus	2.17	0.68	20	1	(Africa)	same	generalist	>500	herbivore
Caro et al.			Various megafauna		(Hippopotamus					forest				
2003 Caro et al	Table 5	mammal	(mammals) Various megafauna	mammal	amphibius) spotted hvena	5.15	0	20	1	(Africa) forest	same	generalist	>500	herbivore
2003	Table 5	mammal	(mammals)	mammal	(Crocuta crocuta)	0.19	0	20	1	(Africa)	same	generalist	>500	herbivore

						Co-oo	ccurring							
						species a	abundance							
												Umbrella		
				Co-								species		
		Umbrella		occurring		umbrella	a umbrella				Across or	generalist		
		species		species	Co-occurring	species	species	Sample			same	or	Size class	Trophic
Reference	Source	class	Umbrella species	class	species	present	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
Caro et al.			Various megafauna		vervet monkey					forest				
2003	Table 5	mammal	(mammals)	mammal	(Chlorocebus sp.) warthog	0.47	0.1	20	1	(Africa)	same	generalist	>500	herbivore
Caro et al.			Various megafauna		(Phacochoierus					forest				
2003 Caro et al.	Table 5	mammal	(mammals) Various megafauna	mammal	<i>aethiopicus</i>) side-striped jackal	1.34	0.56	20	1	(Africa) forest	same	generalist	>500	herbivore
2003 Caro et al.	Table 7	mammal	(mammals) Various megafauna	mammal	(Canis adustus) banded mongoose	75	18.2	23	1	(Africa) forest	same	generalist	>500	herbivore
2003 Caro et al.	Table 7	mammal	(mammals) Various megafauna	mammal	(<i>Mungos mungo</i>) dwarf mongoose	66.7	0	23	1	(Africa) forest	same	generalist	>500	herbivore
2003	Table 7	mammal	(mammals)	mammal	(Helogale paruva) white-tailed	8.3	0	23	1	(Africa)	same	generalist	>500	herbivore
Caro et al. 2003	Table 7	mammal	Various megafauna (mammals)	mammal	mongoose (<i>Ichneumia</i> <i>albicauda</i>) black-tipped mongoose	8.3	9.1	23	1	forest (Africa)	same	generalist	>500	herbivore
Caro et al.			Various megafauna		(Galerella					forest				
2003 Caro et al.	Table 7	mammal	(mammals) Various megafauna	mammal	sanguinea) spotted hyena (C.	8.3	27.3	23	1	(Africa) forest	same	generalist	>500	herbivore
2003 Caro et al.	Table 7	mammal	(mammals) Various megafauna	mammal	<i>crocuta</i>) common genet	41.7	18.2	23	1	(Africa) forest	same	generalist	>500	herbivore
2003 Caro et al.	Table 7	mammal	(mammals) Various megafauna	mammal	(Genetta genetta) civet (Vivera	50	45.5	23	1	(Africa) forest	same	generalist	>500	herbivore
2003 Caro et al.	Table 7	mammal	(mammals) Various megafauna	mammal	<i>civetta</i>) wild cat (<i>Felis</i>	83.3	9.1	23	1	(Africa) forest	same	generalist	>500	herbivore
2003 Caro et al.	Table 7	mammal	(mammals) Various megafauna	mammal	lybica) serval (Leptailurus	66.7	0	23	1	(Africa) forest	same	generalist	>500	herbivore
2003 Caro et al.	Table 7	mammal	(mammals) Various megafauna	mammal	serval) leopard (Panthera	16.7	9.1	23	1	(Africa) forest	same	generalist	>500	herbivore
2003 Caro et al.	Table 7	mammal	(mammals) Various megafauna	mammal	pardus)	8.3	0	23	1	(Africa) forest	same	generalist	>500	herbivore
2003	Table 7	mammal	(mammals)	mammal	lion (Panthera leo)	8.3	0	23	1	(Africa)	same	generalist	>500	herbivore

						Co-oc	curring							
						species a	abundance							
												Umbrella		
				Co-								species		
		Umbrella		occurring		umbrella	umbrella				Across or	generalist		
		species		species	Co-occurring	species	species	Sample			same	or	Size class	Trophic
Reference	Source	class	Umbrella species	class	species	present	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
Candran					multimammate					farrat				
Garuner	Table 4		various megalauria		mouse (<i>iviasioniys</i>	0.00	4.00	20	4	(Africa)			. 500	h
et al. 2007	Table 1	mammai	(mammais)	mammai	red rock rat	0.66	1.02	20	1	(Africa)	same	generalist	>500	nerbivore
Gardner			Various megafauna		(Aethomys					forest				
et al. 2007	Table 1	mammal	(mammals)	mammal	chrisophilus)	0.37	0.28	20	1	(Africa)	same	generalist	>500	herbivore
Gardner			Various megafauna		gray-bellied pygmy					forest				
et al. 2007	Table 1	mammal	(mammals)	mammal	mouse (<i>Mus triton</i>) African pygmy	0.02	0	20	1	(Africa)	same	generalist	>500	herbivore
Gardner			Various megafauna		mouse (<i>Mus</i>					forest				
et al. 2007	Table 1	mammal	(mammals)	mammal	musculoides)	0	0.32	20	1	(Africa)	same	generalist	>500	herbivore
			_											
Gardner			Various megafauna		Phrynobatrachus					forest				
et al. 2007	Table 1	mammal	(mammals)	amphibian	mabiensis	61.98	77.28	20	1	(Africa)	across	generalist	>500	herbivore
					frog									
Gardner			Various megafauna		(Phrynohatrachus					forest				
et al 2007	Table 1	mammal	(mammals)	amnhihian	(I III ynobuti uchus natalensis)	93 59	33.96	20	1	(Africa)	across	generalist	>500	herhivore
Ct al. 2007	Table I	mannia	(marininais)	ampinoian	marbled snout-	53.55	55.90	20	T	(Anica)	aci 033	generalist	>300	nerbivore
Gardner			Various megafauna		burrower (Hemisus					forest				
et al. 2007	Table 1	mammal	(mammals)	amphibian	marmoratus)	17.88	11.5	20	1	(Africa)	across	generalist	>500	herbivore
Gardner			Various megafauna		Muller's platanna					forest				
et al. 2007	Table 1	mammal	(mammals)	amphibian	(Xenopus melleri)	19.67	8.01	20	1	(Africa)	across	generalist	>500	herbivore
Gardner			Various megafauna		toad (Bufo					forest				
et al. 2007	Table 1	mammal	(mammals)	amnhihian	auttaralis)	8 15	3 55	20	1	(Africa)	across	generalist	>500	herhivore
2007		manna	(umpriorum	gattarano y	0.15	5.55	20	-	(,	401055	Berlerunst	- 500	neronore
Gardner			Various megafauna							forest				
et al. 2007	Table 1	mammal	(mammals)	insect	Bicyclus safitza	26.14	32.64	20	1	(Africa)	across	generalist	>500	herbivore
Gardner			Various megafauna							forest				
et al. 2007	Table 1	mammal	(mammals)	insect	Bicyclus anynana	27.67	26.04	20	1	(Africa)	across	generalist	>500	herbivore

						Co-oc	curring							
						species a	abundance							
												Umbrella		
				Co-								species		
		Umbrella		occurring		umbrella	umbrella				Across or	generalist		
		species		species	Co-occurring	species	species	Sample			same	or	Size class	Trophic
Reference	Source	class	Umbrella species	class	species	present	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
					Common evening									
Gardner			Various megafauna		brown (<i>Melanitus</i>					forest				
et al. 2007	Table 1	mammal	(mammals)	insect	leda)	24.23	4.51	20	1	(Africa)	across	generalist	>500	herbivore
Gardner			Various megafauna							forest				
et al. 2007	Table 1	mammal	(mammals)	insect	H. Daedalus	12.19	1.04	20	1	(Africa)	across	generalist	>500	herbivore
Gardner			Various megafauna							forest				
et al. 2007	Table 1	mammal	(mammals)	insect	Bicyclus cottrelli Ring-necked Dove	5	12.85	20	1	(Africa)	across	generalist	>500	herbivore
Gardner			Various megafauna		(Streptopelia					forest				
et al. 2007	Table 1	mammal	(mammals)	bird	<i>capicola</i>) Tawny-flanked	0.58	12.75	20	1	(Africa)	across	generalist	>500	herbivore
Gardner			Various megafauna		Prinia (<i>Prinia</i>					forest				
et al. 2007	Table 1	mammal	(mammals)	bird	subflava)	5.75	2.88	20	1	(Africa)	across	generalist	>500	herbivore
Gardner			Various megafauna							forest				
et al. 2007	Table 1	mammal	(mammals)	bird	Pyconotus barbatus Lesser Blue-eared	3.17	14.25	20	1	(Africa)	across	generalist	>500	herbivore
					Glossy-starling									
Gardner			Various megafauna		(Lamprotornis					forest				
et al. 2007	Table 1	mammal	(mammals)	bird	<i>chloropterus</i>) Meyer's Parrot	8.75	2.25	20	1	(Africa)	across	generalist	>500	herbivore
Gardner			Various megafauna		(Poicephalus					forest				
et al. 2007	Table 1	mammal	(mammals)	bird	meyeri)	5	5.25	20	1	(Africa)	across	generalist	>500	herbivore
Gardner			Various megafauna		Markhamia					forest				
et al. 2007	Table 1	mammal	(mammals)	plant	obtusifolia	45.89	3.93	20	1	(Africa)	across	generalist	>500	herbivore
Gardner			Various megafauna		Combretum					forest				
et al. 2007	Table 1	mammal	(mammals)	plant	purpureiflorum	25.05	0.07	20	1	(Africa)	across	generalist	>500	herbivore
Gardner			Various megafauna							forest				
et al. 2007	Table 1	mammal	(mammals)	plant	Friesodilsia obovata	19.83	6.83	20	1	(Africa)	across	generalist	>500	herbivore

						Co-oc	curring							
						species a	abundance							
												Umbrella		
				Co-								species		
		Umbrella		occurring		umbrella	umbrella				Across or	generalist		
		species		species	Co-occurring	species	species	Sample			same	or	Size class	Trophic
Reference	Source	class	Umbrella species	class	species	present	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
Gardner			Various megafauna							forest				
et al. 2007	Table 1	mammal	(mammals)	plant	Grewia Bicolor	16.42	0.53	20	1	(Africa)	across	generalist	>500	herbivore
Carlana										6 1				
Gardner			various megatauna		0			••		forest				
et al. 2007	Table 1	mammal	(mammais) Siberian flying	plant	Grewia flavescens	24.17	0	20	1	(ATRICA)	across	generalist	>500	herbivore
Hurmo ot			souirrel (Pteromys							agricultural				
al 2008	Annondiv A	mammal	volans)	lichon	Lobaria nulmonaria	1	0	20	1	(Europe)	across	specialist	<0.25	harhivora
ai. 2000	Appendix A	mannia	Siberian flying	nenen		T	0	20	T	forest/	aci 033	specialist	20.25	nerbivore
Hurme et			squirrel (<i>Pteromys</i>							agricultural				
al. 2008	Appendix A	mammal	volans)	lichen	Nephroma bellum	92	34	20	1	(Europe)	across	specialist	≤0.25	herbivore
	P.P		Siberian flying		-					forest/		-1		
Hurme et			squirrel (<i>Pteromys</i>							agricultural				
al. 2008	Appendix A	mammal	volans)	lichen	N. parile	4	1	20	1	(Europe)	across	specialist	≤0.25	herbivore
			Siberian flying							forest/				
Hurme et			squirrel (<i>Pteromys</i>							agricultural				
al. 2008	Appendix A	mammal	volans)	lichen	N. resupinatum	12	5	20	1	(Europe)	across	specialist	≤0.25	herbivore
			Siberian flying							forest/				
Hurme et			squirrel (<i>Pteromys</i>							agricultural				
al. 2008	Appendix A	mammal	volans)	lichen	Pannaria pezizoides	12	3	20	1	(Europe)	across	specialist	≤0.25	herbivore
11			Siberian flying		A mar da avatia					torest/				
Hurme et			squirrei (<i>Pteromys</i>	<i>c</i>	Amylocystis					agricultural			.0.25	
al. 2008	Appendix A	mammal	VOIGNS) Siborian flying	fungus	lapponica	11	4	20	1	(Europe)	across	specialist	≤0.25	herbivore
Hurmo ot			souirrel (Dteromys		Antrodia					agricultural				
al 2008	Appondix A	mammal	volans)	fungue	albohrunnea	6	0	20	1	(Europe)	across	coocialist	<0.25	horbiyoro
ai. 2000	Appendix A	mannia	Siberian flying	Tungus	uibobiunneu	0	0	20	T	forest/	acioss	specialist	50.25	nerbivore
Hurme et			squirrel (<i>Pteromvs</i>							agricultural				
al. 2008	Appendix A	mammal	volans)	fungus	A. pulvinacens	3	0	20	1	(Europe)	across	specialist	<0.25	herbivore
			Siberian flying			5	5		-	forest/			_00	
Hurme et			squirrel (Pteromys		Antrodiella					agricultural				
al. 2008	Appendix A	mammal	volans)	fungus	citrinella	1	0	20	1	(Europe)	across	specialist	≤0.25	herbivore

						Co-oc	curring							
						species a	abundance							
												Umbrella		
				Co-								species		
		Umbrella		occurring		umbrella	umbrella				Across or	generalist		
		species		species	Co-occurring	species	species	Sample			same	or	Size class	Trophic
Reference	Source	class	Umbrella species	class	species	present	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
			Siberian flying							forest/				
Hurme et			squirrel (Pteromys			_				agricultural				
al. 2008	Appendix A	mammal	<i>volans</i>) Siberian flying	fungus	Cinereomyces lenis	5	1	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (<i>Pteromys</i>		Diplommitoporus					agricultural				
al. 2008	Appendix A	mammal	<i>volans</i>) Siberian flying	fungus	crustilinus	3	0	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (Pteromys							agricultural				
al. 2008	Appendix A	mammal	<i>volans</i>) Siberian flying	fungus	Fomitopsis rosea	5	1	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (Pteromys		Junghuhnia					agricultural				
al. 2008	Appendix A	mammal	<i>volans</i>) Siberian flying	fungus	colabens	1	0	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (Pteromys		Junghuhnia					agricultural				
al. 2008	Appendix A	mammal	<i>volans</i>) Siberian flying	fungus	luteoalba	1	0	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (Pteromys							agricultural				
al. 2008	Appendix A	mammal	volans) Siberian flying	fungus	Leptoporus mollis	2	0	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (Pteromys		Oligoporus					agricultural				
al. 2008	Appendix A	mammal	<i>volans</i>) Siberian flying	fungus	lateritius	2	0	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (<i>Pteromys</i>		Oligoporus					agricultural				
al. 2008	Appendix A	mammal	<i>volans</i>) Siberian flying	fungus	sericeomollis	1	1	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (<i>Pteromvs</i>		Phellinus					agricultural				
al. 2008	Appendix A	mammal	<i>volans</i>) Siberian flying	fungus	chrysoloma	36	9	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (<i>Pteromys</i>		Phellinus					agricultural				
al. 2008	Appendix A	mammal	<i>volans</i>) Siberian flying	fungus	ferrugineofuscus	6	1	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (<i>Pteromvs</i>							, agricultural				
al. 2008	Appendix A	mammal	volans)	fungus	Phellinus lundellii	16	2	20	1	(Europe)	across	specialist	≤0.25	herbivore

						Co-oc	curring							
						species a	abundance							
												Umbrella		
				Co-								species		
		Umbrella		occurring		umbrella	umbrella				Across or	generalist		
		species		species	Co-occurring	species	species	Sample			same	or	Size class	Trophic
Reference	Source	class	Umbrella species	class	species	present	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
			Siberian flying							forest/				
Hurme et			squirrel (<i>Pteromys</i>		Phellinus					agricultural				
al. 2008	Appendix A	mammal	<i>volans</i>) Siberian flying	fungus	nigrolimitatus	32	15	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (<i>Pteromys</i>							agricultural				
al. 2008	Appendix A	mammal	<i>volans</i>) Siberian flying	fungus	Phellinus pini	1	0	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (Pteromys							agricultural				
al. 2008	Appendix A	mammal	<i>volans</i>) Siberian flying	fungus	Phellinus viticola	254	72	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (Pteromys		Skeletocutis					agricultural				
al. 2008	Appendix A	mammal	<i>volans</i>) Siberian flying	fungus	brevispora	0	1	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (Pteromys							agricultural				
al. 2008	Appendix A	mammal	volans) Siberian flying	fungus	Skeletocutis odora	1	0	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (Pteromys							agricultural				
al. 2008	Appendix A	mammal	volans) Siberian flying	fungus	Skeletocutis stellae	3	2	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (Pteromys		Acmaeops					agricultural				
al. 2008	Appendix A	mammal	volans) Siberian flying	insect	septentrionis	6	13	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (Pteromys		Agathidium					agricultural				
al. 2008	Appendix A	mammal	volans) Siberian flying	insect	pallidum	5	1	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (<i>Pteromys</i>							agricultural				
al. 2008	Appendix A	mammal	volans) Siberian flying	insect	Atomario abietina	1	0	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (Pteromys		Atomario					agricultural				
al. 2008	Appendix A	mammal	volans) Siberian flying	insect	elongatula	3	0	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (<i>Pteromys</i>							agricultural				
al. 2008	Appendix A	mammal	volans)	insect	Atrecus longiceps	4	1	20	1	(Europe)	across	specialist	≤0.25	herbivore

						Co-oo	curring							
						species a	abundance							
												Umbrella		
				Co-								species		
		Umbrella		occurring		umbrella	umbrella				Across or	generalist		
		species		species	Co-occurring	species	species	Sample			same	or	Size class	Trophic
Reference	Source	class	Umbrella species	class	species	present	absent	size	Variance	Habitat	taxa	specialist	(kg)	level
			Siberian flying		_					forest/				
Hurme et			squirrel (Pteromys		Cercyon					agricultural				
al. 2008	Appendix A	mammal	<i>volans</i>) Siberian flying	insect	emarginatus	1	2	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (Pteromys		Cryptophagus					agricultural				
al. 2008	Appendix A	mammal	<i>volans</i>) Siberian flying	insect	lysholmi	15	2	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (Pteromys							agricultural				
al. 2008	Appendix A	mammal	<i>volans</i>) Siberian flying	insect	Cyphea latiuscula	4	12	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (Pteromys							agricultural				
al. 2008	Appendix A	mammal	volans) Siberian flying	insect	Enicmus apicalis	6	1	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Hurme et			squirrel (Pteromys		Euclilodes					agricultural				
al. 2008	Appendix A	mammal	volans)	insect	<i>caucasicus</i> Red-breasted	3	1	20	1	(Europe) forest/	across	specialist	≤0.25	herbivore
Pakkala et			Capercaillie (Tetrao		Flycatcher (Ficedula					agricultural			>0.25 -	
al. 2003	text	bird	urogallus)	bird	parva) Pygmy Owl	4.2	1	82	1	(Europe) forest/	same	specialist	0.5	omnivore
Pakkala et			Capercaillie (Tetrao		(Glaucidium					agricultural			>0.25 -	
al. 2003	text	bird	urogallus)	bird	passerinum) Three-toed	8.5	1	82	1	(Europe)	same	specialist	0.5	carnivore
					Woodpecker					forest/				
Pakkala et			Capercaillie (Tetrao		(Picoides					agricultural			>0.25 -	
al. 2003	text	bird	urogallus)	bird	tridactylus)	19.3	1	82	1	(Europe)	same	specialist	0.5	herbivore

Taxonomic abundance of cooccurring species

				Co-							Umbrella		
		Umbrella		occurring	umbrella	umbrella				Across	species	Size	
		species		species	species	species	Sample			or same	generalist	class	Trophic
Reference	Source	class	Umbrella species	class	present	absent	size	Variance	Habitat	taxa	or specialist	(kg)	level
			Various										assumed
			megafauna						Forest				majority
Caro 2001	Table 1	mammal	(mammals) Various	mammal mammal	0.84	8.28	20	1	(Africa)	same	generalist	>500	herbivore assumed
Caro et al.			megafauna	(medium					Forest				majority
2003	Table 5	mammal	(mammals) Various	to large)	9.72	1.92	20	1	(Africa)	same	generalist	>500	herbivore assumed
Caro et al.			megafauna	mammals					Forest				majority
2003	Table 6	mammal	(mammals)	(small)	0.57	8.20	24	1	(Africa) Forest	same	generalist	>500	herbivore
Caro et al.			Jaguar (<i>Panthera</i>						(Central			>50 -	
2004	Table 2	mammal	onca)	amphibian	1.30	8.47	4	1	America) Forest	across	generalist	100	carnivore
Caro et al.			Jaguar (<i>Panthera</i>						(Central			>50 -	
2004	Table 2	mammal	onca)	mammal	1.70	5.73	4	1	America) Forest	same	generalist	100	carnivore
Caro et al.			Jaguar (<i>Panthera</i>						(Central			>50 -	
2004	Table 2	mammal	onca)	mammal	2.90	2.47	4	1	America) Forest	same	generalist	100	carnivore
Caro et al.			Jaguar (<i>Panthera</i>						(Central			>50 -	
2004	Table 2	mammal	onca)	mammal	0.50	4.33	4	1	America) Forest	same	generalist	100	carnivore
Caro et al.			Jaguar (<i>Panthera</i>						(Central			>50 -	
2004	Table 2	mammal	onca)	bird	73.50	55.47	4	1	America) Forest	across	generalist	100	carnivore
Caro et al.			Baird's tapir						(Central			>100 -	
2004	Table 2	mammal	(Tapirus bairdii)	amphibian	21.50	1.73	4	1	America)	across	specialist	500	herbivore

	Taxonomic												
					abundai	nce of co-							
					occurrin	g species							
				_									
				Co-							Umbrella		
		Umbrella		occurring	umbrella	umbrella				Across	species	Size	
		species		species	species	species	Sample			or same	generalist	class	Trophic
Reference	Source	class	Umbrella species	class	present	absent	size	Variance	Habitat	taxa	or specialist	(kg)	level
Cana at al			De indle ten in						Forest			× 100	
Caro et al.			Baird's tapir						(Central			>100 -	
2004	Table 2	mammal	(Tapırus bairdii)	mammal	6.00	4.30	4	1	America) Forest	same	specialist	500	herbivore
Caro et al.			Baird's tapir						(Central			>100 -	
2004	Table 2	mammal	(Tapirus bairdii)	mammal	2.40	7.90	4	1	America) Forest	same	specialist	500	herbivore
Caro et al.			Baird's tapir						(Central			>100 -	
2004	Table 2	mammal	(Tapirus bairdii)	mammal	0.20	3.77	4	1	America) Forest	same	specialist	500	herbivore
Caro et al.			Baird's tapir						(Central			>100 -	
2004	Table 2	mammal	(<i>Tapirus bairdii</i>) White-lipped	bird	63.00	58.97	4	1	America) Forest	across	specialist	500	herbivore
Caro et al.			peccary (Dicotyles						(Central				
2004	Table 2	mammal	pecari) White-linned	amphibian	3.50	7.73	4	1	America)	across	generalist	>20 - 50	herbivore
Caro et al.			peccary (Dicotyles						(Central				
2004	Table 2	mammal	<i>pecari</i>) White-lipped	mammal	10.50	2.80	4	1	America) Forest	same	generalist	>20 - 50	herbivore
Caro et al.			peccary (<i>Dicotyles</i>						(Central				
2004	Table 2	mammal	<i>pecari</i>) White-lipped	mammal	3.90	2.13	4	1	America) Forest	same	generalist	>20 - 50	herbivore
Caro et al.			peccary (<i>Dicotyles</i>						(Central				
2004	Table 2	mammal	<i>pecari</i>) White-lipped	mammal	4.60	2.30	4	1	America) Forest	same	generalist	>20 - 50	herbivore
Caro et al.			peccary (Dicotyles						(Central				
2004	Table 2	mammal	pecari)	bird	58.90	60.33	4	1	America)	across	generalist	>20 - 50	herbivore

	Taxonomic												
					abundai	nce of co-							
					occurrin	ig species							
				6.							t taskas lla		
		Unabaalla		C0-						A	Umbrella	C:	
		Umbrella		occurring	umbrella	umprella	C			Across	species	Size	Table
D (6	species		species	species	species	Sample			or same	generalist	class	Irophic
Reference	Source	class	Umbrella species	class	present	absent	size	Variance	Forest	taxa	or specialist	(Kg)	level
Caro et al.			Spider monkey						(Central				
2004	Table 2	mammal	(Ateles geoffroyi)	amphibian	0.40	8.77	4	1	America) Forest	across	generalist	>10 - 20	herbivore
Caro et al.			Spider monkey						(Central				
2004	Table 2	mammal	(Ateles geoffroyi)	mammal	0.70	6.07	4	1	America) Forest	same	generalist	>10 - 20	herbivore
Caro et al.			Spider monkey						(Central				
2004	Table 2	mammal	(Ateles geoffroyi)	mammal	1.10	9.20	4	1	America) Forest	same	generalist	>10 - 20	herbivore
Caro et al.			Spider monkey						(Central				
2004	Table 2	mammal	(Ateles geoffroyi)	mammal	6.70	1.60	4	1	America) Forest	same	generalist	>10 - 20	herbivore
Caro et al.			Spider monkey						(Central				
2004	Table 2	mammal	(<i>Ateles geoffroyi</i>) Various	bird	44.50	65.13	4	1	America)	across	generalist	>10 - 20	herbivore assumed
Fontaine			megafauna						Forest				majority
et al. 2007		mammal	(mammals) Various	molluscs	7.70	8.80	145	1	(Africa)	across	generalist	>500	herbivore assumed
Gardner			megafauna						Forest				majority
et al. 2007	Table 1	mammal	(mammals) Various	mammal	2.20	3.70	20	1	(Africa)	same	generalist	>500	herbivore assumed
Gardner			megafauna						Forest				majority
et al. 2007	Table 1	mammal	(mammals) Various	amphibian	210.80	131.30	20	1	(Africa)	across	generalist	>500	herbivore assumed
Gardner			megafauna						Forest				majority
et al. 2007	Table 1	mammal	(mammals)	insect	133.20	131.60	20	1	(Africa)	across	generalist	>500	herbivore

Taxonomic abundance of cooccurring species

				Co-							Umbrella		
		Umbrella		occurring	umbrella	umbrella				Across	species	Size	
		species		species	species	species	Sample			or same	generalist	class	Trophic
Reference	Source	class	Umbrella species	class	present	absent	size	Variance	Habitat	taxa	or specialist	(kg)	level
			Various										assumed
Gardner			megafauna						Forest				majority
et al. 2007	Table 1	mammal	(mammals) Various	bird	186.80	95.50	20	1	(Africa)	across	generalist	>500	herbivore assumed
Gardner			megafauna						Forest				majority
et al. 2007	Table 1	mammal	(mammals) Siberian flying	plant	202.10	91.50	20	1	(Africa)	across	generalist	>500	herbivore
Hurme et	Appendix		squirrel (<i>Pteromys</i>						Forest				
al. 2008	А	mammal	<i>volans</i>) Siberian flying	lichen	10.10	5.40	20	1	(Europe)	across	yes	≤0.25	herbivore
Hurme et	Appendix		squirrel (Pteromys						Forest				
al. 2008	A	mammal	<i>volans</i>) Siberian flying	fungus	32.50	13.60	20	1	(Europe)	across	yes	≤0.25	herbivore
Hurme et	Appendix		squirrel (<i>Pteromys</i>						Forest				
al. 2008	A Table 1	mammal	volans)	insect	4.70	5.90	20	1	(Europe) Forest/	across	yes	≤0.25	herbivore
Ozaki et	(home		Northern goshawk						agricultural				
al. 2006	range) Table 1	bird	(Accipter gentilis)	bird	49.90	33.50	80	1	(Japan) Forest/	same	no	>0.5 - 1	carnivore
Ozaki et	(home		Northern goshawk						agricultural				
al. 2006	range) Table 1	bird	(Accipter gentilis)	insect	295.40	208.30	80	1	(Japan) Forest/	across	no	>0.5 - 1	carnivore
Ozaki et	(home		Northern goshawk						agricultural				
al. 2006	range) Table 1	bird	(Accipter gentilis)	plant	108.80	96.80	80	1	(Japan) Forest/	across	no	>0.5 - 1	carnivore
Ozaki et	(home		Northern goshawk						agricultural				
al. 2006	range)	bird	(Accipter gentilis)	insect	288.30	312.80	80	1	(Japan)	across	no	>0.5 - 1	carnivore

					Тахо	nomic							
					abundai	nce of co-							
					occurrin	ng species	_						
		Umbrella species		Co- occurring species	umbrella	umbrella species	Sample			Across or same	Umbrella species generalist	Size	Trophic
Reference	Source	class	Umbrella species	class	present	absent	size	Variance	Habitat	taxa	or specialist	(kg)	level
Pakkala et al. 2003	text	bird	Capercaillie (Tetrao urogallus)	bird	10.67	1.00	82	1	Forest/ agricultural (Europe)	same	yes	>1 - 5	carnivore
Sergio et al. 2006	Figure 1	bird	Northern Goshawk (A. gentilis), Pygmy Owl (Glaucidium passerinum), Tengmalms Owl (Aegolius funereus), Tawny Owl (S. aluco), Long-Eared Owl	bird	17.19	8.39	50	1	Alpine	same	no	>0.25 - 0.5	carnivore
			rubecula), Blackbird (Turdus merula), Blackcap (Sylvia atricapilla), crested tit (Parus cristatus), Chaffinch (Fringilla coelebs), European										
Sergio et			Goldfinch				- -					>0.02 -	majority
al. 2006	Figure 1	bird	(Carduelis	bird	8.57	8.46	50	1	Alpine	same	no	0.1	omnivore

					Taura								
					Taxo	nomic							
					abunda	nce of co-							
					occurrin	ng species	_						
							-						
				Co-							Umbrella		
		Umbrella		occurring	umbrella	a umbrella				Across	species	Size	
		species		species	species	species	Sample			or same	generalist	class	Trophic
Reference	Source	class	Umbrella species	class	present	absent	size	Variance	Habitat	taxa	or specialist	(kg)	level
			(Bonasa bonasia),										
			European Nightjar										
			(Caprimulgus										
			europaeus), Green										
			Woodpecker										
			(Picus viridis),										
			Grey-headed										
			Woodpecker										
			(Picus canus),										
			Gmelin and										
Sergio et			Eurasian									>0.02 -	majority
al. 2006	Figure 1	bird	Treecreeper	bird	9.64	8.84	50	1	Alpine	same	yes	0.1	omnivore

Appendix B Summary of Diversity, Habitat Complexity and Ecosystem Function by Pond and Season

						Maximum		
Watershed_		Project age	Elevation			temperature		
Pond #	Restoration type	(years)	(m)	Area (m ²)	Water source	(°C)*	Chlorophyll a	Algae†
Chilliwack_1	reconnected, flooded	11	158	13419	surface	18.33	1282.67	0.00
Chilliwack_2	reconnected, flooded	10	381	4211	combined	15.52	706.17	0.01
Chilliwack_3	excavated	2	11	1280	surface	22.07	1000.33	0.00
Chilliwack_4	excavated	8	18	5525	surface	15.76	883.00	0.74
Chilliwack_5	reconnected	20	15	3000	ground	21.47	na	0.19
Chilliwack_6	excavated	2	38	825	surface	15.86	617.00	0.37
Chilliwack_7	excavated	8	19	519	surface	16.40	610.67	0.11
Chilliwack_8	reconnected, flooded	8	422	7231	surface	11.10	923.33	0.10
Chilliwack_9	excavated	8	19	1717	surface	16.64	915.83	0.87
Coquitlam _1	excavated	23	90	4308	surface	20.37	353.75	0.00
Coquitlam _2	excavated	23	124	4045	surface	18.75	736.00	0.00
Coquitlam _3	excavated	5	84	1462	ground	12.75	732.20	0.00
Coquitlam _4	excavated	13	28	3566	surface	19.40	1780.17	0.00
Seymour_1	flooded	7	152	3667	surface	14.75	715.33	0.00
Seymour_2		8	104	532	ground	9.13	970.10	0.00
Seymour_3	flooded	14	167	2679	ground	10.58	502.42	0.00
Seymour_4	flooded	7	168	12000	combined	15.94	368.20	0.00

* Average for warmest consecutive 7-day period
† Proportion of measurements with structural component

Table B.1 Summary of Restoration Techniques and Characteristics of Restored Ponds

						Coefficient of		Depth at
Watershed_	Aquatic					variation in	Maximum depth	water's edge
Pond #	vegetation†	Boulder (>25 cm	Organic matter†	Riparian cover†	Wood†	depth	(cm)	(cm)
Chilliwack_1	0.80	0.00	0.02	0.03	0.17	0.48	235	5.70
Chilliwack_2	0.40	0.01	0.04	0.01	0.57	0.67	179	1.83
Chilliwack_3	1.05	0.00	0.02	0.00	0.05	0.53	177	28.10
Chilliwack_4	1.09	0.00	0.00	0.00	0.35	0.76	390	1.67
Chilliwack_5	1.15	0.00	0.00	0.04	0.17	0.51	156	1.38
Chilliwack_6	0.53	0.00	0.00	0.17	0.32	0.52	171	0.86
Chilliwack_7	0.64	0.00	0.09	0.20	0.42	0.56	261	9.00
Chilliwack_8	0.27	0.06	0.10	0.00	0.65	0.78	241	4.17
Chilliwack_9	0.04	0.06	0.00	0.15	0.25	0.54	185	9.17
Coquitlam _1	0.83	0.04	0.03	0.12	0.69	0.57	218	0.00
Coquitlam _2	0.10	0.05	0.35	0.12	0.70	0.5	248	5.10
Coquitlam _3	0.00	0.18	0.02	0.01	0.98	0.95	351	4.50
Coquitlam _4	0.28	0.00	0.03	0.00	1.00	0.62	174	4.75
Seymour_1	0.09	0.00	0.17	0.01	1.43	0.72	224	24.60
Seymour_2	0.38	0.00	0.09	0.04	0.91	0.43	87	0.00
Seymour_3	0.27	0.02	0.20	0.01	0.68	0.68	227	11.17
Seymour_4	0.31	0.00	0.32	0.08	1.38	0.51	152	0.75

* Average for warmest consecutive 7-day period
† Proportion of measurements with structural component

		Species richness			Abundance (number individuals per trap night)						
	Trapping								Fish_no		
Watershed_pond	session	Listed	Fish	Amphibians	Benthos	O. kisutch	Listed	Fish	stickleback	Amphibians	Benthos
Chilliwack_1	1	2	1.63	2.67	46	0.46	0.05	0.05	0.05	0.57	2654
Chilliwack_2	1	1.77	1.9	1.83	42.33	0.86	0.14	0.00	0.00	0.23	988
Chilliwack_3	1	0	0.92	1.22	36.66	0.00	0.00	21.12	0.88	0.09	1525
Chilliwack_4	1	0	1.06	1	38.66	0.00	0.00	4.15	0.13	0.01	5696
Chilliwack_5	1	1.77	0.79	1.75	39	0.04	0.11	2.13	0.09	0.69	2420
Chilliwack_6	1	2.43	0.84	1.94	41.66	0.00	0.09	20.38	0.11	0.18	1175
Chilliwack_7	1	1	0.71	1.62	43.33	0.08	0.05	11.40	0.03	0.08	2858
Chilliwack_8	1	1.09	1.12	0.99	42	0.85	1.05	0.93	0.93	0.13	806
Chilliwack_9	1	0	1.04	1	42	0.19	0.00	1.46	0.03	0.01	16913
Coquitlam _1	1	1.84	2.76	1.51	42.66	0.40	0.10	0.18	0.18	0.23	3203
Coquitlam _2	1	1.48	1.17	0.5	38.33	0.49	0.00	2.73	0.03	0.05	1511
Coquitlam _3	1	2.1	2.29	1.71	30.33	3.66	0.03	0.17	0.17	0.00	1226
Coquitlam _4	1	1	1.31	1.5	43	0.05	0.08	7.93	0.27	0.13	3492
Seymour_1	1	1.73	3	2.38	32.33	2.63	0.93	0.15	0.15	0.80	1310
Seymour_2	1	1.74	1.98	1.77	25	0.52	0.00	0.17	0.17	0.17	2361
Seymour_3	1	1.49	2.08	0.99	22.33	2.21	0.40	0.40	0.40	0.07	2095
Seymour_4	1	1.64	0.7	0.98	37	1.49	0.31	0.38	0.38	0.04	3552
Chilliwack_1	2	2	1.63	2.67	na	0.20	0.00	0.00	0.00	0.20	na
Chilliwack_2	2	1.77	1.9	1.83	na	0.54	0.49	0.13	0.13	0.67	na
Chilliwack_3	2	0	0.92	1.22	na	0.00	0.00	6.90	0.37	0.43	na
Chilliwack_4	2	0	1.06	1	na	0.13	0.00	8.87	0.11	0.00	na
Chilliwack_5	2	1.77	0.79	1.75	na	0.08	0.13	25.78	0.20	0.53	na
Chilliwack_6	2	2.43	0.84	1.94	na	0.16	0.06	9.16	0.06	0.16	na
Chilliwack_7	2	1	0.71	1.62	na	0.19	0.16	7.42	0.03	0.16	na
Chilliwack_8	2	1.09	1.12	0.99	na	1.59	0.73	0.69	0.69	0.04	na
Chilliwack_9	2	0	1.04	1	na	0.31	0.00	3.66	0.03	0.03	na
Coquitlam _1	2	1.84	2.76	1.51	na	0.10	0.00	0.35	0.33	0.13	na
Coquitlam _2	2	1.48	1.17	0.5	na	0.78	0.05	5.53	0.20	0.03	na
Coquitlam _3	2	2.1	2.29	1.71	na	6.10	0.13	0.30	0.30	0.10	na
Coquitlam _4	2	1	1.31	1.5	na	0.08	0.03	2.93	0.25	0.15	na
Seymour_1	2	1.73	3	2.38	na	4.03	0.51	0.51	0.51	0.03	na
Seymour_2	2	1.74	1.98	1.77	na	2.46	0.38	0.15	0.15	0.27	na
Seymour_3	2	1.49	2.08	0.99	na	4.18	0.45	0.45	0.45	0.00	na
Seymour_4	2	1.64	0.7	0.98	na	2.97	0.21	0.21	0.21	0.13	na

Table B.2 Summary of Species Richness, Abundance and Biomass of Co-occurring Species Groups

			Species r	ichness			Abundanc	ce (number	individuals pe	er trap night)	
	Trapping								Fish_no		
Watershed_pond	session	Listed	Fish	Amphibians	Benthos	O. kisutch	Listed	Fish	stickleback	Amphibians	Benthos
Chilliwack_1	3	2	1.63	2.67	na	0.18	0.00	0.03	0.03	0.21	na
Chilliwack_2	3	1.77	1.9	1.83	na	0.20	0.10	0.12	0.12	0.12	na
Chilliwack_3	3	0	0.92	1.22	na	0.07	0.00	5.70	0.30	0.10	na
Chilliwack_4	3	0	1.06	1	na	0.06	0.00	2.60	0.03	0.00	na
Chilliwack_5	3	1.77	0.79	1.75	na	0.37	0.13	10.42	0.18	1.82	na
Chilliwack_6	3	2.43	0.84	1.94	na	0.38	0.03	10.34	0.09	0.13	na
Chilliwack_7	3	1	0.71	1.62	na	0.23	0.00	2.60	0.00	0.00	na
Chilliwack_8	3	1.09	1.12	0.99	na	1.61	0.39	0.39	0.39	0.00	na
Chilliwack_9	3	0	1.04	1	na	0.37	0.00	1.74	0.03	0.00	na
Coquitlam _1	3	1.84	2.76	1.51	na	0.75	0.05	0.30	0.30	0.48	na
Coquitlam _2	3	1.48	1.17	0.5	na	0.55	0.08	0.68	0.30	2.93	na
Coquitlam _3	3	2.1	2.29	1.71	na	4.43	0.00	0.29	0.29	0.14	na
Coquitlam _4	3	1	1.31	1.5	na	0.27	0.00	2.34	0.39	0.24	na
Seymour_1	3	1.73	3	2.38	na	2.24	0.19	0.24	0.24	0.11	na
Seymour_2	3	1.74	1.98	1.77	na	1.96	0.08	0.12	0.12	0.42	na
Seymour_3	3	1.49	2.08	0.99	na	3.88	0.32	0.41	0.41	0.12	na
Seymour_4	3	1.64	0.7	0.98	na	2.26	0.58	0.87	0.87	0.71	na

	Biomass (grams per trap night)									
				Fish_no						
Watershed_pond	O. kisutch	Listed	Fish	stickleback	Amphibians	Benthos				
Chilliwack_1	0.63	2.50	3.79	3.79	3.31	2.68				
Chilliwack_2	1.65	0.17	0.00	0.00	2.57	0.32				
Chilliwack_3	0.00	0.00	31.31	12.76	0.70	0.49				
Chilliwack_4	0.00	0.00	10.11	3.81	0.40	1.17				
Chilliwack_5	0.05	0.22	2.25	0.36	8.29	0.96				
Chilliwack_6	0.00	1.16	20.24	2.07	2.78	0.31				
Chilliwack_7	0.40	0.02	18.54	1.21	0.94	0.48				
Chilliwack_8	3.43	35.62	35.52	35.52	0.10	0.27				
Chilliwack_9	0.16	0.00	3.26	0.99	0.21	1.05				
Coquitlam _1	0.71	0.06	5.15	5.15	2.37	0.91				
Coquitlam _2	0.56	0.00	4.10	1.01	0.22	0.6				
Coquitlam _3	4.68	1.45	10.25	10.25	0.00	0.34				
Coquitlam _4	0.10	0.11	17.39	10.63	0.48	0.66				
Seymour_1	3.02	14.50	13.57	13.57	0.95	0.39				
Seymour_2	1.07	0.00	3.26	3.26	0.83	0.55				
Seymour_3	4.83	11.00	11.00	11.00	1.08	0.18				
Seymour_4	3.41	10.20	11.52	11.52	0.52	0.97				
Chilliwack_1	0.84	0.00	1.24	1.24	0.00	na				
Chilliwack_2	2.15	2.50	2.10	2.10	6.33	na				
Chilliwack_3	0.00	0.00	10.50	6.05	0.87	na				
Chilliwack_4	0.47	0.00	16.00	2.16	0.00	na				
Chilliwack_5	0.13	0.13	12.48	1.49	3.55	na				
Chilliwack_6	0.59	2.87	13.04	2.87	0.43	na				
Chilliwack_7	1.11	0.55	11.59	1.46	0.55	na				
Chilliwack_8	8.48	29.03	28.87	28.87	0.15	na				
Chilliwack_9	1.45	0.00	8.98	0.76	0.55	na				
Coquitlam _1	0.21	0.00	8.05	8.01	0.36	na				
Coquitlam _2	1.66	2.07	13.48	7.69	0.40	na				
Coquitlam _3	15.52	6.78	16.98	16.98	1.42	na				
Coquitlam _4	0.26	0.06	8.34	5.04	3.60	na				
Seymour_1	12.02	23.10	23.10	23.10	0.76	na				
Seymour_2	11.10	9.04	8.09	8.09	1.17	na				
Seymour_3	9.06	10.76	10.76	10.76	0.00	na				
Seymour_4	7.73	7.40	7.40	7.40	1.74	na				

	Biomass (grams per trap night)											
				Fish_no								
Watershed_pond	O. kisutch	Listed	Fish	stickleback	Amphibians	Benthos						
Chilliwack_1	1.84	0.00	2.03	2.03	0.00	na						
Chilliwack_2	1.14	0.49	1.34	1.34	0.55	na						
Chilliwack_3	0.71	0.00	5.10	1.91	0.42	na						
Chilliwack_4	0.46	0.00	2.69	0.77	0.00	na						
Chilliwack_5	1.83	2.16	7.29	1.90	23.04	na						
Chilliwack_6	2.33	0.05	7.81	1.59	0.82	na						
Chilliwack_7	2.09	0.00	2.25	0.00	0.00	na						
Chilliwack_8	11.30	14.68	14.68	14.68	0.00	na						
Chilliwack_9	0.18	0.00	1.94	0.83	0.00	na						
Coquitlam _1	4.25	1.37	10.48	10.48	8.80	na						
Coquitlam _2	2.33	0.18	15.41	15.01	55.15	na						
Coquitlam _3	21.84	0.00	6.26	6.26	2.02	na						
Coquitlam _4	2.18	0.00	11.84	10.05	4.37	na						
Seymour_1	10.60	11.36	11.97	11.97	1.75	na						
Seymour_2	8.95	2.20	2.51	2.51	8.61	na						
Seymour_3	13.51	11.92	14.07	14.07	1.77	na						
Seymour_4	9.00	18.05	23.19	23.19	13.72	na						

	_	Catos	tomus	_						Onc	orhynchu	S
Watershed	Trapping		Salish	Centrarchid	Cottus	Cyprinidae	Gasterosteus	Lampetra				
_Pond	session	spp.	sucker*	spp	sp.	(spp.)	aculeatus	spp.	clarki*	kistuch	mykiss	tshawytscha
Chilliwack_1	1	0	0	0	1	0	0	0	0	17	0	0
Chilliwack_2	1	0	0	0	0	0	0	0	0	30	0	0
Chilliwack_3	1	2	0	0	6	0	667	0	0	0	0	0
Chilliwack_4	1	0	0	0	10	0	301	0	0	0	0	0
Chilliwack_5	1	0	3	0	0	0	92	1	0	2	0	0
Chilliwack_6	1	0	3	0	1	0	912	1	0	0	0	0
Chilliwack_7	1	0	0	0	1	0	455	0	0	3	0	0
Chilliwack_8	1	0	0	0	0	0	0	0	0	34	0	0
Chilliwack_9	1	0	0	0	2	0	96	0	0	13	0	0
Coquitlam _1	1	0	0	0	5	0	0	0	0	16	2	0
Coquitlam _2	1	0	0	0	1	0	100	0	0	18	0	0
Coquitlam _3	1	0	0	0	0	0	0	0	1	128	5	0
Coquitlam _4	1	0	0	0	8	0	306	0	0	2	0	0
Seymour_1	1	0	0	0	0	0	0	0	1	105	0	0
Seymour_2	1	0	0	0	0	0	0	0	0	15	5	0
Seymour_3	1	0	0	0	0	0	0	0	1	93	3	0
Seymour_4	1	0	0	0	0	0	0	0	0	67	3	0
Chilliwack_1	2	0	0	0	0	0	0	0	0	8	0	0
Chilliwack_2	2	0	0	0	0	0	0	0	0	21	4	0
Chilliwack_3	2	1	0	1	8	0	197	0	0	0	0	0
Chilliwack_4	2	0	0	0	2	0	412	3	0	6	0	0
Chilliwack_5	2	0	5	0	0	0	1023	0	0	3	3	0
Chilliwack_6	2	0	1	0	0	0	291	0	1	5	0	0
Chilliwack_7	2	0	0	0	1	0	229	0	0	6	0	0
Chilliwack_8	2	0	0	0	0	0	0	0	1	78	0	0
Chilliwack_9	2	0	0	0	0	0	127	0	0	11	1	0
Coquitlam _1	2	1	0	0	8	0	1	0	0	4	4	0
Coquitlam _2	2	0	0	0	3	2	213	0	2	31	0	0
Coquitlam _3	2	0	0	0	0	0	0	0	3	183	5	1
Coquitlam _4	2	0	0	2	5	0	107	0	0	3	0	0
Seymour_1	2	0	0	0	0	0	0	0	5	141	0	0
Seymour_2	2	0	0	0	0	0	0	0	4	64	0	0
Seymour_3	2	0	0	0	0	0	0	0	2	159	0	0
Seymour_4	2	0	0	0	0	0	0	0	5	116	0	0

		Catos	tomus							Onc	orhynchu	5
Watershed _Pond	Trapping session	spp.	Salish sucker*	Centrarchid spp	Cottus sp.	Cyprinidae (spp.)	Gasterosteus aculeatus	Lampetra spp.	clarki*	kistuch	mykiss	tshawytscha
Chilliwack_1	3	0	0	0	0	0	0	0	0	2	1	0
Chilliwack_2	3	0	0	0	0	0	0	0	0	8	5	0
Chilliwack_3	3	0	0	0	9	0	162	0	0	2	0	0
Chilliwack_4	3	0	0	0	1	0	90	0	0	2	0	0
Chilliwack_5	3	0	5	0	0	0	389	0	0	14	2	0
Chilliwack_6	3	0	1	0	2	0	328	0	0	12	0	0
Chilliwack_7	3	0	0	0	0	0	78	0	0	7	0	0
Chilliwack_8	3	0	0	0	0	0	0	0	1	79	0	0
Chilliwack_9	3	0	0	0	1	0	60	0	0	13	0	0
Coquitlam _1	3	0	0	0	5	0	0	0	1	30	6	0
Coquitlam _2	3	0	0	0	9	0	15	0	2	22	1	0
Coquitlam _3	3	0	0	0	0	0	0	0	0	124	8	0
Coquitlam _4	3	1	0	0	11	0	80	0	0	11	0	0
Seymour_1	3	0	0	0	0	0	0	0	2	83	3	0
Seymour_2	3	0	0	0	0	0	0	0	2	51	1	0
Seymour_3	3	0	0	0	0	0	0	0	5	132	0	0
Seymour_4	3	0	0	0	0	0	0	0	2	86	11	0

	Trapping	Ptychocheilus	Rhinichthys	Salvelinus	Ambystoma	Lithobates	L.	Pseudacris	Rana	Taricha
Watershed_Pond	session	spp.	cataractae	malma*	gracile	catesbiana	clamitans	regilla	aurora*	granulosa
Chilliwack_1	1	0	0	1	16	0	0	0	1	4
Chilliwack_2	1	0	0	0	0	0	0	0	5	3
Chilliwack_3	1	22	0	0	0	0	3	0	0	0
Chilliwack_4	1	0	0	0	1	0	0	0	0	0
Chilliwack_5	1	0	0	0	8	0	19	0	2	2
Chilliwack_6	1	0	0	0	0	0	7	0	1	0
Chilliwack_7	1	0	0	0	1	0	0	0	2	0
Chilliwack_8	1	0	0	37	0	0	0	0	5	0
Chilliwack_9	1	0	0	0	0	0	0	0	0	1
Coquitlam _1	1	0	0	0	5	0	0	0	4	0
Coquitlam _2	1	0	0	0	2	0	0	0	0	0
Coquitlam _3	1	0	0	0	0	0	0	0	0	0
Coquitlam _4	1	3	0	0	2	0	0	0	3	0
Seymour_1	1	0	0	5	0	0	0	1	31	0
Seymour_2	1	0	0	0	4	0	0	1	0	0
Seymour_3	1	0	0	16	3	0	0	0	0	0
Seymour_4	1	0	0	13	1	0	0	0	1	0
Chilliwack_1	2	0	0	0	8	0	0	0	0	0
Chilliwack_2	2	0	0	1	7	0	0	0	18	1
Chilliwack_3	2	0	0	0	0	0	13	0	0	0
Chilliwack_4	2	0	0	0	0	0	0	0	0	0
Chilliwack_5	2	0	0	0	13	1	6	0	0	1
Chilliwack_6	2	0	0	0	2	0	3	0	0	0
Chilliwack_7	2	0	0	0	0	0	0	0	5	0
Chilliwack_8	2	0	0	33	0	0	0	0	2	0
Chilliwack_9	2	0	0	0	0	0	0	0	0	1
Coquitlam _1	2	0	0	0	5	0	0	0	0	0
Coquitlam _2	2	0	1	0	1	0	0	0	0	0
Coquitlam _3	2	0	0	0	2	0	0	0	0	0
Coquitlam _4	2	3	0	0	5	0	0	0	1	0
Seymour_1	2	0	0	13	1	0	0	0	0	0
Seymour_2	2	0	0	0	1	0	0	0	6	0
Seymour_3	2	0	0	15	0	0	0	0	0	0
Seymour_4	2	0	0	3	5	0	0	0	0	0

	Trapping	Ptychocheilus	Rhinichthys	Salvelinus	Ambystoma	Lithobates	L.	Pseudacris	Rana	Taricha
Watershed_Pond	session	spp.	cataractae	malma*	gracile	catesbiana	clamitans	regilla	aurora*	granulosa
Chilliwack_1	3	0	0	0	8	0	0	0	0	0
Chilliwack_2	3	0	0	0	1	0	0	0	4	0
Chilliwack_3	3	0	0	0	0	1	2	0	0	0
Chilliwack_4	3	0	0	0	0	0	0	0	0	0
Chilliwack_5	3	0	0	0	56	3	9	0	0	1
Chilliwack_6	3	0	0	0	2	0	2	0	0	0
Chilliwack_7	3	0	0	0	0	0	0	0	0	0
Chilliwack_8	3	0	0	18	0	0	0	0	0	0
Chilliwack_9	3	0	0	0	0	0	0	0	0	0
Coquitlam _1	3	0	0	0	18	0	0	0	1	0
Coquitlam _2	3	0	0	0	116	0	0	0	1	0
Coquitlam _3	3	0	0	0	4	0	0	0	0	0
Coquitlam _4	3	4	0	0	10	0	0	0	0	0
Seymour_1	3	0	0	4	3	0	0	0	1	0
Seymour_2	3	0	0	0	11	0	0	0	0	0
Seymour_3	3	0	0	6	4	0	0	0	0	0
Seymour_4	3	0	0	20	25	0	0	0	0	2

	_	Catos	stomus	_						Ond	corhynchus	
Watershed_	Trapping		Salish	Centrarchid		Cyprinidae	Gasterosteus	Lampetra				
Pond	session	spp.	sucker*	spp	Cottus	(spp.)	aculeatus	spp.	clarki*	kistuch	mykiss	tshawytscha
Chilliwack_1	1	0.00	0.00	0.00	68.00	0.00	0.00	0.00	0.00	23.25	0.00	0.00
Chilliwack_2	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	55.50	0.00	0.00
Chilliwack_3	1	11.60	0.00	0.00	111.30	0.00	611.88	0.00	0.00	0.00	0.00	0.00
Chilliwack_4	1	0.00	0.00	0.00	286.00	0.00	472.42	0.00	0.00	0.00	0.00	0.00
Chilliwack_5	1	0.00	3.80	0.00	0.00	0.00	36.20	12.60	0.00	2.30	0.00	0.00
Chilliwack_6	1	0.00	49.70	0.00	38.20	0.00	817.80	5.20	0.00	0.00	0.00	0.00
Chilliwack_7	1	0.00	0.00	0.00	48.50	0.00	692.98	0.00	0.00	16.00	0.00	0.00
Chilliwack_8	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	137.10	0.00	0.00
Chilliwack_9	1	0.00	0.00	0.00	66.50	0.00	152.04	0.00	0.00	10.80	0.00	0.00
Coquitlam _1	1	0.00	0.00	0.00	191.05	0.00	0.00	0.00	0.00	28.35	15.00	0.00
Coquitlam _2	1	0.00	0.00	0.00	37.20	0.00	114.65	0.00	0.00	20.75	0.00	0.00
Coquitlam _3	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.45	163.73	307.80	7.80
Coquitlam _4	1	0.00	0.00	0.00	395.95	0.00	276.32	0.00	0.00	3.80	0.00	0.00
Seymour_1	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.05	120.90	0.00	0.00
Seymour_2	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	31.00	94.65	0.00
Seymour_3	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.32	51.50	0.00	0.00
Seymour_4	1	0.00	0.00	0.00	0.00	0.00	0.00	12.00	0.00	153.31	52.00	0.00
Chilliwack_1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	34.60	0.00	0.00
Chilliwack_2	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	83.90	49.91	0.00
Chilliwack_3	2	0.95	0.00	7.50	173.16	0.00	133.34	0.00	0.00	0.00	0.00	0.00
Chilliwack_4	2	0.00	0.00	0.00	84.40	0.00	650.57	17.10	0.00	21.90	0.00	0.00
Chilliwack_5	2	0.00	5.20	0.00	0.00	0.00	38.63	0.00	0.00	5.30	54.40	0.00
Chilliwack_6	2	0.00	77.90	0.00	0.00	0.00	325.57	0.00	0.43	19.01	0.00	0.00
Chilliwack_7	2	0.00	0.00	0.00	45.20	0.00	314.16	0.00	0.00	34.40	0.00	0.00
Chilliwack_8	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.99	415.41	0.00	0.00
Chilliwack_9	2	0.00	0.00	0.00	0.00	0.00	287.84	0.00	0.00	50.60	26.50	0.00
Coquitlam _1	2	7.54	0.00	0.00	289.40	0.00	1.71	0.00	0.00	8.52	23.46	0.00
Coquitlam _2	2	0.00	0.00	0.00	165.00	56.80	231.47	0.00	2.07	66.35	0.00	0.00
Coquitlam _3	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.74	465.51	299.30	0.00
Coquitlam _4	2	0.00	0.00	8.70	114.30	0.00	132.08	0.00	0.00	10.40	0.00	0.00
Seymour_1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.56	420.60	0.00	0.00
Seymour_2	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.09	288.49	0.00	0.00
Seymour_3	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.70	341.32	0.00	0.00
Seymour_4	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.26	301.39	0.00	0.00

		Catos	stomus							Ond	corhynchus	
Watershed_	Trapping		Salish	Centrarchid		Cyprinidae	Gasterosteus	Lampetra				
Pond	session	spp.	sucker*	spp	Cottus	(spp.)	aculeatus	spp.	clarki*	kistuch	mykiss	tshawytscha
Chilliwack_1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	69.91	4.80	0.00
Chilliwack_2	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	40.79	55.07	0.00
Chilliwack_3	3	0.00	0.00	0.00	57.37	0.00	95.63	0.00	0.00	21.24	0.00	0.00
Chilliwack_4	3	0.00	0.00	0.00	27.01	0.00	67.00	0.00	0.00	16.12	0.00	0.00
Chilliwack_5	3	0.00	213.24	0.00	0.00	0.00	24.07	0.00	0.00	82.89	11.29	0.00
Chilliwack_6	3	0.00	1.52	0.00	49.47	0.00	198.99	0.00	0.00	74.51	0.00	0.00
Chilliwack_7	3	0.00	0.00	0.00	0.00	0.00	67.64	0.00	0.00	62.77	0.00	0.00
Chilliwack_8	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.65	553.83	0.00	0.00
Chilliwack_9	3	0.00	0.00	0.00	29.11	0.00	38.83	0.00	0.00	6.37	0.00	0.00
Coquitlam _1	3	0.00	0.00	0.00	337.26	0.00	0.00	0.00	1.25	169.98	32.02	0.00
Coquitlam _2	3	0.00	0.00	0.00	568.35	0.00	114.65	0.00	0.21	93.35	30.15	0.00
Coquitlam _3	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	611.43	175.33	0.00
Coquitlam _4	3	25.22	0.00	0.00	0.00	0.00	73.23	0.00	0.00	0.00	0.00	0.00
Seymour_1	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.51	392.14	27.56	0.00
Seymour_2	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.20	31.00	7.98	0.00
Seymour_3	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.79	459.21	73.04	0.00
Seymour_4	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.10	341.91	195.67	0.00

Watershed_	Trapping	Ptychocheilus	Rhinichthys	Salvelinus	Ambystoma	Lithobates	L.	Pseudacris	Rana	Taricha
Pond	session	spp.	cataractae	malma*	gracile	catesbiana	clamitans	regilla	aurora*	granulosa
Chilliwack_1	1	0.00	0.00	38.70	101.45	0.00	0.00	0.00	0.50	53.95
Chilliwack_2	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.90	84.20
Chilliwack_3	1	298.30	0.00	0.00	0.00	0.00	23.10	0.00	0.00	0.00
Chilliwack_4	1	0.00	0.00	0.00	29.70	0.00	0.00	0.00	0.00	0.00
Chilliwack_5	1	0.00	0.00	0.00	69.30	0.00	269.40	0.00	28.60	28.60
Chilliwack_6	1	0.00	0.00	0.00	0.00	0.00	122.60	0.00	0.00	0.00
Chilliwack_7	1	0.00	0.00	0.00	36.50	0.00	0.00	0.00	0.00	0.00
Chilliwack_8	1	0.00	0.00	1420.82	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_9	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	14.00	0.00
Coquitlam _1	1	0.00	0.00	0.00	92.20	0.00	0.00	0.00	2.40	0.00
Coquitlam _2	1	0.00	0.00	0.00	8.10	0.00	0.00	0.00	0.00	0.00
Coquitlam _3	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coquitlam _4	1	29.25	0.00	0.00	14.60	0.00	0.00	0.00	0.00	0.00
Seymour_1	1	0.00	0.00	18 0 .9	0.00	0.00	0.00	0.90	37.25	0.00
Seymour_2	1	0.00	0.00	0.00	21.10	0.00	0.00	3.00	0.00	0.00
Seymour_3	1	0.00	0.00	339.70	45.50	0.00	0.00	0.00	0.00	0.00
Seymour_4	1	0.00	0.00	454.25	18.50	0.00	0.00	0.00	0.00	0.00
Chilliwack_1	2	0.00	0.00	0.00	50.75	0.00	0.00	0.00	0.00	0.00
Chilliwack_2	2	0.00	0.00	32.10	169.10	0.00	0.00	0.00	62.25	12.50
Chilliwack_3	2	0.00	0.00	0.00	0.00	0.00	26.12	0.00	0.00	0.00
Chilliwack_4	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_5	2	0.00	0.00	0.00	114.24	7.70	8.55	0.00	0.00	11.60
Chilliwack_6	2	0.00	0.00	0.00	4.80	0.00	8.80	0.00	0.00	0.00
Chilliwack_7	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	16.97	0.00
Chilliwack_8	2	0.00	0.00	1366.55	0.00	0.00	0.00	0.00	7.41	0.00
Chilliwack_9	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	19.10
Coquitlam _1	2	0.00	0.00	0.00	14.33	0.00	0.00	0.00	0.00	0.00
Coquitlam _2	2	0.00	3.00	0.00	15.80	0.00	0.00	0.00	0.00	0.00
Coquitlam _3	2	0.00	0.00	0.00	41.40	0.00	0.00	0.00	0.00	0.00
Coquitlam _4	2	78.50	0.00	0.00	141.60	0.00	0.00	0.00	2.50	0.00
Seymour_1	2	0.00	0.00	683.70	26.75	0.00	0.00	0.00	0.00	0.00
Seymour_2	2	0.00	0.00	0.00	5.85	0.00	0.00	0.00	24.61	0.00
Seymour_3	2	0.00	0.00	382.43	0.00	0.00	0.00	0.00	0.00	0.00
Seymour_4	2	0.00	0.00	161.60	67.90	0.00	0.00	0.00	0.00	0.00

Watershed_	Trapping	Ptychocheilus	Rhinichthys	Salvelinus	Ambystoma	Lithobates	L.	Pseudacris	Rana	Taricha
Pond	session	spp.	cataractae	malma*	gracile	catesbiana	clamitans	regilla	aurora*	granulosa
Chilliwack_1	3	0.00	0.00	0.00	72.49	0.00	0.00	0.00	0.00	0.00
Chilliwack_2	3	0.00	0.00	0.00	2.42	0.00	0.00	0.00	5.20	0.00
Chilliwack_3	3	0.00	0.00	0.00	0.00	6.14	6.52	0.00	0.00	0.00
Chilliwack_4	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_5	3	0.00	0.00	0.00	69.30	16.85	37.47	0.00	0.00	8.60
Chilliwack_6	3	0.00	0.00	0.00	21.60	0.00	4.52	0.00	0.00	0.00
Chilliwack_7	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_8	3	0.00	0.00	687.58	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_9	3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coquitlam _1	3	0.00	0.00	0.00	347.09	0.00	0.00	0.00	0.00	0.00
Coquitlam _2	3	0.00	0.00	0.00	2201.18	0.00	0.00	0.00	0.00	5.00
Coquitlam _3	3	0.00	0.00	0.00	56.46	0.00	0.00	0.00	0.00	0.00
Coquitlam _4	3	13.81	0.00	0.00	179.17	0.00	0.00	0.00	0.00	0.00
Seymour_1	3	0.00	0.00	1039.51	59.69	0.00	0.00	0.00	5.00	0.00
Seymour_2	3	0.00	0.00	0.00	223.73	0.00	0.00	0.00	0.00	0.00
Seymour_3	3	0.00	0.00	106.56	60.29	0.00	0.00	0.00	0.00	0.00
Seymour_4	3	0.00	0.00	454.25	493.29	0.00	0.00	0.00	0.00	28.08

Watershed_	Trapping							Polycentropo
Pond	Session	Baetidae	Leptophlebiidae	Leuctridae	Capnidae	Nemouridae	Chloroperlidae	didae
Chilliwack_1	1	12	324	0	0	3	1	3
Chilliwack_2	1	25	9	1	0	1	0	0
Chilliwack_3	1	20	0	0	0	0	0	0
Chilliwack_4	1	81	3	0	0	0	0	0
Chilliwack_5	1	9	0	0	0	0	0	0
Chilliwack_6	1	16	1	0	0	0	0	0
Chilliwack_7	1	13	52	0	0	0	0	0
Chilliwack_8	1	14	4	0	0	0	0	0
Chilliwack_9	1	13	327	0	8	9	0	6
Coquitlam _1	1	6	6	6	6	6	6	6
Coquitlam _2	1	5	78	0	0	39	0	1
Coquitlam _3	1	1	32	1	1	1	6	0
Coquitlam _4	1	6	34	0	0	0	0	0
Seymour_1	1	26	293	7	0	12	3	19
Seymour_2	1	14	35	0	0	4	0	0
Seymour_3	1	0	18	0	1	0	0	0
Seymour_4	1	18	56	0	0	4	0	1

Watershed_	Lepidostomat					Hydrophiloi			
Pond	idae	Limnephilidae	Hydroptilidae	Leptoceridae	Trichoptera	dea	Haliplidae	Gyrinidae	Gyrinidae
Chilliwack_1	33	60	0	0	0	3	18	0	0
Chilliwack_2	2	12	19	0	0	0	0	0	0
Chilliwack_3	6	4	0	2	2	1	0	0	0
Chilliwack_4	5	4	12	0	0	9	60	0	0
Chilliwack_5	0	9	16	2	1	1	14	0	0
Chilliwack_6	3	1	0	0	1	15	1	0	0
Chilliwack_7	3	24	1	0	0	0	24	0	0
Chilliwack_8	3	16	0	0	0	0	5	0	0
Chilliwack_9	2	103	2	0	25	0	5	0	0
Coquitlam _1	6	6	6	6	6	6	6	6	6
Coquitlam _2	5	24	0	0	0	0	0	2	5
Coquitlam _3	2	9	0	0	0	0	0	0	0
Coquitlam _4	1	3	0	2	7	1	0	0	2
Seymour_1	0	3	0	1	0	0	0	0	0
Seymour_2	13	1	0	0	0	0	0	0	0
Seymour_3	0	2	0	0	0	0	0	0	0
Seymour_4	12	7	0	1	0	0	0	0	1

Watershed_							Ceratopog	
Pond	Megaloptera	Chironomini	Tanytarsini	Tanypodinae	Orthocladinae	Chironomidae	onidae	Tipulidae
Chilliwack_1	3	21	31	60	32	33	114	2
Chilliwack_2	3	3	75	326	15	7	7	0
Chilliwack_3	10	40	265	114	128	23	20	0
Chilliwack_4	12	0	5	23	41	54	94	18
Chilliwack_5	0	92	57	106	38	29	22	0
Chilliwack_6	0	25	225	2	23	23	245	3
Chilliwack_7	35	34	126	79	190	44	54	0
Chilliwack_8	0	0	7	206	9	9	26	1
Chilliwack_9	1	64	799	0	2980	444	85	123
Coquitlam _1	6	6	6	6	6	6	6	6
Coquitlam _2	0	4	321	133	140	58	20	1
Coquitlam _3	0	0	4	18	114	3	12	0
Coquitlam _4	19	468	907	100	156	92	45	0
Seymour_1	0	6	133	85	174	34	44	6
Seymour_2	0	18	634	92	156	38	27	0
Seymour_3	4	1	230	65	222	42	1	2
Seymour_4	3	1	116	69	137	33	198	6

Watershed_

Pond	Tabanidae	Dixidae	Culicidae	Empididae	Zigoptera	Anysoptera	Gerridae	Corixidae	Naididae
Chilliwack_1	6	1	3	0	12	8	0	0	31
Chilliwack_2	0	0	0	1	1	1	0	0	19
Chilliwack_3	1	1	2	0	5	0	0	9	108
Chilliwack_4	0	0	0	0	2	3	0	0	1148
Chilliwack_5	0	0	0	0	4	0	0	0	851
Chilliwack_6	1	16	1	0	0	0	2	56	3
Chilliwack_7	0	1	1	0	4	0	1	20	880
Chilliwack_8	3	4	0	0	0	1	0	0	139
Chilliwack_9	0	0	0	1	0	0	0	0	7935
Coquitlam _1	6	6	6	6	6	6	6	6	6
Coquitlam _2	3	12	0	0	49	5	1	0	27
Coquitlam _3	4	0	0	0	0	0	0	0	796
Coquitlam _4	0	36	0	0	5	19	0	0	256
Seymour_1	4	0	0	0	0	9	0	0	77
Seymour_2	0	22	0	0	0	14	3	0	197
Seymour_3	1	0	0	3	0	0	0	1	26
Seymour_4	3	4	0	3	0	8	0	0	396
Table B.5 Summary of Benthic Invertebrate Abundance

Watershed_			Lumbriculi							
Pond	Tubificidae	Lumbricidae	dae	Enchytraeidae	Hydracarina	Oribatida	Turbellaria	Nematoda	Hirudinaea	Planorbidae
Chilliwack_1	4	4	862	11	107	1	1	5	0	12
Chilliwack_2	3	0	29	1	14	0	0	16	0	17
Chilliwack_3	105	0	0	0	8	0	0	2	3	3
Chilliwack_4	21	6	198	125	556	0	0	288	0	10
Chilliwack_5	3	0	2	0	56	3	0	11	2	150
Chilliwack_6	0	0	1	0	77	0	0	1	0	16
Chilliwack_7	61	0	82	6	126	0	0	139	0	53
Chilliwack_8	20	0	78	0	7	10	0	1	0	22
Chilliwack_9	56	24	151	44	384	0	0	614	1	185
Coquitlam _1	6	6	6	6	6	6	6	6	6	6
Coquitlam _2	13	0	102	0	113	3	0	9	0	86
Coquitlam _3	1	0	155	10	10	0	1	0	0	0
Coquitlam _4	13	0	143	1	79	4	2	12	0	34
Seymour_1	5	0	128	4	12	0	0	10	0	14
Seymour_2	73	0	0	0	339	0	0	43	0	187
Seymour_3	0	0	91	5	43	4	0	1212	0	0
Seymour_4	1485	0	268	10	63	0	0	298	0	34

Table B.5 Summary of Benthic Invertebrate Abundance

Watershed_

Pond	Physa	Lymnaea	Ancylidae	Sphaeridae	Amphipoda	Ostracoda	Hydra
Chilliwack_1	1	3	0	83	326	4	0
Chilliwack_2	0	0	0	262	2	17	0
Chilliwack_3	3	7	1	74	427	28	0
Chilliwack_4	3	0	0	0	59	2227	0
Chilliwack_5	24	0	7	107	80	508	2
Chilliwack_6	263	14	0	0	13	0	0
Chilliwack_7	60	32	0	60	0	55	0
Chilliwack_8	0	0	0	109	0	4	0
Chilliwack_9	17	2	0	9	0	231	15
Coquitlam _1	6	6	6	6	6	6	6
Coquitlam _2	0	0	0	81	0	3	0
Coquitlam _3	0	0	0	0	0	6	0
Coquitlam _4	4	18	0	29	460	8	1
Seymour_1	0	0	0	12	0	1	1
Seymour_2	0	0	0	138	0	14	0
Seymour_3	0	0	0	1	0	0	0
Seymour_4	0	0	0	15	0	1	0

Appendix C Summary of Measures of Diversity, Habitat Complexity and Ecosystem Function and Non-significant Results

				Mea	asures of div	/ersitv			Habitat	complexity		Measures	of ecosyste	em function
		Years				ereny			Coefficient			BI bm	Vert bm	
Watershed	Trapping	since						Habitat	of variation		Complexity	(a/3 min	(g/trap	Chl <i>a</i> bm
pond	session	restoration	BI SR	BI FR	BI FT SD	Vert SR	Vert FR	richness	of depth	Complexity	category	kick	night)	(µa/cm2)
Chilliwack 1	1	11	46	4.66	0.76	7	6.63	2.34	0.48	0.51	low	2.68	7.73	1282.67
Chilliwack 2	1	10	42.33	6	1.3	4.69	5.55	2.9	0.67	0.67	medium	0.32	4.23	706.17
Chilliwack 3	1	2	36.66	6	0.63	2.76	2.09	2.08	0.53	0.51	low	0.49	32.01	1000.33
Chilliwack 4	1	8	38.66	4.66	0.6	2.48	3.29	2.98	0.76	0.74	hiah	1.17	10.51	883.00
Chilliwack 5	1	20	39	6	0.74	3.63	4.78	2.91	0.51	0.60	medium	0.96	10.60	0.00
Chilliwack 6	1	2	41.66	4	1.1	2.29	1.84	3	0.52	0.61	medium	0.31	23.03	617.00
Chilliwack 7	1	8	43.33	5	0.72	2.82	5.08	3.79	0.56	0.73	high	0.48	19.87	610.67
Chilliwack 8	1	8	42	5	1.21	3.21	6.01	4.42	0.78	0.91	high	0.27	39.05	923.33
Chilliwack 9	1	8	42	5.33	0.45	3.76	3.89	3.33	0.54	0.66	medium	1.05	3.63	915.83
Coquitlam 1	1	13	42.66	5.66	0.72	7.57	5.51	2.82	0.57	0.64	medium	0.91	8.23	353.75
Coquitlam 2	1	13	38.33	5	1.11	4.22	3.3	3.55	0.5	0.66	medium	0.6	4.88	736.00
Coquitlam 3	1	5	30.33	3	0.26	3.26	4.18	2.29	0.95	0.76	high	0.34	14.92	732.20
Coquitlam 4	1	13	43	5	0.45	5.27	3.34	2.47	0.62	0.61	medium	0.66	17.96	1780.17
Seymour 1	1	7	32.33	5.33	0.65	3.76	2.98	2.71	0.72	0.70	high	0.39	17.55	715.33
Seymour_2	1	8	25	4.66	1.05	5.05	5.95	2.9	0.43	0.56	low	0.55	5.16	970.10
Seymour 3	1	14	22.33	3	0.4	3.61	5.17	3.42	0.68	0.74	high	0.18	16.92	502.42
Seymour_4	1	7	37	5	0.63	5.04	5	2.97	0.51	0.61	medium	0.97	15.44	368.20
Chilliwack_1	2	11	46	4.66	0.76	7	3	2.34	0.48	0.51	low	2.68	2.08	1282.67
Chilliwack_2	2	10	42.33	6	1.3	4.69	4.96	2.9	0.67	0.67	medium	0.32	10.58	706.17
Chilliwack_3	2	2	36.66	6	0.63	2.76	2.38	2.08	0.53	0.51	low	0.49	11.37	1000.33
Chilliwack_4	2	8	38.66	4.66	0.6	2.48	2.44	2.98	0.76	0.74	high	1.17	16.47	883.00
Chilliwack_5	2	20	39	6	0.74	3.63	1.99	2.91	0.51	0.60	medium	0.96	16.16	0.00
Chilliwack_6	2	2	41.66	4	1.1	2.29	2.21	3	0.52	0.61	medium	0.31	14.06	617.00
Chilliwack_7	2	8	43.33	5	0.72	2.82	3.28	3.79	0.56	0.73	high	0.48	13.25	610.67
Chilliwack_8	2	8	42	5	1.21	3.21	3.7	4.42	0.78	0.91	high	0.27	37.50	923.33
Chilliwack_9	2	8	42	5.33	0.45	3.76	3.04	3.33	0.54	0.66	medium	1.05	10.97	915.83
Coquitlam _1	2	13	42.66	5.66	0.72	7.57	6.08	2.82	0.57	0.64	medium	0.91	8.62	353.75
Coquitlam _2	2	13	38.33	5	1.11	4.22	3.17	3.55	0.5	0.66	medium	0.6	15.53	736.00
Coquitlam _3	2	5	30.33	3	0.26	3.26	3.77	2.29	0.95	0.76	high	0.34	33.92	732.20
Coquitlam _4	2	13	43	5	0.45	5.27	3.85	2.47	0.62	0.61	medium	0.66	12.20	1780.17
Seymour_1	2	7	32.33	5.33	0.65	3.76	5.84	2.71	0.72	0.70	high	0.39	35.88	715.33
Seymour_2	2	8	25	4.66	1.05	5.05	4	2.9	0.43	0.56	low	0.55	20.36	970.10
Seymour_3	2	14	22.33	3	0.4	3.61	4.28	3.42	0.68	0.74	high	0.18	19.83	502.42
Seymour_4	2	7	37	5	0.63	5.04	4.4	2.97	0.51	0.61	medium	0.97	16.87	368.20
Chilliwack_1	3	11	46	4.66	0.76	7	4	2.34	0.48	0.51	low	2.68	3.87	1282.67
Chilliwack_2	3	10	42.33	6	1.3	4.69	3.75	2.9	0.67	0.67	medium	0.32	3.04	706.17
Chilliwack_3	3	2	36.66	6	0.63	2.76	1.96	2.08	0.53	0.51	low	0.49	6.23	1000.33

Table C.1 Summary of Years Since Restoration, Measures of Diversity, Habitat Complexity and Ecosystem Function by Season and Pond

Table C.1 Summary of Years Since Restoration, Measures of Diversity, Habitat Complexity and Ecosystem Function by Season and Pond

				Measures of diversity					Habitat	complexity		Measures of ecosystem function		
		Years							Coefficient			BI_bm	Vert_bm	
Watershed_	Trapping	since						Habitat	of variation		Complexity	(g/3 min	(g/trap	Chla bm
pond	session	restoration	BI_SR	BI_FR	BI_FT_SD	Vert_SR	Vert_FR	richness	of depth	Complexity	category	kick	night)	(µg/cm2)
Chilliwack_4	3	8	38.66	4.66	0.6	2.48	3.14	2.98	0.76	0.74	high	1.17	3.15	883.00
Chilliwack_5	3	20	39	6	0.74	3.63	2.78	2.91	0.51	0.60	medium	0.96	32.17	0.00
Chilliwack_6	3	2	41.66	4	1.1	2.29	2.4	3	0.52	0.61	medium	0.31	10.96	617.00
Chilliwack_7	3	8	43.33	5	0.72	2.82	4.63	3.79	0.56	0.73	high	0.48	4.35	610.67
Chilliwack_8	3	8	42	5	1.21	3.21	3.89	4.42	0.78	0.91	high	0.27	25.98	923.33
Chilliwack_9	3	8	42	5.33	0.45	3.76	2.79	3.33	0.54	0.66	medium	1.05	2.13	915.83
Coquitlam _1	3	13	42.66	5.66	0.72	7.57	4.77	2.82	0.57	0.64	medium	0.91	23.53	353.75
Coquitlam _2	3	13	38.33	5	1.11	4.22	3.62	3.55	0.5	0.66	medium	0.6	72.90	736.00
Coquitlam _3	3	5	30.33	3	0.26	3.26	3.5	2.29	0.95	0.76	high	0.34	30.12	732.20
Coquitlam _4	3	13	43	5	0.45	5.27	4.75	2.47	0.62	0.61	medium	0.66	18.39	1780.17
Seymour_1	3	7	32.33	5.33	0.65	3.76	4.16	2.71	0.72	0.70	high	0.39	24.32	715.33
Seymour_2	3	8	25	4.66	1.05	5.05	3.51	2.9	0.43	0.56	low	0.55	20.07	970.10
Seymour_3	3	14	22.33	3	0.4	3.61	5.07	3.42	0.68	0.74	high	0.18	29.35	502.42
Seymour_4	3	7	37	5	0.63	5.04	4.98	2.97	0.51	0.61	medium	0.97	45.91	368.20

Benthic invertebrate = BI Vertebrate = Vert Species richness = SR Functional richness = FR Shannon diversity index = FT_SD habitat complexity = complexity

Table C.2 Non-significant Results from Mixed Models

Response variable	Explanatory variables	Sample siz	ze F ratio	P value	Model Pseudo R ²
vertebrate biomass*	complexity	51	$F_{1,45} = 0.06$	0.81	0.19
	BI_SR	51	$F_{1,45} = 0.89$	0.35	
	complexity X BI_SR	51	$F_{1,45} = 0.41$	0.52	
	BI_FR	51	F _{1,47} = 1.26	0.27	0.04
	complexity*	51	F _{1,45} = 2.13	0.15	0.13
	BI_FR*	51	$F_{1,45} = 1.18$	0.28	
	complexity X BI_FR*	51	F _{1,45} = 1.23	0.27	
	BI_FT_SD	51	$F_{1,47} = 0.16$	0.69	-0.01
	complexity	51	$F_{1,45} = 0.30$	0.58	0.09
	BI_FT_SD	51	F _{1,45} = 1.83	0.18	
	complexity X BI_FT_SD	51	$F_{1,45} = 2.03$	0.16	
	complexity	51	F _{1,45} = 0.01	0.94	0.11
	vert_SR	51	$F_{1,45} = 0.48$	0.49	
	complexity X vert_SR	51	$F_{1,45} = 0.24$	0.63	
	vert_FR	51	$F_{1,47} = 0.13$	0.72	0.1
	years	51	$F_{1,47} = 0.12$	0.73	-0.01

Table C.2 Non-significant Results from Mixed Models

Response variable	Explanatory variables	Sample size	e F ratio	P value	Model Pseudo R ²
benthic invertebrate	complexity	17	$F_{1,13} = 0.00$	0.99	0.39
biomass	BI_SR	17	$F_{1,13} = 0.49$	0.49	
	complexity X BI_SR	17	$F_{1,13} = 0.15$	0.7	
	BI_FR	17	$F_{1,15} = 2.30$	0.15	0.12
	complexity	17	F _{1,13} = 1.86	0.2	0.31
	BI_FR	17	$F_{1,13} = 0.94$	0.35	
	complexity X BI_FR	17	$F_{1,13} = 1.20$	0.29	
	BI_FT_SD	17	$F_{1,15} = 0.79$	0.39	0.04
	complexity	17	F _{1,13} = 3.23	0.1	0.31
	BI_FT_SD	17	F _{1,13} = 1.55	0.23	
	complexity X BI_FT_SD	17	F _{1,13} = 1.27	0.28	
	vert_FR	17	$F_{1,15} = 0.52$	0.48	0.02
	time	17	F _{1,15} = 1.15	0.3	0.07

Table C.2 Non-significant Results from Mixed Models

Response variable	Explanatory variables	Sample siz	e F ratio	P value	Model Pseudo R ²
chlorophyll a biomass	complexity	16	F _{1,14} = 1.24	0.28	0.07
	BI_SR	16	F _{1,14} = 1.12	0.31	0.07
	complexity	16	$F_{1,12} = 0.06$	0.81	0.13
	BI_SR	16	$F_{1,12} = 0.00$	0.95	
	complexity X BI_SR	16	$F_{1,12} = 0.01$	0.94	
	BI_FR	16	F _{1,14} = 0.22	0.65	0.01
	complexity	16	F _{1,12} = 0.29	0.6	0.08
	BI_FR	16	$F_{1,12} = 0.14$	0.71	
	complexity X BI_FR	16	$F_{1,12} = 0.16$	0.7	
	BI_FT_SD	16	F _{1,14} = 0.18	0.68	0.01
	vert_SR	16	F _{1,14} = 0.21	0.65	0.01
	vert_FR	16	F _{1,14} = 0.12	0.74	0.01
	complexity	16	$F_{1,12} = 0.19$	0.67	0.08
	vert_FR	16	$F_{1,12} = 0.03$	0.86	
	complexity X vert_FR	16	$F_{1,12} = 0.02$	0.88	
	years	16	F _{1,14} = 0.22	0.65	0.01

Benthic invertebrate = BI Vertebrate = vert Species richness = SR Functional richness = FR Functional trait Shannon diversity index = FT_SD habitat complexity = complexity

* square root transformed † squared

 $\pm \log_{10}$ transformed

Appendix D Summary of Species Abundance and Biomass

Watershed_	Trapping	chinook salmon	coho salmon	cutthroat	longnose	Dolly Varden	lamprey	pike	rainbow trout	Salish
Chilliwack 1	1	0.00	0.46	0.00	0.00	0.03	0.00	0.00	0.00	0.00
Chilliwack 2	1	0.00	0.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack 3	1	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00
Chilliwack_4	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_5	1	0.00	0.04	0.00	0.00	0.00	0.02	0.00	0.00	0.07
Chilliwack_6	1	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.07
Chilliwack_7	1	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_8	1	0.00	0.85	0.00	0.00	0.93	0.00	0.00	0.00	0.00
Chilliwack_9	1	0.00	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coquitlam _1	1	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.05	0.00
Coquitlam _2	1	0.00	0.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coquitlam _3	1	0.03	3.66	0.03	0.00	0.00	0.00	0.00	0.14	0.00
Coquitlam _4	1	0.00	0.05	0.00	0.00	0.00	0.00	0.08	0.00	0.00
Seymour_1	1	0.00	2.63	0.03	0.00	0.13	0.00	0.00	0.00	0.00
Seymour_2	1	0.00	0.52	0.00	0.00	0.00	0.00	0.00	0.17	0.00
Seymour_3	1	0.00	2.21	0.02	0.00	0.38	0.00	0.00	0.00	0.00
Seymour_4	1	0.00	1.49	0.00	0.00	0.29	0.27	0.00	0.07	0.00
Chilliwack_1	2	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_2	2	0.00	0.54	0.00	0.00	0.03	0.00	0.00	0.10	0.00
Chilliwack_3	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_4	2	0.00	0.13	0.00	0.00	0.00	0.06	0.00	0.00	0.00
Chilliwack_5	2	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.08	0.13
Chilliwack_6	2	0.00	0.16	0.03	0.00	0.00	0.00	0.00	0.00	0.03
Chilliwack_7	2	0.00	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_8	2	0.00	1.59	0.02	0.00	0.67	0.00	0.00	0.00	0.00
Chilliwack_9	2	0.00	0.31	0.00	0.00	0.00	0.00	0.00	0.03	0.00
Coquitlam _1	2	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.10	0.00
Coquitlam _2	2	0.00	0.78	0.05	0.03	0.00	0.00	0.00	0.00	0.00
Coquitlam _3	2	0.00	6.10	0.10	0.00	0.00	0.00	0.00	0.17	0.00
Coquitlam _4	2	0.00	0.08	0.00	0.00	0.00	0.00	0.08	0.00	0.00
Seymour_1	2	0.00	4.03	0.14	0.00	0.37	0.00	0.00	0.00	0.00
Seymour_2	2	0.00	2.46	0.15	0.00	0.00	0.00	0.00	0.00	0.00
Seymour_3	2	0.00	4.18	0.05	0.00	0.39	0.00	0.00	0.00	0.00
Seymour_4	2	0.00	2.97	0.13	0.00	0.08	0.00	0.00	0.00	0.00

Watershed_ pond #	Trapping session	chinook salmon	coho salmon	cutthroat trout	longnose dace	Dolly Varden	lamprey	pike minnow	rainbow trout	Salish sucker
Chilliwack_1	3	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.03	0.00
Chilliwack_2	3	0.00	0.20	0.00	0.00	0.00	0.00	0.00	0.12	0.00
Chilliwack_3	3	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_4	3	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_5	3	0.00	0.37	0.00	0.00	0.00	0.00	0.00	0.05	0.13
Chilliwack_6	3	0.00	0.38	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Chilliwack_7	3	0.00	0.18	0.00	0.00	0.53	0.00	0.00	0.00	0.00
Chilliwack_8	3	0.00	1.61	0.02	0.00	14.03	0.00	0.00	0.00	0.00
Chilliwack_9	3	0.00	0.37	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coquitlam _1	3	0.00	0.75	0.03	0.00	0.00	0.00	0.00	0.15	0.00
Coquitlam _2	3	0.00	0.55	0.05	0.00	0.00	0.00	0.00	0.03	0.00
Coquitlam _3	3	0.00	4.43	0.00	0.00	0.00	0.00	0.00	0.29	0.00
Coquitlam _4	3	0.00	0.27	0.00	0.00	0.00	0.00	0.10	0.00	0.00
Seymour_1	3	0.00	2.24	0.05	0.00	0.11	0.00	0.00	0.08	0.00
Seymour_2	3	0.00	1.96	0.08	0.00	0.00	0.00	0.00	0.04	0.00
Seymour_3	3	0.00	3.88	0.15	0.00	0.18	0.00	0.00	0.09	0.00
Seymour_4	3	0.00	2.87	0.07	0.00	0.60	0.00	0.00	0.37	0.00

			three-							rough-	
Watershed_		red-sided	spined		juvenile			NW	red-legged	skinned	
pond #	sculpin	shiner	stickleback	sucker (sp.)	centrarchid	bullfrog	green frog	salamander	frog	newt	tree frog
Chilliwack_1	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.43	0.03	0.11	0.00
Chilliwack_2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.09	0.00
Chilliwack_3	0.18	0.00	20.21	0.06	0.00	0.00	0.09	0.00	0.00	0.00	0.00
Chilliwack_4	0.13	0.00	4.01	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Chilliwack_5	0.00	0.00	2.04	0.00	0.00	0.00	0.42	0.18	0.04	0.04	0.00
Chilliwack_6	0.02	0.00	20.27	0.00	0.00	0.00	0.16	0.00	0.02	0.00	0.00
Chilliwack_7	0.03	0.00	11.38	0.00	0.00	0.00	0.00	0.03	0.05	0.00	0.00
Chilliwack_8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00
Chilliwack_9	0.03	0.00	1.43	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
Coquitlam _1	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.10	0.00	0.00
Coquitlam _2	0.03	0.00	2.70	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00
Coquitlam _3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coquitlam _4	0.20	0.00	7.65	0.00	0.00	0.00	0.00	0.05	0.08	0.00	0.00
Seymour_1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.78	0.00	0.03
Seymour_2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.03
Seymour_3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00
Seymour_4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.00
Chilliwack_1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00
Chilliwack_2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.46	0.03	0.00
Chilliwack_3	0.27	0.00	6.57	0.03	0.03	0.00	0.43	0.00	0.00	0.00	0.00
Chilliwack_4	0.04	0.00	8.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_5	0.00	0.00	25.58	0.00	0.00	0.03	0.15	0.33	0.00	0.03	0.00
Chilliwack_6	0.00	0.00	9.09	0.00	0.00	0.00	0.09	0.06	0.00	0.00	0.00
Chilliwack_7	0.03	0.00	7.39	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00
Chilliwack_8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00
Chilliwack_9	0.00	0.00	3.63	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00
Coquitlam _1	0.20	0.00	0.03	0.03	0.00	0.00	0.00	0.13	0.00	0.00	0.00
Coquitlam _2	0.08	0.05	5.33	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Coquitlam _3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00
Coquitlam _4	0.13	0.00	2.68	0.00	0.05	0.00	0.00	0.13	0.03	0.00	0.00
Seymour_1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Seymour_2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.23	0.00	0.00
Seymour_3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Seymour_4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00

			three-							rough-	
Watershed_		red-sided	spined		juvenile			NW	red-legged	skinned	
pond #	sculpin	shiner	stickleback	sucker (sp.)	centrarchid	bullfrog	green frog	salamander	frog	newt	tree frog
Chilliwack_1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00
Chilliwack_2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.12	0.00	0.00
Chilliwack_3	0.30	0.00	5.40	0.00	0.00	0.03	0.07	0.00	0.00	0.00	0.00
Chilliwack_4	0.03	0.00	2.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_5	0.00	0.00	10.24	0.00	0.00	0.08	0.24	1.47	0.00	0.03	0.00
Chilliwack_6	0.06	0.00	10.25	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00
Chilliwack_7	0.00	0.00	2.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_9	0.03	0.00	1.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coquitlam _1	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.45	0.03	0.00	0.00
Coquitlam _2	0.23	0.00	0.38	0.00	0.00	0.00	0.00	2.90	0.03	0.00	0.00
Coquitlam _3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.00
Coquitlam _4	0.27	0.00	1.95	0.02	0.00	0.00	0.00	0.24	0.00	0.00	0.00
Seymour_1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.11	0.00	0.00
Seymour_2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.42	0.00	0.00	0.00
Seymour_3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.00	0.00
Seymour_4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.83	0.00	0.07	0.00

Watershed_	Trapping	chinook	coho	cutthroat	longnose	Dolly		pike	rainbow	Salish	
pond #	session	salmon	salmon	trout	dace	Varden	lamprey	minnow	trout	sucker	sculpin
Chilliwack_1	1	0.00	0.63	0.00	0.00	1.05	0.00	0.00	0.00	0.00	1.84
Chilliwack_2	1	0.00	1.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_3	1	0.00	0.00	0.00	0.00	0.00	0.00	6.01	0.00	0.00	3.37
Chilliwack_4	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.81
Chilliwack_5	1	0.00	0.05	0.00	0.00	0.00	0.28	0.00	0.00	0.08	0.00
Chilliwack_6	1	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.00	1.10	0.85
Chilliwack_7	1	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.21
Chilliwack_8	1	0.00	3.43	0.00	0.00	35.52	0.00	0.00	0.00	0.00	0.00
Chilliwack_9	1	0.00	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.99
Coquitlam _1	1	0.00	0.71	0.00	0.00	0.00	0.00	0.00	0.38	0.00	4.78
Coquitlam _2	1	0.00	0.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.01
Coquitlam _3	1	0.22	4.68	1.45	0.00	0.00	0.00	0.00	8.79	0.00	0.00
Coquitlam _4	1	0.00	0.10	0.00	0.00	0.00	0.00	0.73	0.00	0.00	9.90
Seymour_1	1	0.00	3.02	9.05	0.00	4.52	0.00	0.00	0.00	0.00	0.00
Seymour_2	1	0.00	1.07	0.00	0.00	0.00	0.00	0.00	3.26	0.00	0.00
Seymour_3	1	0.00	1.23	2.32	0.00	8.09	0.00	0.00	0.00	0.00	0.00
Seymour_4	1	0.00	3.41	0.00	0.00	10.09	0.27	0.00	1.16	0.00	0.00
Chilliwack_1	2	0.00	0.84	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_2	2	0.00	2.15	0.00	0.00	0.82	0.00	0.00	1.28	0.00	0.00
Chilliwack_3	2	0.00	0.28	0.00	0.00	0.00	0.00	0.00	0.78	0.00	9.65
Chilliwack_4	2	0.00	8.95	2.65	0.00	14.55	0.00	0.00	0.00	0.00	0.00
Chilliwack_5	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.33
Chilliwack_6	2	0.00	9.02	6.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_7	2	0.00	0.71	0.00	0.00	0.00	0.55	0.00	0.00	0.00	2.72
Chilliwack_8	2	0.00	0.11	0.00	0.00	0.00	0.00	0.00	1.11	0.11	0.00
Chilliwack_9	2	0.00	0.54	0.39	0.00	0.00	0.00	0.00	0.00	2.23	0.00
Coquitlam _1	2	0.00	8.53	0.66	0.00	9.56	0.00	0.00	0.00	0.00	0.00
Coquitlam _2	2	0.00	7.53	3.18	0.00	4.04	0.00	0.00	0.00	0.00	0.00
Coquitlam _3	2	0.00	1.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.51
Coquitlam _4	2	0.00	10.39	1.21	0.00	34.16	0.00	0.00	0.00	0.00	0.00
Seymour_1	2	0.00	1.90	2.36	0.09	0.00	0.00	0.00	0.00	0.00	4.71
Seymour_2	2	0.00	17.90	7.78	0.00	0.00	0.00	0.00	11.51	0.00	0.00
Seymour_3	2	0.00	0.27	0.00	0.00	0.00	0.00	2.07	0.00	0.00	3.01
Seymour_4	2	0.00	1.30	0.00	0.00	0.00	0.00	0.00	0.68	0.00	0.00

Watershed_	Trapping	chinook	coho	cutthroat	longnose	Dolly		pike	rainbow	Salish	
pond #	session	salmon	salmon	trout	dace	Varden	lamprey	minnow	trout	sucker	sculpin
Chilliwack_1	3	0.00	1.84	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00
Chilliwack_2	3	0.00	0.99	0.00	0.00	0.00	0.00	0.00	1.34	0.00	0.00
Chilliwack_3	3	0.00	5.67	1.66	0.00	0.00	0.00	0.00	1.07	0.00	11.24
Chilliwack_4	3	0.00	11.20	6.88	0.00	29.70	0.00	0.00	0.79	0.00	0.00
Chilliwack_5	3	0.00	0.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.51
Chilliwack_6	3	0.00	0.97	1.79	0.00	0.00	0.00	0.00	0.25	0.00	0.00
Chilliwack_7	3	0.00	0.54	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.90
Chilliwack_8	3	0.00	1.69	0.00	0.00	0.00	0.00	0.00	0.23	4.35	0.00
Chilliwack_9	3	0.00	2.13	0.00	0.00	0.00	0.00	0.00	0.00	0.04	1.41
Coquitlam _1	3	0.00	11.48	7.47	0.00	2.66	0.00	0.00	1.84	0.00	0.00
Coquitlam _2	3	0.00	8.55	1.99	0.00	11.36	0.00	0.00	4.89	0.00	0.00
Coquitlam _3	3	0.00	2.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coquitlam _4	3	0.00	13.51	0.78	0.00	16.77	0.00	0.00	0.00	0.00	0.00
Seymour_1	3	0.00	2.52	0.22	0.00	0.00	0.00	0.00	0.81	0.00	15.36
Seymour_2	3	0.00	23.52	0.00	0.00	0.00	0.00	0.00	6.74	0.00	0.00
Seymour_3	3	0.00	0.00	0.00	0.00	0.00	0.00	0.41	0.00	0.00	0.00
Seymour_4	3	0	0.17	0	0	0	0	0	0	0	0.77

		three-							rough	
Watershed_	red-sided	spined		juvenile			NW	red-legged	skinned	
pond #	shiner	stickleback	sucker (sp.)	centrarchid	bullfrog	green frog	salamander	frog	newt	tree frog
Chilliwack_1	0.00	0.00	0.00	0.00	0.00	0.00	2.74	0.01	1.46	0.00
Chilliwack_2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	2.41	0.00
Chilliwack_3	0.00	18.54	0.35	0.00	0.00	0.70	0.00	0.00	0.00	0.00
Chilliwack_4	0.00	6.30	0.00	0.00	0.00	0.00	0.40	0.00	0.00	0.00
Chilliwack_5	0.00	0.80	0.00	0.00	0.00	5.99	1.54	0.13	0.64	0.00
Chilliwack_6	0.00	18.17	0.00	0.00	0.00	2.72	0.00	0.06	0.00	0.00
Chilliwack_7	0.00	17.32	0.00	0.00	0.00	0.00	0.91	0.02	0.00	0.00
Chilliwack_8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00
Chilliwack_9	0.00	2.27	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00
Coquitlam _1	0.00	0.00	0.00	0.00	0.00	0.00	2.31	0.06	0.00	0.00
Coquitlam _2	0.00	3.10	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00
Coquitlam _3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coquitlam _4	0.00	6.91	0.00	0.00	0.00	0.00	0.37	0.11	0.00	0.00
Seymour_1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.93	0.00	0.02
Seymour_2	0.00	0.00	0.00	0.00	0.00	0.00	0.73	0.00	0.00	0.10
Seymour_3	0.00	0.00	0.00	0.00	0.00	0.00	1.08	0.00	0.00	0.00
Seymour_4	0.00	0.00	0.00	0.00	0.00	0.00	0.41	0.10	0.00	0.00
Chilliwack_1	0.00	0.00	0.00	0.00	0.00	0.00	1.24	0.00	0.00	0.00
Chilliwack_2	0.00	0.00	0.00	0.00	0.00	0.00	4.34	1.60	0.32	0.00
Chilliwack_3	0.00	0.06	0.25	0.00	0.00	0.00	0.48	0.00	0.00	0.00
Chilliwack_4	0.00	0.00	0.00	0.00	0.00	0.00	0.57	0.00	0.00	0.00
Chilliwack_5	0.00	3.33	0.02	0.19	0.00	0.65	0.00	0.00	0.00	0.00
Chilliwack_6	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.77	0.00	0.00
Chilliwack_7	0.00	20.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_8	0.00	0.79	0.00	0.00	0.16	0.17	2.33	0.00	0.24	0.00
Chilliwack_9	0.00	9.30	0.00	0.00	0.00	0.25	0.14	0.00	0.00	0.00
Coquitlam _1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coquitlam _2	0.00	0.00	0.00	0.00	0.00	0.00	1.70	0.00	0.00	0.00
Coquitlam _3	0.00	10.47	0.00	0.00	0.00	0.00	0.00	0.57	0.00	0.00
Coquitlam _4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.00	0.00
Seymour_1	1.62	6.61	0.00	0.00	0.00	0.00	0.45	0.00	0.00	0.00
Seymour_2	0.00	0.00	0.00	0.00	0.00	0.00	1.59	0.00	0.00	0.00
Seymour_3	0.00	3.48	0.00	0.23	0.00	0.00	3.73	0.07	0.00	0.00
Seymour_4	0.00	7.38	0.00	0.00	0.00	0.00	0.00	0.00	0.49	0.00

		three-							rough	
Watershed_	red-sided	spined		juvenile			NW	red-legged	skinned	
pond #	shiner	stickleback	sucker (sp.)	centrarchid	bullfrog	green frog	salamander	frog	newt	tree frog
Chilliwack_1	0.00	0.00	0.00	0.00	0.00	0.00	1.91	0.00	0.00	0.00
Chilliwack_2	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.61	0.00	0.00
Chilliwack_3	0.00	0.00	0.00	0.00	0.00	0.00	11.57	0.17	0.00	0.00
Chilliwack_4	0.00	0.00	0.00	0.00	0.00	0.00	1.71	0.57	0.00	0.00
Chilliwack_5	0.00	2.52	0.00	0.00	0.16	0.17	0.00	0.00	0.00	0.00
Chilliwack_6	0.00	0.00	0.00	0.00	0.00	0.00	6.99	0.00	0.00	0.00
Chilliwack_7	0.00	2.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chilliwack_8	0.00	0.49	0.00	0.00	0.34	0.76	1.41	0.00	0.18	0.00
Chilliwack_9	0.00	5.69	0.00	0.00	0.00	0.13	0.62	0.00	0.00	0.00
Coquitlam _1	0.00	0.00	0.00	0.00	0.00	0.00	1.51	0.00	0.00	0.00
Coquitlam _2	0.00	0.00	0.00	0.00	0.00	0.00	12.33	0.00	0.70	0.00
Coquitlam _3	0.00	2.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coquitlam _4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Seymour_1	0.00	3.10	0.00	0.00	0.00	0.00	59.49	0.14	0.00	0.00
Seymour_2	0.00	0.00	0.00	0.00	0.00	0.00	2.17	0.00	0.00	0.00
Seymour_3	0.00	2.15	0.74	0.00	0.00	0.00	5.27	0.00	0.00	0.00
Seymour_4	0	1.02	0	0	0	0	0	0	0	0