THE DEVELOPMENT OF GEOMORPHIC AND HYDRAULIC COMPLEXITY WITHIN STREAMS AND ITS INFLUENCE ON FISH COMMUNITIES FOLLOWING GLACIAL RECESSION IN GLACIER BAY, ALASKA

by

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Abstract

Studies of landscape development via primary successional processes are an important area of research for understanding how landscapes evolve into stable, diverse ecosystems. This research sought to assess how geomorphic and hydraulic complexity alter as streams develop following glacial recession. Investigations revealed that younger streams were dominated by fast flowing geomorphic units such as rapids and riffles with little hydraulic or landscape diversity. As stream age increased, however, slower flowing habitat units such as glides and pools became more dominant, resulting in increased geomorphic, hydraulic and riverscape diversity. Determination of these changes in hydromorphic complexity which occur as streams develop, twinned with an assessment of the role of coarse woody debris in creating such complexity at the reach and microscale levels revealed the importance of coarse woody debris in driving these changes. Coarse woody debris was found to influence the development of biocomplexity and interaction between stream, terrestrial and floodplain environments. These changes in geomorphic and hydraulic complexity result in the creation and maintenance of instream habitat which biota such as juvenile Pacific salmonids may utilise.

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A revised version of Chapter 2 of this thesis has been published in River Research and Applications, a copy of which is included in Appendix 3 (page 168).

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Abbreviations Used

Abbreviation	Full name
ADCP	Acoustic Doppler Current Profiler
BBS	Berg Bay South Stream
CGU	Channel Geomorphic Unit
CPUE	Catch Per Unit Effort
CWD	Coarse Woody Debris
GBNP	Glacier Bay National Park
IVS	Ice Valley Stream
NFS	North Fingers South stream
PCA	Principal Components Analysis
RPC	Rush Point Creek
WPC	Wolf Point Creek

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The role of geomorphic and hydraulic complexity in creating habitat diversity within stream environments

The importance of geomorphic and hydraulic complexity in determining the quantity and quality of instream habitat is a well known within the field of aquatic ecology. What is less known, however, are the processes involved in creating and maintaining such complexity. By utilising the unique environmental conditions present within Glacier Bay, Alaska, it is possible to monitor how hydromorphic complexity develops over time, resulting in the development of linkages between hydrology, geomorphology and biota. The study of landscape development in this sense will help clarify the underlying mechanisms which link biological pattern and physical processes, resulting in increased biocomplexity within stream and terrestrial environments. Such knowledge will benefit restoration efforts, which seek to reinstate degraded aquatic habitats through the creation of geomorphic and hydraulic complexity.

1.1 Introduction

Historic use and management of river systems has led to the ‘severe’ alteration of over 77% of rivers within North America, Europe and the former Soviet Union (Cowx and Welcomme, 1998). Practices such as channel modification, flow regulation, abstraction and the removal of instream woody debris have negatively impacted the structure and functioning of rivers to such an extent that many are no longer able to support viable aquatic communities due to the removal and degradation of instream habitat (Brierley and Fryirs, 2005; Thomson et al., 2001) twinned with declines in water quality . The availability of instream habitat for aquatic biota is determined by the physical template provided by a river’s channel morphology combined with the discharge and hydraulic characteristics of the flow regime (Maddock, 1999). Changes in the quality and quantity of geomorphic and hydraulic features, such as those due to human intervention, can therefore affect the diversity and abundance of instream habitat and species composition (Bartley and Rutherford, 2005; Beisel et al., 2000; Sullivan et al., 2006).

Research focusing on the hydraulic component of habitat availability has become an increasingly important subject area, due to the need for the sustainable management of water resources (Janauer, 2000; Zalewski, 2000; Zalewski, 2002) twinned with an increasing understanding of the importance of maintaining the structural functioning of ecosystems in order to ensure the continued production of resources (Zalewski, 2000). Research into this area has prompted the creation of the new discipline of hydro-ecology or eco-hydrology (Hannah et al., 2004; Zalewski and Robarts, 2003), which seeks to predict the response of freshwater biota and ecosystems to the variation of abiotic factors over a range of spatial and temporal scales (Dunbar and Acreman, 2001). Ecohydraulics, a sub discipline of hydroecology, which focuses on the interaction of ecology and hydraulic engineering (Nestler et al., 2007) has also increased in popularity.

The majority of research within this field has focused on the impacts of water abstraction and reduced water flow on the biological integrity of the riverine ecosystem. Temporal and spatial heterogeneity of river flows are important factors in determining the quality and quantity of instream habitat as a varied flow is required to create and maintain the geomorphic and ecological integrity of the river system (Naiman et al., 2008; Stalnaker et al., 1996). Early research sought to ascertain the minimum water flows required within a riverine ecosystem, which still allows such processes to be maintained, whilst providing maximum usage of dwindling freshwater supplies. More recently, the importance of the entire flow regime (including intermediate and flood flows cf. Poff et al., (1997)) has been recognised, and therefore, researchers have attempted to define environmentally acceptable flow regimes, or 'environmental flows' (Dunbar and Acreman, 2001).

More recent investigations within this field have highlighted the lack of studies focused on the role of geomorphic diversity and complexity in influencing habitat availability within the aquatic environment (Clark et al., 2008; Yarnell et al., 2006). The geomorphic assemblage of the river environment reflects catchment and reach scale controls (e.g. gradient, sediment supply and geology) that determine the distribution of energy and associated erosional and depositional forms, which together, create the geomorphic complexity observed within river environments. These processes determine the availability of physical habitat upon which a number of biophysical processes may interact (Brierley and Fryirs, 2005).

Recently, attention has turned to the need for an integrative approach to the assessment of linkages between ecology and physical habitat (Hannah et al., 2007; Vaughan et al., 2009). In particular, the role of geomorphic complexity in the provision of instream habitat on the diversity of fish (Geist and Dauble, 1998; Sullivan et al., 2006), macroinvertebrates (Beisel et al., 2000; Brown, 2003; Principe et al., 2007) and plants (Gurnell et al., 2007) has received greater attention. Research has shown that stream hydrology, geomorphology and biota are intimately linked at a number of spatial and temporal scales. Investigations into these linkages (Figure 1.1) have begun to increase in number, due in part to the introduction of the EU Water Framework Directive, which specifically identifies hydrology and fluvial geomorphology (hydromorphology) as key components in defining the ecological integrity of water bodies (European Commission, 2000).

Current research within this field is predominantly focused on the understanding of form- function processes and linkages over a range of spatial and temporal scales. This research seeks to continue the shift in scientific thinking, away from a prescriptive to a more holistic and integrative approach to environmental management.

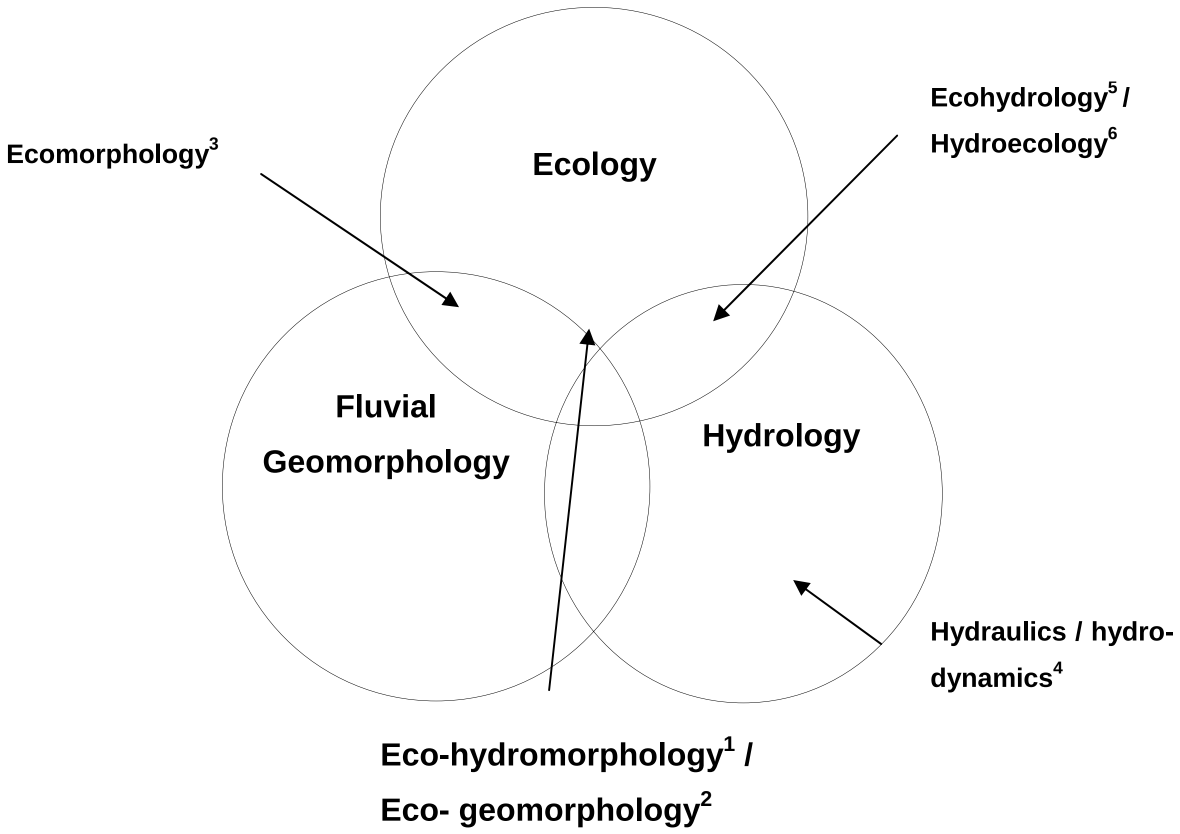

Figure 1.1: Recent research has begun to investigate the interaction between ecology, fluvial morphology and hydrology. An initial suggestion for the name of such multidisciplinary research is [1]eco-hydromorphology (Thorp et al., 2006). Eco-hydromorphology encompasses a number of other disciplines, including [2]Eco-geomorphology- Thoms and Parsons, (2002); [3]Ecomorphology- Fisher et al., (2007); [4]Hydro-dynamics- Harvey and Clifford, (2008); [5]Eco-hydrology- Zalewski, (2000); and [6]Hydro-ecology (Acreman, 2001).

Observational studies of the links between biological pattern and physical processes have been extensive in the past (Vaughan et al., 2009), but very few have focussed on the underlying mechanisms which drive these relationships, particularly from their initial onset following stream development. The formation of a conceptual framework which addresses the theory of biocomplexity as a measure of ecosystem structuring and functioning (Cadenasso et al., 2006) has provided a useful template for addressing these questions. Such research is concerned with the variety and arrangement of terrestrial and aquatic habitats, and the diversity and distribution of the species in which they support (Gurnell et al., 2005). The structural framework of biocomplexity proposed by Cadenasso et al. (2006) provides three axes of measurement of biocomplexity; spatial heterogeneity, organisational connectivity and temporal contingency (Figure 1.2), all of which provide a measure of spatial and structural complexity within the river system. Assessment of biocomplexity at these dimensions will be utilised within this research as an approach to exploring structure-function relationships (Cadenasso et al., 2006) and their role in the development of hydromorphic and structural complexity following deglaciation.

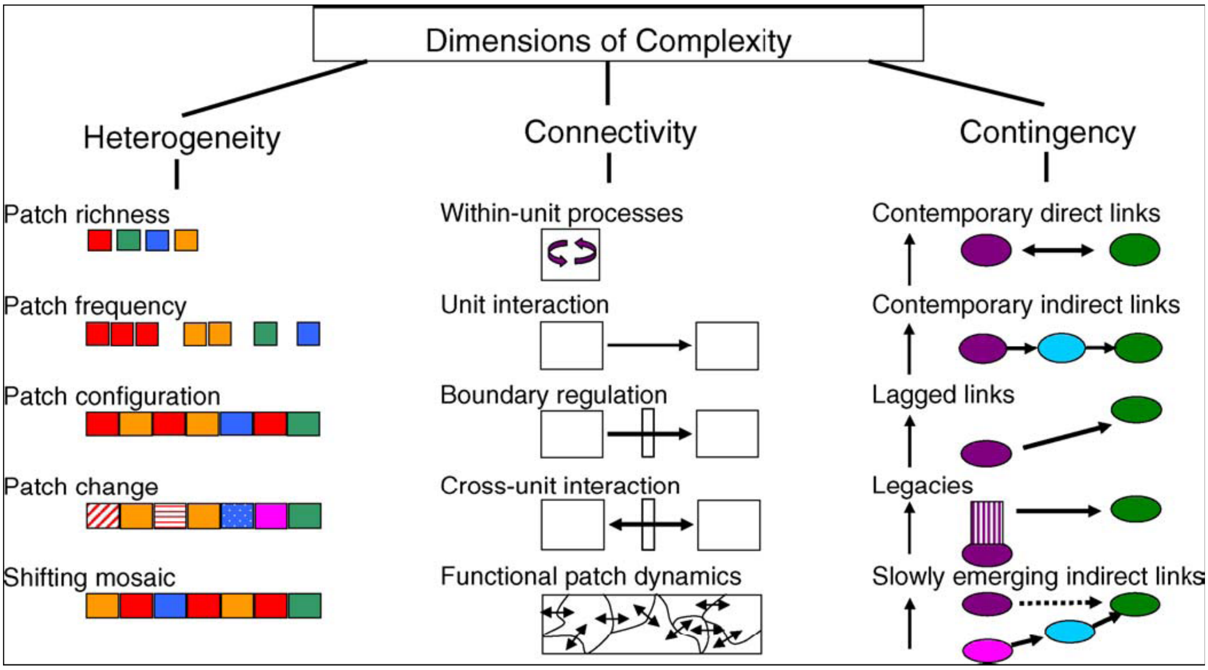

Figure 1.2: Framework for biocomplexity proposed by Cadenasso et al. (2006), which utilises three dimensions of biocomplexity. Components of the framework are arrayed along each axis increasing in complexity.

Emerging research within near-pristine environments has begun to recognise the complexity of biotic- abiotic interactions, which are often lacking within degraded river systems. This research has highlighted the lack of understanding of how changes in the physical heterogeneity of habitats influence ecosystem level processes such as primary production and nutrient cycling, as well as the external drivers of landscape form and processes (Renschler et al., 2007). For example, research within Kruger National Park, South Africa, has shown that coarse woody debris (CWD) plays an important role in riverine and riparian heterogeneity, and landscape recovery following ecosystem disturbance (Pettit and Naiman, 2005). In this instance, CWD was found to create a mosaic of patches of surviving organisms and propagules following a wide scale flood, the presence of which strongly influenced the subsequent recovery and trajectory of vegetative community succession (Pettit et al., 2005). Current river management and restoration techniques fail to consider the dynamic processes which operate within natural systems, preventing the creation and maintenance of these natural processes within degraded systems.

Traditionally, restoration techniques have focused on reinstating the geomorphic form of rivers to a condition often seen in natural or pristine rivers. The foundation of such techniques rested on the observation that geomorphic processes determine which biota may be found locally within a stream (Dauwalter et al., 2008), and accordingly, changes in geomorphic processes lead to predictable changes in stream habitat and the presence of selected species. Restoration techniques which restore geomorphic processes and channel morphology to a ‘natural’ state are therefore predicted to produce specific responses from aquatic biota. The most widely used tool for the enhancement or creation of instream habitat is the use of CWD (Manners and Doyle, 2008). Wood- based restoration techniques mimic the recruitment of large, complex riparian vegetation into the stream environment, which is a natural phenomenon within undisturbed riverine ecosystems. The introduction of CWD into the stream channel in this way has been shown to play an important role in creating and maintaining geomorphic complexity at the reach and microscale, which instream biota may utilise, resulting in an increase in species diversity and habitat stability.

Although the use of CWD as a technique for restoring geomorphic complexity to degraded habitats is widely used (Manners and Doyle, 2008), little attention has focused the complex interactions between hydrology and geomorphology and the landscape and ecological processes which form them. These linkages naturally occur within undisturbed sites, creating the hydromorphic complexity which restoration techniques seek to emulate, however, a lack of knowledge of how these processes function and are maintained prevent such efforts from fully benefiting.

Glacier Bay National Park (GBNP), Alaska, provides the unique opportunity to study the process of geomorphic and hydraulic development within a number of streams, as large temporal differences (up to 250 years) may be analysed in a small spatial scale (< 200 km). This study aims to utilise investigations into landscape evolution twinned with the monitoring of Pacific salmon colonisation to clarify the linkages between fluvial geomorphology, hydrology and ecology. Attention will also be given to feedback mechanisms which operate between geomorphological form and ecosystem function and vice versa; that is, functional eco-geomorphology (Fisher et al., 2007) at the terrestrial / aquatic interface.

1.1.1 Landscape Ecology- a measurement of geomorphic complexity

Landscape ecology is the area of science concerned with the influence of spatial pattern on ecological processes (Brierley and Fryirs, 2005; Wiens, 2002). Ecosystem connectivity, composition and structure have increasingly been found to play important roles in determining species and habitat diversity (Amoros and Bornette, 2002; Cadenasso et al., 2006; Ward, 1998; Ward et al., 1999). The use of spatial and temporal indices of landscape composition within the aquatic environment (‘riverscapes’ *sensu* Wiens (2002)) over a large scale (e.g. stream reaches >1km over a period covering 200 years of stream development as used within this study) provides information at a scale relevant to a wide range of species and communities (Fausch et al., 2002). Analysis of geomorphic composition across the riverscape provides an assessment of river character at a number of scales and processes, which are relevant to instream biota over a large spatial and temporal scale (Poole, 2002). For the purposes of this thesis, geomorphic complexity has been defined as the quantity and arrangement of geomorphic (and associated hydraulic) units within a defined reach.

Using this level of analysis, it is possible to investigate how landscape form influences ecosystems processes, and also to consider how ecological processes and interactions may shape ecosystem morphology (Fisher et al., 2007).

1.2 Landscape Evolution

Studies of landscape development over time are an important area of research for the understanding of how landscapes evolve and develop into stable, diverse ecosystems. A large proportion of research within this area is limited to instances of secondary succession following disturbance such as floods, droughts, and fire. Although such research has provided a great deal of information on the process of colonisation and habitat development, the presence of remnant landscapes and biota within these habitats prevents a true study of the process of landscape development to be studied. Extreme ecosystem disturbance, such as volcanic activity and glacial processes provide the opportunity to study ecosystem development via primary successional processes due to the removal of all previous biological communities from the affected area. Investigations of primary successional development provide the opportunity to study the development of natural processes, which may then be used to inform restoration programs which seek to emulate such complexity and interactions (Tockner et al., 2003).

Extensive glacial activity within southeast Alaska twinned with well-documented rapid glacial recession within Glacier Bay National Park, Alaska has provided the unique opportunity to study the development of newly created ecosystems. Classic studies on the process of colonisation of terrestrial vegetation at Glacier Bay (Crocker and Major, 1955) have helped form the theory of facilitative succession (Begon et al., 1996). The development of stream ecosystems within Glacier Bay has also been documented (Milner, 1987; Milner et al., 2000; Sidle and Milner, 1988), leading to the synthesis of the interactions and linkages between terrestrial, lake, stream and marine intertidal ecosystems during landscape evolution within Glacier Bay (Milner et al., 2007).

This research has highlighted the shift from physical controls (e.g. temperature and turbidity) to increasing biotic control (e.g. nutrient availability and competition) of successional processes over time (Milner et al., 2007). Linkages between terrestrial and aquatic landscape processes were also found to play an important role in all ecosystems, altering in strength and nature over time, as outlined in Figure 1.3.

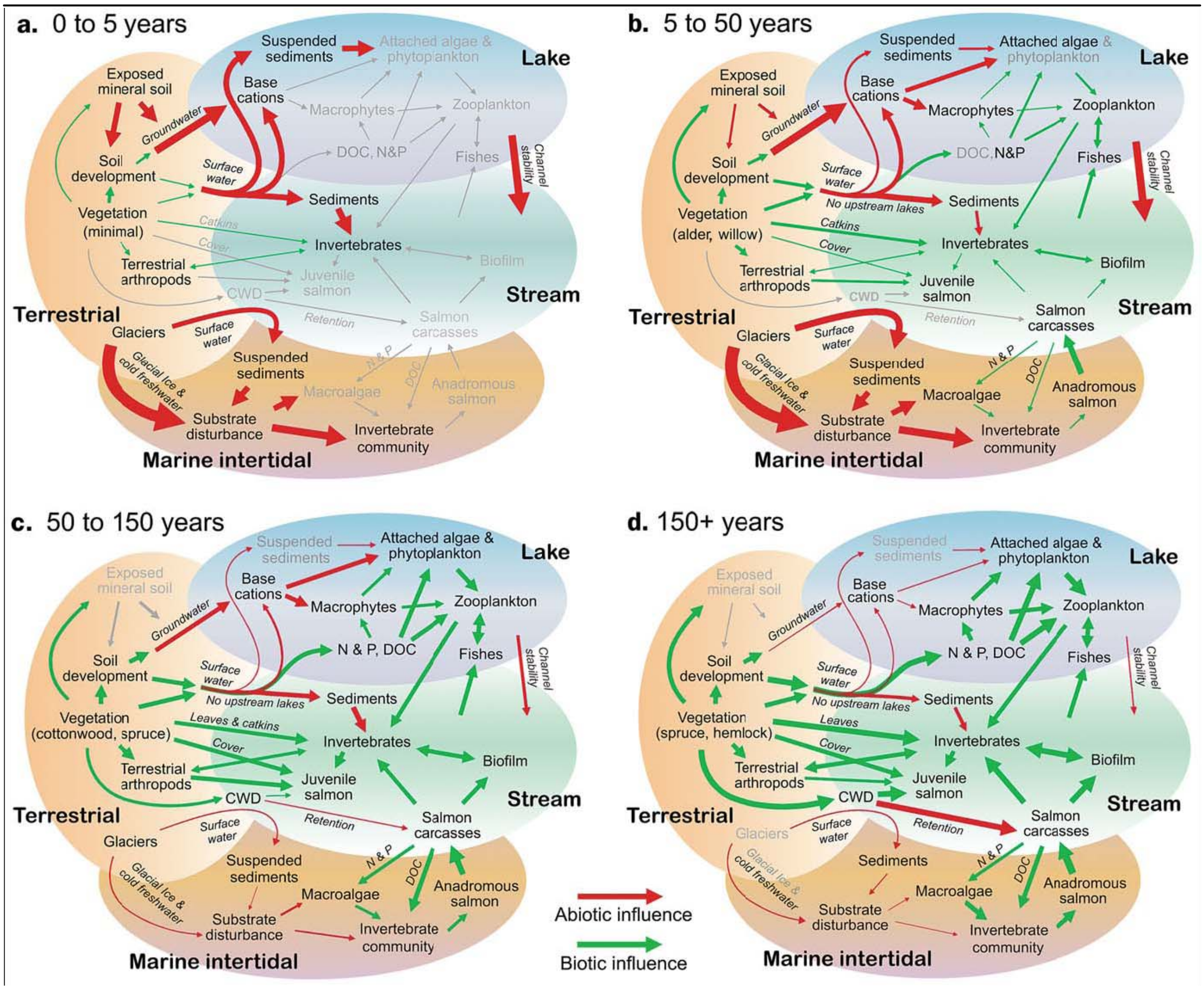

Figure 1.3: Major linkages among and within stream, lake, terrestrial and marine intertidal environments at Glacier Bay during four selected time periods following glacial retreat. The thickness of the arrows indicates the strength of the influence, which may be positive or negative. Grey components have little or no importance in

the time period shown. Abbreviations: CWD- coarse woody debris; DOC- dissolved organic carbon; N- nitrogen; P- phosphorus. From Milner et al., (2007).

This thesis will develop further our understanding of those processes and linkages operating between terrestrial and stream ecosystems, highlighting the role of CWD in facilitating such linkages, and thus further strengthening interactions between ecosystems. It is important to note that throughout the research, the term riparian vegetation is used as a term to describe vegetation across the floodplain, including terraces and vegetation within 10- 30m of stream which may at times interact with water at very high flows, often resulting in the subsequent recruitment of this vegetation into the stream channel. Such a broad spatial zone was chosen due to the dynamic nature of streams within GBNP, which continue to form new channels and recruit vegetation from adjacent terrestrial sources.

1.3 Study aims and objectives

The overall aim of the research was to **assess how geomorphic and hydraulic complexity alters as streams develop, thereby influencing the complexity of biological communities following glacial recession within Glacier Bay, Alaska.**
In order to achieve the project aim, the following objectives were identified;

a. To identify those variables driving geomorphic and hydraulic complexity across the stream chronosequence as a result of stream development
b. To evaluate the response of juvenile salmonid populations to changes in hydromorphic and structural complexity
c. To assess the dynamics of coarse woody debris accumulations resulting from differences in riparian and floodplain vegetative development and their influence on hydromorphic variation across the stream chronosequence
d. To highlight the linkages between riparian vegetation, coarse woody debris and landscape development within Glacier Bay

1.4 Thesis structure

The thesis is structured as a series of draft papers which will be subsequently submitted to peer reviewed journals, focussing on four interlinked aspects of the development of geomorphic, hydraulic and structural diversity within recently deglaciated catchments, and the influence of such development on the subsequent success of juvenile Pacific salmon.

Following the brief contextual grounding of the research theme provided within this chapter, the mechanism by which hydraulic, geomorphic and structural complexity alters over time within five study streams representing 200 years of stream development will be discussed in **Chapter 2**. Analysis of the differences in habitat availability within the streams provided information of the geomorphic processes, which operate during stream development, creating the differences in geomorphic and hydraulic diversity observed.

Chapter 3 examines the role of woody debris in creating the changes in hydromorphic complexity observed within the study streams in Chapter 2. Novel survey techniques allowed detailed assessment of the hydraulic characteristics surrounding woody debris to be assessed, revealing a linkage between adjacent riparian vegetation and geomorphic and hydraulic complexity. The chapter introduces a theoretical relationship between physical habitat heterogeneity, stream development and relative sediment supply which may explain the trends observed across the stream chronosequence within Glacier Bay.

The response of juvenile salmonids to the geomorphic and hydraulic development reported in Chapters 2 and 3 is examined within **Chapter 4.** This chapter identifies those coarse woody debris characteristics resulting from the development of adjacent riparian vegetation over time, which result in the creation of hydromorphic and structural complexity, which juvenile fish may utilise, resulting in an increase in fish densities as stream age increases.

The role of coarse woody debris in landscape evolution and ecosystem functioning is investigated within **Chapter 5**. The chapter utilises the temporal chronosequence present within Glacier Bay to expand upon emerging research, which suggests that riparian vegetation is a significant landform control factor within natural river systems, highlighting the importance of biotic- abiotic interactions in the natural functioning of riverine ecosystems.

Finally, the overall synthesis of the research is summarised in **Chapter 6**, in which the applicability of this research in elucidating the process of stream development within Glacier Bay is discussed.

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2

The development of geomorphic and hydraulic complexity in recently formed streams in Glacier Bay National Park, Alaska

Geomorphic and hydraulic complexity within five streams representing 200 years of stream development were examined in Glacier Bay National Park, Alaska. Channel geomorphic units were mapped using a hierarchical approach, which defined stream habitat according to morphological and hydraulic characteristics. Detailed hydraulic assessment within the geomorphic units allowed differences in hydraulic characteristics across the 200-year chronosequence to be documented. Channel geomorphology and hydrology changed as stream age increased. Younger streams were dominated by fast flowing geomorphic units such as rapids and riffles with little hydraulic or landscape diversity. As stream age increased, slower flowing habitat units such as glides and pools became more dominant, resulting in increased geomorphic, hydraulic and landscape diversity. These results suggest that geomorphic and hydraulic complexity develop over time within Glacier Bay streams, creating habitat features likely to be favoured by instream biota, enhancing biodiversity.

2.1 Introduction

The availability of instream habitat within rivers is determined by the interaction of channel geomorphology and hydrology (Maddock, 1999). Changes in the diversity and complexity of hydraulic features have been found to influence habitat and species diversity (Bartley and Rutherford, 2005; Maddock, 1999; Sullivan et al., 2006), contributing to increased biodiversity within the stream environment (Crowder and Diplas, 2006; Dyer and Thoms, 2006; Principe et al., 2007; Stalnaker et al., 1996). In comparison, there has been far less research on how changes in geomorphic diversity and complexity influence habitat availability within the aquatic environment (Clarke et al., 2008; Yarnell et al., 2006).

Geomorphological complexity may be defined as the complexity in both composition and configuration of geomorphological elements within a river channel. Changes in the geomorphic composition of a river influence community diversity, productivity and stability (Beisel et al., 2000; Sullivan et al., 2006) as geomorphic complexity creates spatial heterogeneity which can be utilised by instream biota, such as macroinvertebrates (Beisel et al., 2000) and fish (Inoue and Nakano, 1999; Walters et al., 2003).

A heterogeneous and diverse habitat is generally considered beneficial to biota as such conditions provide a range of habitats over a wide spatial (e.g.- meso and micro habitat) and temporal (e.g.- seasonal or life stage) scale. For example, habitat preferences of juvenile coho salmon in summer include high energy geomorphic units such as riffle tails which offer easy access to food resources (Fausch, 1993), whilst in winter months, the preferred habitats are low velocity units, such as backwaters, which offer refuge from high velocities (Nickelson et al., 1992). Microhabitat preferences within these habitats are also apparent; for example choice of pool habitat by juvenile coho within the winter months is strongly influenced by the degree of overhead cover available (McMahon and Hartman, 1989). Habitat heterogeneity has also been found to exert a stabilising force on local community dynamics by regulating the availability of resources (Brown, 2003; Brown, 2007).

Previous work by Yarnell et al., (2006) suggests that relative sediment supply influences stream habitat heterogeneity, with streams containing a moderate relative sediment supply (i.e.- a balance between sediment supply and transport), supporting the highest habitat diversity as a result of variable deposition and scour at any given flow providing a higher diversity of geomorphic features. Although research has alluded to the importance of geomorphic complexity in creating habitat and hydraulic diversity, our knowledge of how geomorphological complexity develops, its interaction within the ecology-hydrology-geomorphology interface, and the response of instream biota to these changes is negligible. An understanding of the underlying mechanisms and process rates of hydromorphology- ecology linkages would greatly improve the determination of ecological responses to climate change, river regulation, management and restoration practices.

This chapter aims to utilise the stream chronosequence found at Glacier Bay National Park, Alaska, to understand the development of geomorphic and hydraulic complexity within streams over time. Identification of channel geomorphic units (CGUs; e.g.- riffle, run, pool etc) using a hierarchical description of the morphological and hydraulic properties provides an ecologically meaningful (Hawkins et al., 1993) measure of the geomorphic and physical diversity of the instream environment. Analysis of differences in the habitat and hydraulic environments within five streams representing a 200-year age chronosequence will assist in identifying changes in instream habitat, which occur as streams develop. Assessment of these changes at the ‘meso’ scale (100m+) will provide an assessment over the entire riverscape, allowing identification of landscape and hydraulic features at scales relevant to the entire lifecycle of instream biota such as fish (Fausch et al., 2002). Detailed mapping and assessment of smaller representative reaches identified from meso scale mapping is able to quantify the hydraulic (microscale) and habitat changes, which occur as the streams age.

Analysis of the development of geomorphic and hydraulic complexity within pristine riverine environments and its influence on the creation of spatial and temporal heterogeneity within stream environments will assist in understanding how hydromorphological processes affect instream biota. Such knowledge will further clarify how hydromorphological condition may be used as a measure of habitat quality as outlined within the EU Water Framework Directive.

2.2 Methods

2.2.1 Study site

Glacier Bay National Park and Preserve (GBNP) is located in the southeast of Alaska (58°10’- 59°15’N; 135°15’- 138°10’W), approximately 105 kilometres west of the state capital of Juneau. The National Park covers an area of approximately 11,030 km^2, most of which is dominated by a ‘Y’ shaped tidal fjord over 100km in length and 20km

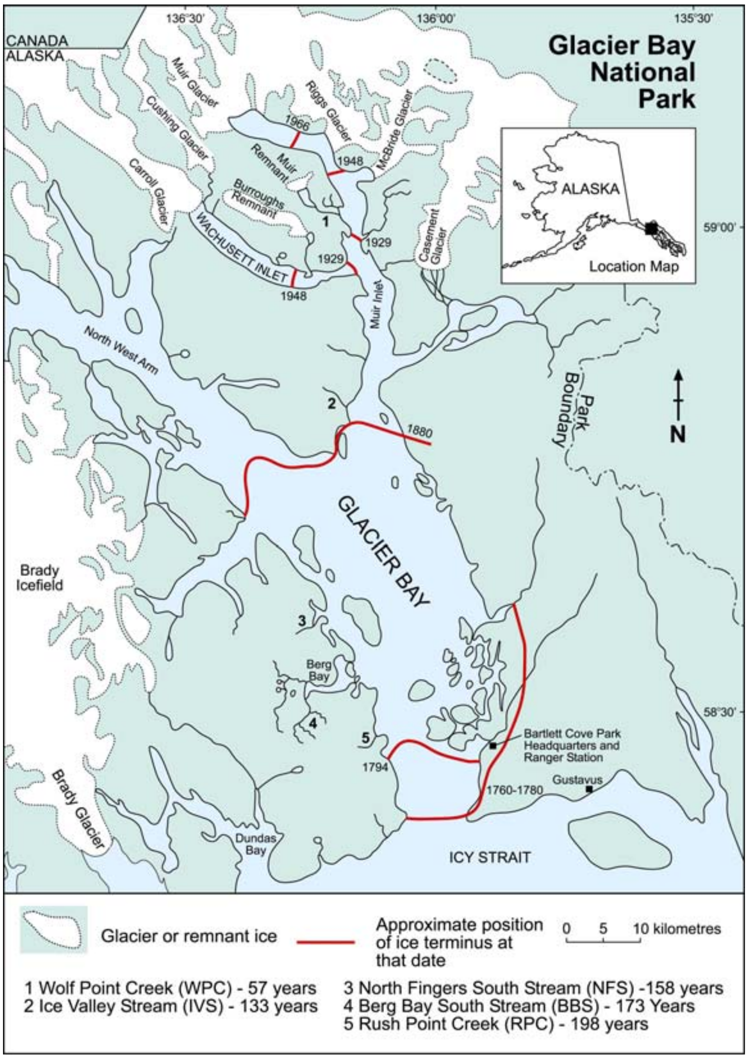


Figure 2.1: Map of Glacier Bay National Park, Alaska, indicating the location of the study streams (and acronyms) and dates of glacial recession.

in width. A Neoglacial ice sheet once covered the entire province surrounding GBNP, reaching its maximum near the mouth of the current fjord around 1700 AD.

Rapid glacial recession of the Glacier Bay ice sheet has created a unique opportunity to monitor the geomorphological development of streams and associated physical and ecological responses over time. Detailed historical, geological and dendrochronological data allows glacial recession within Glacier Bay to be accurately dated, whilst extreme disturbance to the area following deglaciation provides the opportunity to study habitat and community development via primary colonisation processes (Chapin et al., 1994; Crocker and Major, 1955; Reiners et al., 1971). Stream age is related to the distance of a stream from the retreating glacier termini (Figure 2.1), and thus temporal changes in stream complexity can be studied on the basis of spatial differences (Milner et al., 2000). Five streams were chosen for study according to their similarity in catchment and geological characteristics (Table 2.1), and together, represent a range of stream ages and development present within Glacier Bay.

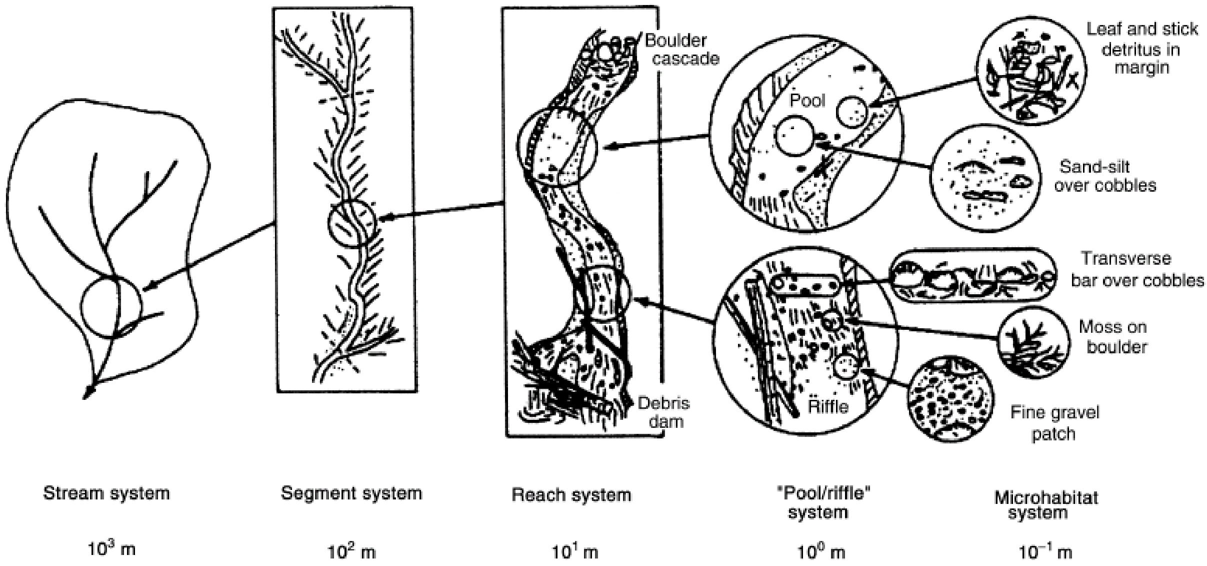
Table 2.1: Summary of physical characteristics of the five study streams. WPC- Wolf Point Creek; IVS- Ice Valley Stream; NFS- North Fingers South Stream; BBS- Berg Bay South Stream; RPC- Rush Point Creek; Bo- boulder; Co- cobble; Gr- gravel; A/W- Alexander/ Wrangellia Terrace. Data sources- * (Robertson and Milner, 2006); ** (Hill et al., 2009).

	Stream age	Reach gradient (%)	Stream length (km)*	Drainage area (km^2)**	Ave discharge (m^3/s)	Stream order *	Dom substrate	Geology
WPC	57	1.14	5.6	29.8	2.29	2	Bo	A/W
IVS	133	0.98	8.3	19.4	3.02	2	Co	A/W
NFS	158	1.14	8.0	16.8	5.65	2	Bo	A/W
BBS	173	0.80	7.2	33.1	4.95	3	Gr	A/W
RPC	198	0.88	6.6	23.3	7.51	2	Co	A/W

2.2.2 Measurement of geomorphic and hydraulic complexity

Measurement of geomorphic structure and variability as an indicator of habitat diversity within streams is a relatively new development (Bartley and Rutherford, 2005; Crowder and Diplas, 2006; Schwartz and Herricks, 2007; Yarnell et al., 2006). For the purposes of this study, identification of channel geomorphic units (CGUs) within each of the five study streams was used in order to quantify geomorphic structure and composition within the streams. CGUs are areas of relatively homogenous depth and flow that are bounded by sharp gradients in both depth and flow which incorporate the morphological and hydraulic properties of channel geomorphic units (Hawkins et al., 1993). Classification of habitat units at the CGU level have been shown to be ecologically meaningful to instream biota (Hanrahan, 2008; Moir and Pasternack, 2008; Thomson et al., 2001; Yarnell et al., 2006) and hence an appropriate indicator of instream habitat availability. Determination of the differences in hydraulic and geomorphic characteristics within and between CGUs will help to determine how instream habitat develops over time.

Mapping at the segment and reach scales (as illustrated in Figure 2.2), were chosen as geomorphological development is likely to occur at the stream level, whilst fish are most likely to respond to these changes at the segment level. The study of habitat complexity at the landscape level is vital as it is at this scale that heterogeneity of spatial patterns become apparent and set the scale for ecological processes (Fausch et al., 2002). The stream chronosequence present in Glacier Bay allows temporal changes in habitat diversity and availability to instream biota to be studied, identifying the processes and timescale of stream development following deglaciation to be determined.



catchment	meso scale (≥ 1.3km)	representative reach (≥300m)	CGU	**Mapping Definitions**

Figure 2.2: The hierarchical classification of stream habitats (Frissel et al., 1986) with associated definitions of terminology used in habitat mapping.

2.2.3 Data collection

Fieldwork conducted in 2006 and 2007 focused on the identification and quantification of the geomorphic composition within the study streams. Analysis of aerial photographs (e.g.- those provided in Appendix 2) provided an initial identification of suitable stream reaches, allowing areas representative of the stream as a whole to be located and later ground-truthed to ensure that the reaches had similar gradient, stream order and geology prior to arrival. CGUs were identified at base flow conditions, over a minimum distance of 1.3 km, starting upstream of the tidal limit, using a modified version of the Hawkins et al., (1993) classification system, which is based on three increasingly fine descriptions of the morphological and hydraulic properties of the CGUs. The total length of the stream reaches were determined by the shortest stream length (at North Fingers South Stream), which contained an extended cascade unit which is likely to limit fish passage, and was therefore used as the upper reach limit. The end points of the other four streams were determined when a minimum of 1.3 km had been reached, and the mapping had reached a full riffle-run-pool cycle. CGU types were identified by a single operator, using standard guidelines to avoid operator variability, according to their surface flow type and channel planform (descriptions are provided in Appendix 1), and mapped by walking within the stream (or bank where necessary) with a mapping grade GPS unit (Trimble GeoXT; accurate to the sub metre level) collecting positional information every five seconds to provide geo-referenced information on the size and location of each CGU. Mapping at this level allowed the stream to be characterised at the ‘meso’ habitat scale, which represents the full scale of habitats utilised by fish (Fausch et al., 2002), and has also been identified as an appropriate scale for assessing river adjustments and development (Brierley and Fryirs, 2005). Mapping at this levels has also been found to be appropriate for developing process- based habitat surveys which allow comparison between functionally similar systems (Thomson et al., 2001).

Mapping of CGUs at the mesoscale (>1km in length within each stream), allowed the identification of representative reaches (a minimum of 300m in length) which were subsequently studied in greater detail to quantify hydraulic and habitat structure at the microscale within CGU types across the stream chronosequence. ‘Representative’ reaches were identified as those which contained an appropriate CGU composition as that found within the meso-scale mapping, thereby representative of this larger area. Care was taken to ensure that these representative areas had similar gradient, tidal influence and location within the stream catchments. Mapping at the meso-scale and reach levels was conducted over a maximum period of two days, at baseflow to limit the influence of differential discharge when identifying CGU classes.

Each CGU within the representative reach was mapped by walking its perimeter in order to obtain area and shape information using the GPS unit. Thirty random water velocity (at 0.6 depth, averaged over 30 seconds using a Model 201D flow meter, Marsh-McBirnley Inc., Frederick MD, U.S.A.) and total water depth measurements were also taken from each CGU type. Froude numbers were calculated using the depth and velocity measurement from each of the CGUs, using the equation:-

$$Fr = \frac{V}{\sqrt{gD}}$$

where V= mean velocity (m/s), g= acceleration due to gravity ($9.8 m/s^2$) and D= hydraulic depth (m)

Descriptive statistics of mean depth, velocity and Froude number within the representative reaches were calculated for each of the streams using SPSS software (version 17.0; SPSS, Chicago, CA, U.S.A.) and a oneway ANOVA used to test for significant differences between the streams. A Tukey HSD test was employed to identify those streams which were significantly different from one another. Size, shape and proximity analysis of CGUs within the representative reaches were assessed using the landscape analysis software FRAGSTATS, detailed in Section 2.2.5.

2.2.4 HydroSignature

Velocity and depth measurements from each sampled CGU were assessed using Hydrosignature software (Le Coarer, 2005), a free-to-use software program which classifies depth and velocity percentages into cross-classed grids, displaying the hydraulic diversity within a site as a velocity/ depth plane, or hydraulic signature. Analysis of the data using HydroSignature allows the hydraulic diversity present within CGU types to be assessed. Plotting hydraulic characteristics on two axes in this way has been shown to provide a greater ability to differentiate between morphological units than standard statistical methods (Moir and Pasternack, 2008).

The data were input as NOXY 2 (pseudo-specialisation method; Scharl and Le Coarer, (2005)), using Froude number as the sorting factor. Surveyed CGUs were grouped together within each stream according to their CGU type, and analysed using HydroSignature's inbuilt 'HydroSignature Comparison Index' (HSC; Scharl and Le Coarer, (2005)). The HSC uses a spatial analysis filter technique to construct a comparison matrix, which provides a relative scale of comparison of two hydraulic signatures. A single 'HSC CGU total' value is then output from HydroSignature (an example of which is provided in Figure 2.3), with values ranging from 0 to 100; 0

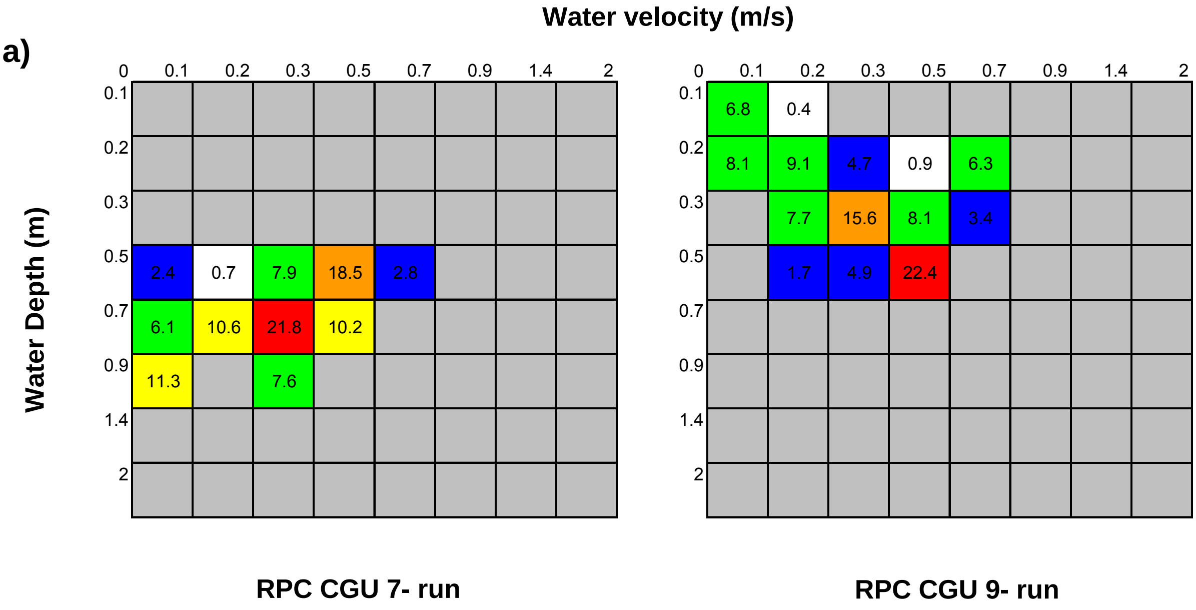
implies two hydraulic signatures are identical or homogenous, whilst a value of 100 suggests that the hydraulic signatures have no similar properties, or are heterogeneous.

HSC was used to evaluate differences in hydraulic diversity in three instances; 1) the 'CGU total' HSC, constructed for each CGU type within each of the five study streams was compared against itself in order to obtain a comparison index, which provides an indication of the amount of natural variation present within a CGU type over the study reach (i.e.- hydraulic variation present between 'run' CGUs within Stream A; Y. Le Coarer, *pers. comm.*) 2) The 'CGU total' hydraulic signatures were then compared within their corresponding CGU type across the chronosequence to evaluate changes in hydraulic diversity within CGU types which may occur as stream age increases (i.e.- 'run total' from Stream A vs 'run total' from Stream B) and 3) A mean HSC value for each CGU type was calculated from point 2 above to assess the degree of change in hydraulic diversity within CGUs across the chronosequence.

2.2.5 Landscape diversity and evenness

Positional data obtained during the mapping exercise was post-processed using Trimble's GPS Pathfinder Office software to improve its accuracy. These data were then converted from *.cor files to ArcMap shape files and displayed within ArcGIS software. ArcGIS is able to directly display the habitat mapping data collected in the field and display them as a geo-referenced map. Maps produced in ArcGIS were then converted from a polygon based feature file into a graded raster image in order to input the files into FRAGSTATS, a computer program used to analyse landscape pattern, diversity and evenness (McGarigal et al., 2002).

a)



b)

	WPC- 57	NUN- 68	IVS- 133	NFS- 158	BBS- 173	RPC- 198
WPC- 57	0					
NUN- 68	50	0				
IVS- 133	26	39	0			
NFS- 158	32	54	37	0		
BBS- 173	56	14	48	60	0	
RPC- 198	71	35	65	78	25	0

Figure 2.3: An illustration of hydraulic signatures and comparison matrices used to calculate differences in hydraulic diversity at three scales, as described above. (a) Example of a comparison of the hydraulic signature of two separate runs within RPC. Comparison in this manner provides an indication of the amount of natural variation present within a single CGU type within a single stream (point 1). Key to colour scheme: **N/A 0 1- 5 6- 10 11- 15 16- 20 21- 40**

(b) an example of a comparison of 'run' CGUs across the stream chronosequence, used to evaluate changes in the hydraulic diversity of CGUs across the chronosequence (point 2 in the measurement of hydraulic diversity described above). Key to HSC values: **N/A 0-10 11-20 21-40 41-60 61-80 81-100**

FRAGSTATS analyses landscape patterns at three scales; the landscape, class and patch levels. The patch level is the smallest unit within the landscape which, in this instance, is each individual CGU (i.e.- CGU number 3, a pool within North Fingers South Stream). This level of detail is too fine scaled for the purposes of this study which focuses on landscape connectivity and diversity, and hence, no patch level metrics were calculated, although the patch level was used as the computational basis for the landscape metrics. The CGU or 'class' level, as defined FRAGSTATS, and associated metrics are the combined cases of each CGU type; i.e.- all of the runs within a single stream. These were calculated outside of the FRAGSTATS platform, as a greater flexibility in the analysis of CGU types could be calculated using descriptive statistics, rather than those calculated in FRAGSTATS. The majority of the metrics calculated using FRAGSTATS were at the landscape level (all CGUs and CGU types within a river), as this represents the spatial pattern and structure of the river unit (or representative reach) studied, enabling a comparison of river habitat development to be assessed.

Two landscape metrics were used to measure spatial configuration. Contagion is a measure of the 'clumpiness' of a landscape, or the tendency for patch types (CGUs) to be in large or 'contagious' distributions (McGarigal et al., 2002). It is also a measure of patch type diversity and dominance. Higher values of contagion are usually found in landscapes which contain a few large patches, whilst landscapes with fewer, smaller habitat types typically have a low contagion value. A complementary metric to contagion is the Interspersion and Juxtaposition Index (IJI), which, like Contagion, measures the spatial configuration of the landscape, and how evenly distributed habitat types are. The benefit of IJI, however, is that instead of the likelihood of raster cells (or pixels) being used to measure the probability of two separate habitat types being adjacent to one another, IJI only uses the patch perimeter to calculate adjacency, and hence, calculates whole patch adjacency, and not just cell adjacency. Such calculation removes the bias of cells located in the centre of a homogenous patch skewing the overall calculation. Higher values of IJI indicate that a landscape contains habitat types which are well interspersed (i.e.- equally adjacent to each other), whereas lower values characterise landscapes which are poorly interspersed (McGarigal et al., 2002).

The cohesion metric was used as a measure of the physical connectivity of habitat types within a stream by calculating the proportional difference between patch area and perimeter which gives an indication of the degree of clumping each habitat type becomes in its distribution. The more clumped the CGU distribution, the more physically connected the habitat. Relative patch richness (RPR) was also calculated. RPR represents the richness, as a percentage, of the maximum potential richness within the landscape. In this case, the maximum potential richness occurred when a stream contained all five CGU types. RPR is therefore related to diversity.

Diversity (Shannon's and Simpson's Diversity indices) and evenness (Shannon's and Simpson's Evenness indices) metrics were calculated using FRAGSTATS at the landscape level to determine CGU richness and evenness as a measure of landscape composition within the riverscapes. The landscape diversity indices calculate the richness, or number of habitat units within the landscape, whilst evenness indices provide information on how the different habitat units are distributed within the landscape (i.e.- clumped or evenly spread). Unlike the Contagion metric, however, Shannon's and Simpson's evenness metrics assess the overall evenness of the landscape, rather than the size of the habitat units. Both of these measures (diversity and evenness) provide information on landscape composition, and have been previously used to provide an ecologically meaningful measure of geomorphic diversity (Yarnell et al., 2006).

2.3 Results

2.3.1 Geomorphic and hydraulic diversity

CGU composition was found to vary over the stream chronosequence (as illustrated in Appendix 2). A summary of the number of CGUs found within each stream is provided in Table 2.2. The youngest streams supported lower geomorphic and hydraulic diversity than older streams, and were characterised by faster flowing CGUs (rapids and riffles; Figure 2.4), with higher velocities and shallower depths, and thus higher Froude numbers (Figure 2.5). As stream age increased, however, slower flowing CGUs (e.g. glides and pools) began to dominate, resulting in a decline in mean velocity and Froude number.

Table 2.2: A summary of the number of CGUs and CGU types recorded in the study reaches within the study streams, Summer 2007.

	Rapid	**Riffle**	**Run**	**Glide**	**Pool**	**No CGUs/ 100m**
WPC	1	16	17	-	-	1.6
IVS	8	13	8	-	1	2.3
NFS	6	14	11	2	2	3.2
BBS	1	30	28	8	6	3.0
RPC	-	14	17	7	2	2.5

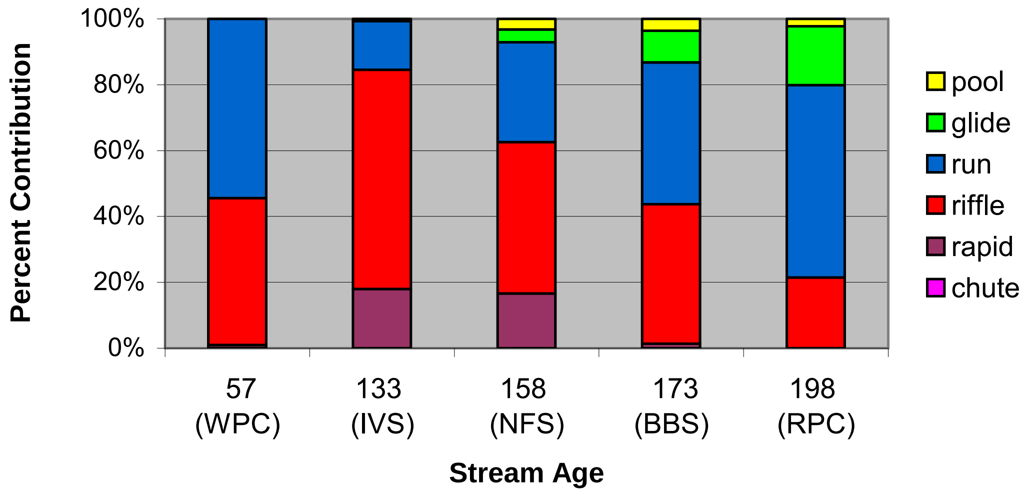


Figure 2.4: Percent contribution of CGU types within study streams, Summer 2007.

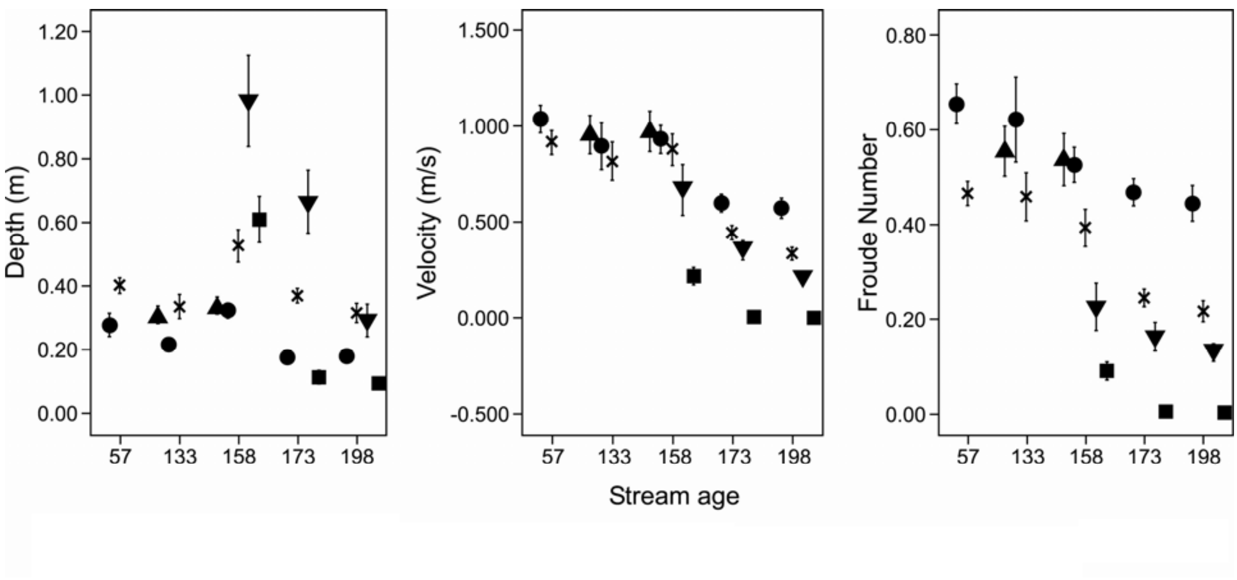


Figure 2.5: Mean CGU depth, velocity and Froude number values across the stream chronosequence. ▲ rapid; ● riffle; **X** run; ▼ glide; ■ pool. Bars represent 95% C.I.

Table 2.3: Summary of average depth, velocity and Froude number values for each CGU type within the study streams.

		Rapid	Riffle	Run	Glide	Pool
WPC	**Depth (m)**	-	0.28	0.4	-	-
	Velocity (m/s)	-	1.036	0.914	-	-
	Froude Number	-	0.63	0.46	-	-
IVS	**Depth (m)**	0.31	0.22	0.34	-	-
	Velocity (m/s)	0.957	0.894	0.816	-	-
	Froude Number	0.55	0.62	0.45	-	-
NFS	**Depth (m)**	0.34	0.32	0.53	0.98	0.61
	Velocity (m/s)	0.973	0.931	0.878	0.667	0.219
	Froude Number	0.53	0.53	0.39	0.22	0.09
BBS	**Depth (m)**	-	0.18	0.37	0.66	0.11
	Velocity (m/s)	-	0.599	0.444	0.354	0.007
	Froude Number	-	0.45	0.23	0.14	0.00
RPC	**Depth (m)**	-	0.18	0.30	0.29	0.10
	Velocity (m/s)	-	0.572	0.337	0.211	0.003
	Froude Number	-	0.43	0.20	0.13	0.00

Results from the oneway ANOVA of average depth, velocity and Froude number values across the stream chronosequence (Table 2.4) reveals North Fingers South Stream to be significantly different from all other streams. In contrast, Ice Valley and Berg Bay South Streams contained the least number of significant differences in stream hydraulics across the chronosequence.

Table 2.4: Summary of oneway ANOVA results of differences in depth, velocity and Froude number values between stream across the age chronosequence. NS= not significant, * = p<0.05, ** = p<0.01.

		WPC	IVS	NFS	BBS	RPC
Depth	WPC	/	*	**	NS	**
	IVS	*	/	**	NS	NS
	NFS	**	**	/	**	**
	BBS	NS	NS	**	/	**
	RPC	**	NS	**	**	/
Velocity	WPC	/	NS	**	**	**
	IVS	NS	/	*	**	**
	NFS	**	*	/	**	**
	BBS	**	**	**	/	NS
	RPC	**	**	**	NS	/
Froude Number	WPC	/	NS	**	**	**
	IVS	NS	/	**	**	**
	NFS	**	**	/	**	**
	BBS	**	**	**	/	NS
	RPC	**	**	**	NS	/

2.3.2 Landscape diversity and evenness

Landscape diversity and number of CGUs per 100m of mapped stream both increased with stream age, peaking at streams of intermediate age, whilst evenness decreased from the younger to older streams (Figure 2.6). It should be noted, however, that the low number of samples (one for each stream) and restriction in terms of replication (additional streams of suitable ages) warrant the use of caution when interpreting the relationships shown in Figure 2.6. Table 2.5 provides a summary of the landscape level metrics calculated using FRAGSTATS. Analysis of the physical connectivity of the landscape (as calculated using the COHESION metric) suggests that there is no difference in the connectivity between streams, as all of the streams resulted in very similar COHESION values, ranging from 99.1 to 99.6, with 100 being the maximum value possible.

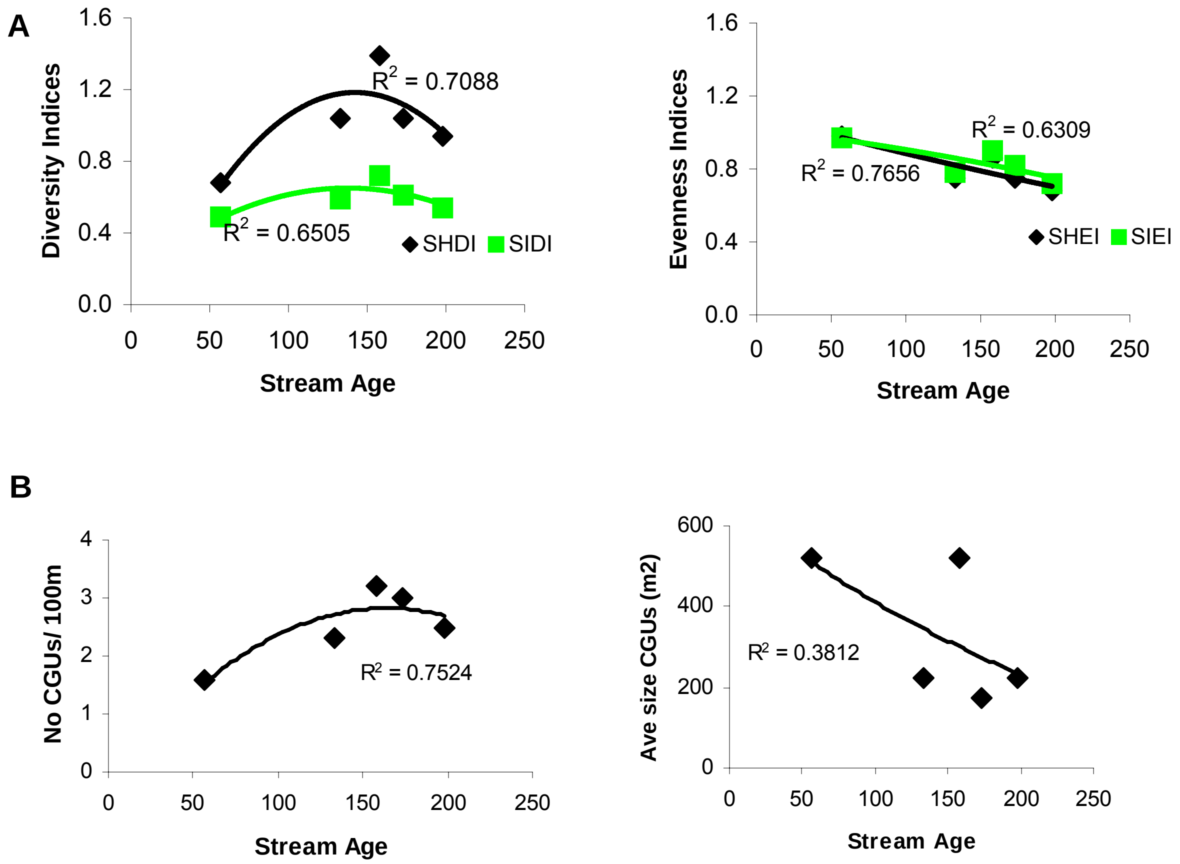


Figure 2.6: Changes in habitat and CGU variables within the study streams (A) Reach landscape and evenness indices within the study streams. SHDI= Shannon's Diversity Index; SIDI= Simpson's Diversity Index; SHEI= Shannon's Evenness Index; SIEI= Simpson's Evenness Index. (B) Number (per 100m) and size (m^2) of CGUs across the stream chronosequence.

Table 2.5: Summary of landscape level metrics calculated using FRAGSTATS

	COHESION	IJI	SHDI	SIDI	RPR	SHEI	SIEI
WPC	99.6	*	0.68	0.49	40	0.98	0.97
IVS	99.1	58.8	1.04	0.59	80	0.75	0.78
NFS	99.6	76.8	1.39	0.72	100	0.86	0.90
BBS	99.1	51.8	1.04	0.61	80	0.75	0.82
RPC	99.2	37.7	0.94	0.54	80	0.68	0.72

* = not possible to calculate metric due to low number of CGUs present at the site (2), as CGUs will always be adjacent to the other CGU type, or itself

Conversely, the IJI metric, which is a measurement of how evenly distributed CGU types are, shows that North Fingers South (NFS) is the most evenly distributed, whilst CGUs within RPC are more isolated, as indicated by a lower IJI value. Diversity metrics, Shannon's Diversity Index (SHDI) and Simpson's Diversity Index (SIDI) follow a similar trend to one another, starting at lower values in the youngest stream, Wolf Point Creek, rising to a peak at North Fingers South, then tailing off in the two older streams, Berg Bay South and Rush Point Creek, indicating that landscape diversity peaks in the intermediate aged stream (as seen at the meso-scale level).

Relative patch richness was highest within North Fingers South, which contained all five CGU types, although it should be noted that its higher score reflects the presence of cascade units which were absent from all the other streams. The presence of cascades does not necessarily add any additional favourable habitats to instream biota due to the high velocities and bedrock substrate found at the cascade unit. The low score at Wolf Point Creek, however, reflects the lack of slower flowing CGUs (pools and glides).

2.3.3 HydroSignature

Table 2.6 summarises results obtained from cross analysis of CGU types, where the average HydroSignature Comparison value (HSC) for a single river CGU type was calculated to determine the amount of natural variation present between CGUs in a within that river system. These results show that glide CGUs within Berg Bay South had the highest dissimilarity from one another (HSC = 40), followed by riffle and run

CGUs within Wolf Point Creek, Berg Bay South and Rush Point Creek. CGUs within Ice Valley Stream and North Fingers South were similar to one another, as suggested by the low HSC values.

Table 2.6: Average value of comparison index of CGU types within the study streams, indicating the amount of natural variation within CGUs across the stream chronosequence. Zero values occur when only one example of a CGU occurred within the study reach; comparison of that HydroSignature with itself will be indentical, and hence have an HSC value of 0. * denotes a lack of that CGU within the river.

	WPC (57)	**IVS** (133)	**NFS** (158)	**BBS** (173)	**RPC** (198)
Rapid	*	5	13	*	*
Riffle	29	0	4	24	16
Run	18	0	0	25	25
Glide	*	*	0	40	0
Pool	*	*	0	0	0

Comparison of the hydraulic composition of CGU types across the chronosequence using Hydrosignature is summarised in Figure 2.7. These data show that a comparison of the hydraulic composition or signature of a riffle within RPC vs a riffle in WPC (the oldest vs the youngest stream) results in a value of 48, indicating that the hydraulic composition of riffles within these two rivers are less similar than a comparison of riffles within RPC and BBS (the two oldest streams) which have an HSC value of 9. Comparison of HSC values across the chronosequence in this way, from WPC to RPC reveals a steady increase in HSC values as the difference in stream age increases, whilst the lowest HSC values occur where the difference in stream age are lowest (e.g. comparison of the two youngest or older two streams). It is interesting to note that riffle and pool CGUs in the two oldest streams (173 and 198 years respectively) have similar hydraulic signatures (HSC = 9 and 2 respectively).

The mean HSC value of each CGU type (i.e. mean HSC value of all ‘run’ CGUs within all of the study streams) was lowest within fast flowing CGUs (Table 2.7), indicating little difference in hydraulic characteristics between streams, whilst the HSC values for slower flowing CGUs was high, suggesting growing disparity in the hydraulic characteristics of these CGUs, in those streams which contained them (NFS, BBS and RPC).

Table 2.7: Summary of average HSC value for each CGU type across the stream chronosequence. The average HSC value indicates the degree of change in hydraulic diversity within CGUs across the chronosequence.

CGU type	Ave HSC value
Rapid	14
Riffle	34
Run	46
Glide	69
Pool	56

Stream Age

Stream Age

rapid	57	133	158	173	198
57					
133	*				
158	*	14			
173	*	*	*		
198	*	*	*	*	

riffle	57	133	158	173	198
57					
133	22				
158	20	18			
173	49	33	46		
198	48	33	45	9	

run	57	133	158	173	198
57					
133	26				
158	32	37			
173	56	48	60		
198	71	65	78	25	

glide	57	133	158	173	198
57					
133	*				
158	*	*			
173	*	*	69		
198	*	*	76	62	

pool	57	133	158	173	198
57					
133	*				
158	*	*			
173	*	*	82		
198	*	*	84	2	

Figure 2.7: Summary of the comparison of hydraulic signatures within CGUs across the 200- year chronosequence. Figures in bold indicate the stream age, whilst figures within the matrix signify the comparison index of the similarity between CGUs within those two streams. A low figure indicates that the hydraulic composition of CGUs within those rivers is similar, whilst a high value indicates that the hydraulic signatures are dissimilar.

2.4 Discussion

Hydraulic and geomorphic composition differed across the stream chronosequence. Differences in channel geomorphology may be due to inherent differences between streams, such as catchment geology, stream discharge and gradient. However, differences in these primary driving variables were taken into account when study streams were selected, and when identifying channel reaches in which hydraulic characteristics were assessed. The scouring action of glacial advance and retreat results in the removal of all previous biological and physical features from stream catchments, effectively creating a 'clean slate' or tabula rasa, from which new stream habitats can evolve within a landscape driven by primary successional process and current hydraulic regimes. Stream variables as described in Table 2.1 do not appear to vary substantially; stream size, gradient and geology are similar across the chronosequence, indicating that inherent differences between the study streams are unlikely. It is therefore proposed that the differences in geomorphic composition within the streams are due to differences which have occurred as a result of changes in channel geomorphology which result from stream development over time.

2.4.1 Geomorphic development

Analysis of the geomorphic composition of the five study streams representing 200 years of stream development revealed that the youngest streams typically contained a lower geomorphic diversity. These streams tended to be dominated by large, fast flowing CGUs such as rapids and riffles, with very few velocity shelters. As stream age increases, however, small, slow flowing CGUs, such as glides and pools become dominant, resulting in decreased flow velocities and increased water depth. The addition of small, slow flowing CGUs results in an increase in the total number of CGUs present, whilst the average size of the CGUs declines with increasing stream age. In turn, these changes lead to a decline in the evenness of the landscape, as habitat units become isolated from one another (e.g.- as measured by the Interspersion and Juxtaposition and Shannon's and Simpson's Evenness Indices) resulting in the landscape becoming increasingly uneven.

Changes in the number, diversity and evenness of geomorphic units across the stream chronosequence results in an increase in habitat diversity as stream age increases, as a result of an increase in the number of microhabitats (aka- ‘ecotones’), such as pool heads and riffle tails which otherwise may be of limited supply. This increased habitat diversity benefits instream biota by allowing a greater number of species to co-exist, across a broad range of life stages (Dolinsek et al., 2007; Floyd et al., 2009).

The changes in geomorphic composition observed are likely to be a result of the continued development of the stream and riparian vegetation, which together, result in the gradual stabilisation of the stream channel. Previous research within Glacier Bay has shown that for the first few years, newly formed streams within deglaciated catchments are typically highly unstable due to channel migration and instability and marked fluctuations in flow following spring snowmelt and autumn storms. Over time, however, streams begin to stabilise following erosional processes, which deepen streambeds, reducing the stream gradient whilst increasing stream capacity (Milner, 1987). Such stability encourages the growth of riparian vegetation, which further promotes channel stability and geomorphic diversity by stabilising stream banks and introducing organic debris into the stream ecosystem which may later be used as a roughness element (detailed in Chapter 3). This development allows geomorphic processes to interact with the stream’s hydrology to create channel units such as glides and pools, as observed.

Such development also influences the relative sediment supply within each stream. As discussed, the youngest streams within Glacier Bay are characterised as having unstable stream channels, as well as a general lack of riparian vegetation, resulting in increased channel erosion and high sediment supply. Older streams, however, are likely to have lower sediment supplies due to the occurrence of established riparian vegetation and increased channel stability. Streams of intermediate age, however, remain relatively unstable, with developing riparian vegetation and a moderate sediment supply (as a result of active erosion of stream channels), which may be utilised to create geomorphic complexity and diversity. Changes in sediment supply such as this has been supported by earlier research by Sidle and Milner (1989) in which the sediment supply of Glacier Bay streams using assessments of total suspended sediment, turbidity and bedload transport rates reported Wolf Point Creek to have the highest sediment input, due to channel instability and migration and sediment input from a glacial remnant, whilst older streams (Ice Valley Stream and Berg Bay South) displayed a gradual reduction in sediment supply, leading to a state of equilibrium in terms of the supply/ capacity ratio. Sediment supply has recently been shown to influence riverine habitat heterogeneity (Yarnell et al., 2006). Using measurements of sediment supply and transport capacity, Yarnell et al. (2006) were able to determine the role of relative sediment supply in driving geomorphic diversity at the reach scale in natural river systems. Streams with a moderate relative sediment supply (in terms of the supply/ capacity ratio) were shown to display the highest habitat heterogeneity due to differential scour and deposition, which creates a greater variety of geomorphic features. Such influence of sediment supply on habitat heterogeneity also appears to be operating within Glacier Bay streams, and could be the cause of the differences in habitat diversity observed between the streams.

It is possible that other processes which govern sediment supply within streams (e.g. valley floor slope, valley confinement, the presence of a sediment rich tributary etc), rather than those processes resulting from stream development over time are responsible for differences in sediment supply within the study streams, however, the earlier research by Sidle and Milner (1989), as well as extensive research of aerial and topography maps have shown that this is not the case. Chapter 3 investigates this theory in further detail.

2.4.2 Hydraulic complexity

Hydraulic signatures become more diverse (i.e. less similar to one another, as a result of increased diversity) in slower flowing CGUs such as glides and pools than faster flowing CGUs, in that the addition of slower flowing CGUs in older streams results in increased hydraulic variation. Differences between hydraulic signatures were also found to increase as differences in stream age increased (i.e. the oldest stream vs the youngest stream), indicating a significant change in stream hydraulics over time.

Harvey and Clifford (2008) have shown that there is a continuum of increasing habitat complexity from glide to riffle, to pool CGUs, resulting from an increase in turbulence and flow structure organisation within observed CGUs. ‘Within- CGU’ (or biotope) variation was also found to increase across the continuum. These data support the observed changes in hydraulic and habitat diversity as slower flowing CGUs, such as glides and pools began to dominate in older streams.

The development of hydraulic complexity within older streams is likely to have important consequences for instream biota. Hydraulic complexity has been shown to be an important aspect in creating habitat diversity. For example, hydraulic diversity, as dictated by a heterogeneous channel morphology, has been shown to influence the selection of suitable microhabitat conditions for spawning chinook salmon (Moir and Pasternack, 2008), yet few habitat assessments take hydraulic habitat into account (Crowder and Diplas, 2006; Shoffner and Royall, 2008).

This study has assessed the geomorphic and hydraulic complexity of river reaches (i.e.- the mesoscale) to be studied, permitting comparisons of five study streams representing 200 years of stream development to be assessed. Analysis of habitat availability at this level provides information on differences in geomorphic composition to be indentified which may help identify the geomorphic processes which operate during stream development, creating geomorphic and hydraulic diversity which contribute to the creation of habitat heterogeneity. Assessment at the reach scale has identified a gradual change in the composition and diversity of streams over time, from fast flowing streams with little geomorphic or hydraulic diversity to slower flowing, complex streams which typically contain greater habitat diversity.

These changes in geomorphic and hydraulic diversity are thought to be due to the process of landscape development following deglaciation. In particular, the development of riparian vegetation and its subsequent recruitment into the stream environment is likely to play a key role in altering geomorphic complexity and hydraulic variation at the microscale, and is studied in greater detail in Chapter 3. An understanding of how geomorphic and hydraulic complexity are formed and maintained is of vital importance in informing restoration techniques, which aim to recreate these natural processes.

2.5 Conclusions

This study has shown that stream hydromorphology differs amongst five streams of varying ages in Glacier Bay National Park. Geomorphic composition, complexity and hydraulic variation increased as stream age increased, resulting in increased habitat and landscape diversity. These results suggest that the geomorphic composition of streams change over time resulting in an increase in hydraulic diversity, creating habitat heterogeneity within streams, which instream biota may utilise. This research suggests that the hydromorphic condition of streams also alters over time, developing favourable conditions for the colonisation of these habitats by macroinvertebrates and Pacific salmonids.

Further research is now needed to identify the drivers responsible for the observed changes in geomorphic and hydraulic complexity observed across the stream chronosequence. Quantification of the response of colonising Pacific salmon to the creation of habitat heterogeneity within these recently deglaciated streams within Chapter 4 will further clarify those features of stream development which drive the continued colonisation of these newly created habitats.

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3

Coarse woody debris and the development of habitat complexity within streams

The physical and structural characteristics of coarse woody debris structures were examined within five streams representing 200 years of stream development within Glacier Bay National Park, Alaska. Debris characteristics were found to alter across the stream chronosequence as a result of adjacent terrestrial development and the subsequent introduction of woody debris into the riverine environment as a result of bank erosion. The influence of coarse woody debris characteristics on the development of geomorphic diversity and hydraulic variability were assessed using detailed habitat mapping and hydraulic assessment using an Acoustic Doppler Current Profiler at a number of transects upstream, downstream and adjacent to woody debris structures. Results show that the size, complexity and orientation of woody debris are the main drivers in determining the degree of influence such structures have on stream habitat and complexity. Adjacent riparian vegetation must be of a sufficient stage of development (in terms of size and maturity) in order to elicit significant changes as a geomorphic agent, which may be of benefit to aquatic biota such as fish, macroinvertebrates and plants.

3.1 Introduction

The natural accumulation of logs, branches and other woody vegetation into the stream environment (coarse woody debris (CWD) accumulations) from adjacent stream banks has been shown to play an important role in altering the physical and ecological behaviour of rivers (Bilby and Likens, 1980; Brooks et al., 2004; Faustini and Jones, 2003; Jeffries et al., 2003). CWD is often used as a tool in restoration projects which seek to create or enhance instream habitat which may be utilised by a variety of biota such as fish (Floyd et al., 2009; Neumann and Wildman, 2002; Sullivan et al., 1987), macroinvertebrates (Drury and Kelso, 2000; Milner and Gloyne-Philips, 2005; Schneider and Winemiller, 2008) and plants (Fetherston et al., 1995; Pettit and Naiman, 2005).

The use of CWD within these projects relies on the function of CWD as a roughness element to the stream channel (Gippel, 1995; Manners and Doyle, 2008), which results in modified flow, erosion and deposition, thus influencing the geomorphic and hydraulic structure (Daniels and Rhoads, 2003; Wondzell and Bisson, 2003) and stability (Montgomery et al., 2003) of rivers. Studies focusing on the re-introduction of CWD into degraded streams have shown that following its installation, pool frequency and depth increased, whilst average velocity was reduced as a result of forced scour, sediment mobilisation and flow diversion (Borg et al., 2007; Brooks et al., 2004; Floyd et al., 2009).

The characteristics of CWD structures (e.g. angle of orientation, size, complexity etc) are known to determine the degree of impact a structure has on stream geomorphology and hydraulics. For example, Hughes et al. (2007), found that the most complex structures were associated with the lowest mean velocities and greatest hydraulic diversity within lowland streams, whilst Gippel et al. (1996b) reported that the angle of orientation and degree of channel cover or blockage were more important in influencing debris drag than the shape and position of debris structures within the stream. Debris occupying a higher percentage of the channel resulted in elevated drag coefficients, producing a larger impact on stream hydraulics (Gippel, 1995; Gippel et al., 1996a). It is important to note, however, that studies have shown that no single characteristic is the sole predictor of the degree of influence CWD structures have on hydraulic complexity. Instead, each of the physical variables appear to act together to influence the hydraulic complexity surrounding the structure (Hughes et al., 2007), and hence, the synergistic effects of CWD characteristics should be taken into account.

Assessment of flow surrounding obstructions such as boulders and CWD using two- and three- dimensional hydrodynamic models have become increasingly popular (Crowder and Diplas, 2000; Crowder and Diplas, 2002; Daniels and Rhoads, 2003; Daniels and Rhoads, 2004; Shen and Diplas, 2008; Shields and Rigby, 2005). These studies illustrate that such obstructions alter the spatial and temporal complexity of the water flow, creating complex localised flow patterns favoured by instream biota. Few studies, however, have assessed how differences in CWD characteristics may alter the three-dimensional flow structure upstream and downstream of a woody debris complex, resulting in changes in the hydraulic and geomorphic composition of streams. Assessment of flow structure at this level is of particular interest as changes in flow are likely to occur rapidly, within a potentially limited space (Daniels and Rhoads, 2003).

The objective of this study was to assess how differences in CWD characteristics influence geomorphic composition and hydraulic variation within developing stream environments. Rapid glacial recession within Glacier Bay National Park and Preserve (GBNP), Alaska, has created a unique opportunity to study the development of habitat complexity following the natural introduction of CWD. By comparing the physical characteristics of CWD accumulations across five streams representing 200 years of stream development, it is possible to analyse how CWD structures alter in structure and formation over time, as a result of vegetation development influencing the degree of geomorphic and hydraulic complexity within the streams. Specifically, the study aim is to determine how differences in CWD characteristics determine the efficiency of CWD in inducing scour, deposition, trapping of fine sediments, and debris retention which in turn, contribute to habitat complexity within the streams.

It is hoped that this, and other recent studies (Manners and Doyle, 2008), will contribute to our knowledge of how CWD jams alter the hydraulic structure of riverine habitats, which in turn, will assist wood-based restoration projects that aim to restore geomorphic and ecological integrity to degraded riverine habitats.

The term ‘coarse woody debris’ is used in this study in order to allow the addition of small woody accumulations to be included in the assessment. Traditionally, the term large woody debris was used to refer to material in stream channels that is sized larger than 0.1m in diameter, and 1.0m in length (Keller and Swanson, 1979). Recent research, however, has shown that accumulations of smaller woody debris exert similar influences to streams as large woody debris (Dolloff and Warren, 2003; Jackson and Sturm, 2002), and are therefore included within this study.

3.2 Methods

3.2.1 Study site

See section 2.2.1 for detailed study site information.

Previous research within GBNP on CWD indicates that woody riparian vegetation does not play an important role within the stream environment until at least 100 years following deglaciation in those stream systems lacking lakes (Sidle and Milner, 1989), and do not become a key component until more than 130 years following deglaciation (Milner and Gloyne-Philips, 2005). The floodplains of streams downstream of lakes, however (such as the youngest stream in this study; Wolf Point Creek) are typically colonised by riparian vegetation at an earlier stage, due to the buffering effect on stream flow within these systems. This limits downstream peak flows, creating a more stable riparian environment which allows the development of bankside vegetation, including species of alder and willow.

CWD characteristics within GBNP change as stream age increases as a result of the continued development of adjacent riparian vegetation. Successional processes of terrestrial habitats within GBNP have been well documented (Chapin et al., 1994; Crocker and Major, 1955; Reiners et al., 1971), revealing a pioneer community of blue-green algae, lichens and liverworts, *Dryas drummondii* and scattered willows for the first 15-25 years following glacial recession. Woody species such as alder begin to dominate approximately 50 years following deglaciation, followed by cottonwood (*Populus trichocarpa*) and scattered Sitka spruce (*Picea sitchensis*) which form a mixed forest approximately 100 years after deglaciation, leading to a climax community of western hemlock (*Tsuga heterophylla*) forest, and later *Sphagnum* dominated muskeg over a period of thousands of years (Chapin et al., 1994; Milner et al., 2000). This process of terrestrial succession results in differences in CWD characteristics within the streams of different ages, as CWD is recruited directly from the adjacent floodplain when streams migrate across them during flooding events, and hence alters across stream age. Figure 3.1 illustrates the differences in CWD characteristics between the five study streams.

3.2.2 Geomorphic and hydraulic complexity

Differences in geomorphic and hydraulic complexity between the five study streams have been highlighted in Chapter 2, which assessed differences in channel geomorphic units (CGUs) by mapping large areas of the study streams using a mapping grade GPS unit to identify the morphological and hydraulic characteristics of each stream. Thirty random water velocity (at 0.6 depth, averaged over 30 seconds using a Model 201D flow meter, Marsh-McBirnley Inc., Frederick, MD, U.S.A.) and total water depth measurements within CGUs present within representative reaches (detailed in Chapter 2) provided detailed hydraulic assessment of the streams. These data were subsequently assessed using HydroSignature software to provide a measurement of hydraulic diversity (Le Coarer, 2005) both within and between the study streams.

WPC

57 years

Alder dominated riparian vegetation with scattered cottonwood

IVS

133 years

Cottonwood and spruce

Alder and willow under story dominates

Some willow and alder on channel bars

NFS

158 years

Dominant cottonwood and some spruce riparian vegetation

BBS

173 years

Tall cottonwood and spruce with scattered hemlock and thick alder fringe

RPC

198 years

Tall, complex spruce and hemlock with some cottonwood and alder

Figure 3.1: Photos of the five streams studied within GBNP, highlighting the differences in riparian vegetation development across the chronosequence.

Pebble counts were conducted within the mapped reaches (Chapter 2) to assess substrate composition. Substrate particles were randomly selected for measurement using a modified version of the Wolman walk (Wolman, 1954) as described by Bevenger and King (1995). A minimum of thirty particles were measured within each CGU along the intermediate, or 'b axis' within each CGU and subsequently grouped by stream. Bed material particle size distribution was then plotted to obtain the median particle size (D_{50}). Calculation of the bank full shear stress was obtained using the DuBoys equation as follows:-

$$\tau = \rho ghS \qquad (1)$$

where ρ is the density of water (set at 1000 kg/m^3), g is the acceleration due to gravity, h is the hydraulic radius, which in this case, due to the rectangular nature of the river, is replaced by the average flow depth and S is the reach slope. When equation 1 is combined with equation 2 below, the minimum stable grain size which is entrained by bankfull flows may be calculated;

$$\tau_c = \theta_c \, gD \, (\rho_s - \rho) \qquad (2)$$

where τ_c is the Shield's parameter, θ_c is the dimensionless constant which is related to particle shape (in this instance, θ_c = 0.04 as the particle size distribution analysis suggests that there are few fines in the surface layer, and is hence a suitable figure (Gordon et al., 2004)), ρ_s is the sediment density (assumed to be 2.65 g/cm^3) and D is the minimum stable grain size at bankfull flow (i.e. the unknown value).

Channel cross sections at two locations within each study stream were used to calculate bankfull capacity. Locations were chosen from historic areas established by Sidle and Milner (1989), and surveyed using a Sokia dumpy level, tripod and staff at breakpoints from the river terrace on either bank and at regular intervals within the stream channel to establish changes in river planform from year to year (not reported here). From these surveys, bankfull capacity was identified.

Landscape evenness and diversity indices were calculated for each of the streams using FRAGSTATS (McGarigal et al., 2002 as detailed in the previous chapter) to provide information on landscape composition and to provide an ecologically meaningful measure of geomorphic diversity (Yarnell et al., 2006).

3.2.3 Assessment of CWD characteristics

The characteristics of coarse woody debris within five study streams were assessed between 2006- 2008, resulting in the characteristics of a total of 131 structures to be assessed. A ground-based survey over a minimum distance of 1.3km (starting directly upstream of the tidal limit) was conducted in 2006 within each stream, allowing the identification, position (using a mapping grade Trimble GeoXT unit with sub metre accuracy and associated Pathfinder Office software; illustrated in Appendix 2) and physical properties (Figure 3.2 / Table 3.1) of each identified CWD structure to be assessed. Key members within each complex were tagged using a small individually numbered metal tree tag to allow relocation of the complex in subsequent years. The locations of tagged CWD structures were visited again in 2007 and 2008 using the recorded GPS co-ordinates, and changes in size, position or properties since their initial identification were noted. New CWD structures were identified and recorded as detailed in Table 3.1. The dimensions of debris dams were measured (length and width) using a laser range finder and recorded, as was the diameter of key members using a tape measure at a fixed distance of 0.2m from the rootwad or at the base of the bole where a rootwad was not present. This height was chosen as the standard measurement at breast height was not always accessible due to the nature of debris dams.

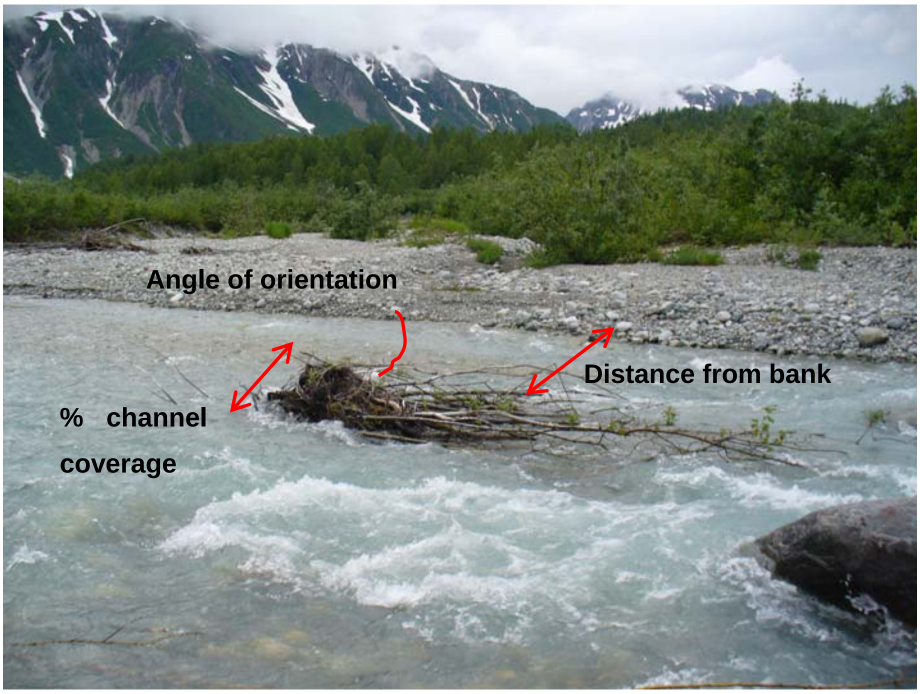


Figure 3.2: Example of a CWD structure within WPC. Identification of the characteristics of this structure included; Dam type- bank input; Position- in channel; Class- active; Control- living rootwad; Anchorage- rooted/ buried in bank; % channel coverage- 5%; Number of pieces- 1; Number of key pieces- 1; Horizontal orientation- 0; Distance from bank- 7; Complexity- 2; Decay state- low.

Positional data of the location of CWD and associated channel geomorphic units were converted from feature based files as collected using the Trimble software, into shapefiles which can be displayed in ArcGIS software using the Export feature within the Trimble Pathfinder Office software. These data were then presented as a map within ArcMap, which assisted in the relocation of CWD structures and interpolation of CWD data.

Oriana2 software (version 2.02c, Kovach Computing Services) was used to create rose diagrams, which illustrate the horizontal orientation of CWD within the study streams to the nearest 15 degrees. These data were input as a range from 0-90° in order to limit any bias in orientation results as a result of differences in orientation between CWD on the left or right bank (0° was identified as the direction of the water flow, i.e.- looking downstream).

3.2.4 ADCP transects around CWD structures

To ascertain the influence of CWD structures in altering hydraulic and geomorphic complexity within the study streams, an Acoustic Doppler Current Profiler (ADCP) was used to measure channel bathymetry, velocity structure and bed shear stress variations in a series of transects upstream, adjacent to and below CWD structures. Selection of structures for ADCP analysis ensured that the chosen structures were 'typical' of that study stream, as determined using the properties previously outlined in Table 3.1. An RDI StreamPro ADCP (RDI Instruments, San Diego, CA, USA) and associated iPAQ (Hewlett-Packard Development Company, Palo Alto, CA, USA) were used, which utilise the RDI 'Transect' software. The StreamPro has the ability to measure the vertical profile of the three-dimensional velocity vector and water depth at a temporal frequency of approximately 1Hz. From these raw data, the chosen parameters may be easily determined. A total of seven CWD complexes were chosen for ADCP transects; a smaller number than originally planned due to inadequate stream depth and / or poor access which prevented the deployment of the ADCP at additional locations. The number of transects completed at each location also differed due to these factors.

The initial set up of the system was conducted in accordance with the manufacturer's instructions (Teledyne, 2005), and a minimum of three consecutive transects were executed at a series of locations upstream, at and downstream of CWD structures. Transects were conducted by slowly traversing from one bank to the other with the ADCP while data were being acquired. Efforts were made to keep the rate of traverse as constant as possible and to keep the angle of traverse as nearly perpendicular to the banks as possible. However, due to the fast currents and uneven footing experienced in many of the transects, the track and rate of traverse of the ADCP were sometimes irregular. The location and number of transects were limited in some circumstances to only those areas with sufficient water depth (typically a minimum of 0.15m) to provide a sufficient transmission return signal.

Transect data were exported from WinRiver and converted into ASCII text files for subsequent analysis within Matlab, which allowed the data to be more easily analysed. To simplify subsequent analysis, the data were interpolated onto a regularly-spaced grid of comparable resolution on a line connecting the starting and ending points of the transect. Velocity and depth data were then smoothed using a moving average (three neighbours on each side) filter.

The bulk channel data that are immediately available from the post-processed data include the discharge (Q) and the hydraulic radius (R_h = A/ P) where A is the cross sectional area and P is the wetted perimeter. To obtain the bed shear stress, additional calculations were required. The vertical profile of streamwise velocity (u) in a turbulent, open channel flow, may be given by

$$u(y) = u^* \left[\frac{1}{\kappa} \log\left(\frac{yu^*}{\nu} \right) + 5 \right] \qquad (3)$$

Where u* is the shear velocity, k is the von Karman constant (0.41), y is the vertical distance above the bed and v is the fluid kinematic viscosity. The shear velocity is related to the shear τ_0 through the following relation

$$u^* 0 \sqrt{\frac{\tau_0}{\rho}}. \tag{4}$$

If the equation for velocity is depth averaged over the local water column depth h, it is found that

$$u_{avg} = u^* \left[\frac{1}{\kappa} \log\left(\frac{hu^*}{\nu} \right) - \frac{1}{\kappa} + 5 \right]. \tag{5}$$

Finally, this equation may be solved for the shear velocity to yield

$$u^* = \frac{u_{avg}\kappa}{lambertW\left[\frac{u_{avg}\kappa h}{\nu} \exp(-1+5\kappa) \right]}. \tag{6}$$

From the StreamPro data, the depth averaged velocity and the water column depth are known. Therefore, the shear velocity, and in turn, the bed shear stress can be determined directly.

In addition to providing quantitative information on depth-averaged velocity, channel discharge and bed shear stress, the ADCP data provide a valuable look at the two-dimensional structure of the flow, and how this structure is altered by the presence of CWD. To help illustrate this, ADCP transects from two of the field sites with contrasting CWD accumulations at Wolf Point Creek and Berg Bay South were considered in detail. The CWD accumulation within Wolf Point Creek consisted of alder brush on the right bank, which was anchored in place by a large boulder. This accumulation is typical of that found within Wolf Point Creek. A total of three transects were taken at this location; 1 upstream and 2 downstream of the accumulation. Additional transects upstream of the accumulation were not possible due to the high flows and deep water located at within this area. Upstream and downstream views of this CWD accumulation are provided in Figure 3.3.

Table 3.1: Coarse woody debris properties recorded within five study streams within Glacier Bay National Park and Preserve. Classification based on Abbe and Montgomery (2003)[1], and Hughes et al., (2007)[2]

CWD variable	*Description*
Identification number	Unique identification number of CWD structure to aid observations in subsequent surveys
Dam type[1]	Wood accumulation typology; bank input/ log step/ valley jam/ flow deflection/ debris flow/ bench/ bar apex/ meander/ raft/ boulder
Position	Position within the channel; in channel/ channel margin/ channel bridging
Class [1]	Degree of influence on the channel; partial/ active/ complete/ high water
Control [1]	Fallen tree/ living upright trunk or branches/ living rootwad/ detached rootwad/ CWD pieces
Anchorage [1]	None apparent/ channel constriction/ living tree/ roots/ riparian vegetation/ rooted or buried in the bank/ overlapping bank/ boulder
% channel coverage	Recorded to the nearest 10%
Dimensions	Height and width of dam or bole in metres
Number of pieces	Number of CWD pieces within the complex
Number of key pieces	Number of pieces key to the maintenance of the CWD structure
Horizontal orientation	Angle to the channel centre line to the nearest 15°
CWD dimension	Length and diameter (at breast height) of key pieces
Distance from bank	From the point closest to the bank, in metres
Complexity [2]	1 (lowest)- 4 (highest)
Decay state	Low, medium or high
Photo	To aid in relocation of the CWD structure in subsequent years

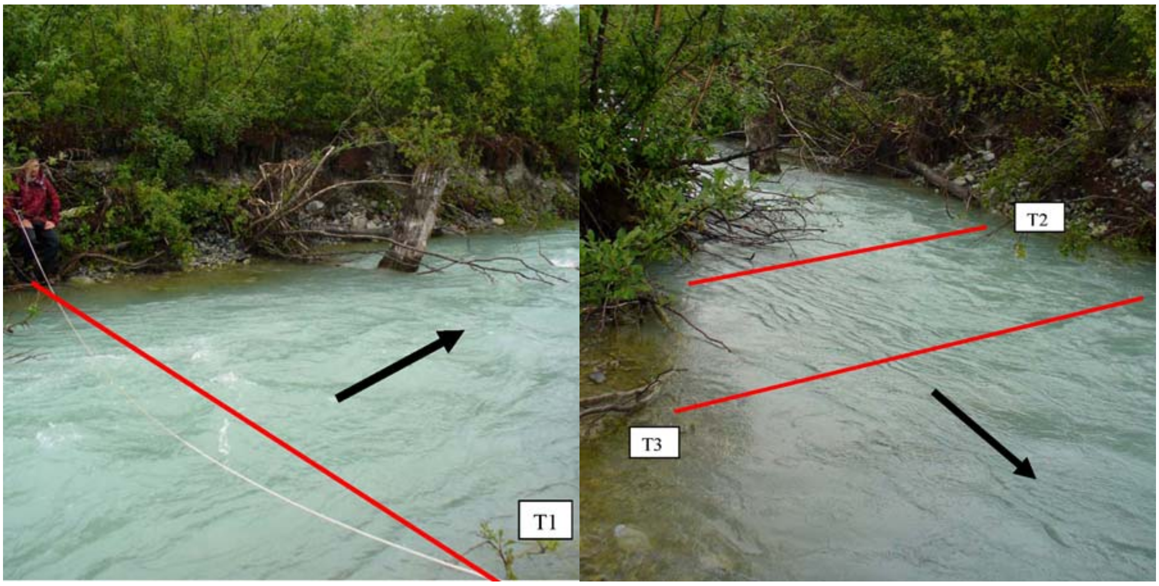


Figure 3.3: Wolf Point Creek field site. The black arrows indicate the direction of flow and the red lines indicate the three transects (T1- upstream, T2 & 3- downstream).

The CWD accumulation at Berg Bay South consisted of a series of CWD piles on the right and left banks. Both accumulations consisted of a single key member comprised of a large spruce tree, and spanned the channel bank which provided an anchorage point behind which smaller debris had accumulated. A total of seven transects were taken at this site; three upstream, two at, and two downstream of the accumulations, as detailed in Figure 3.4.

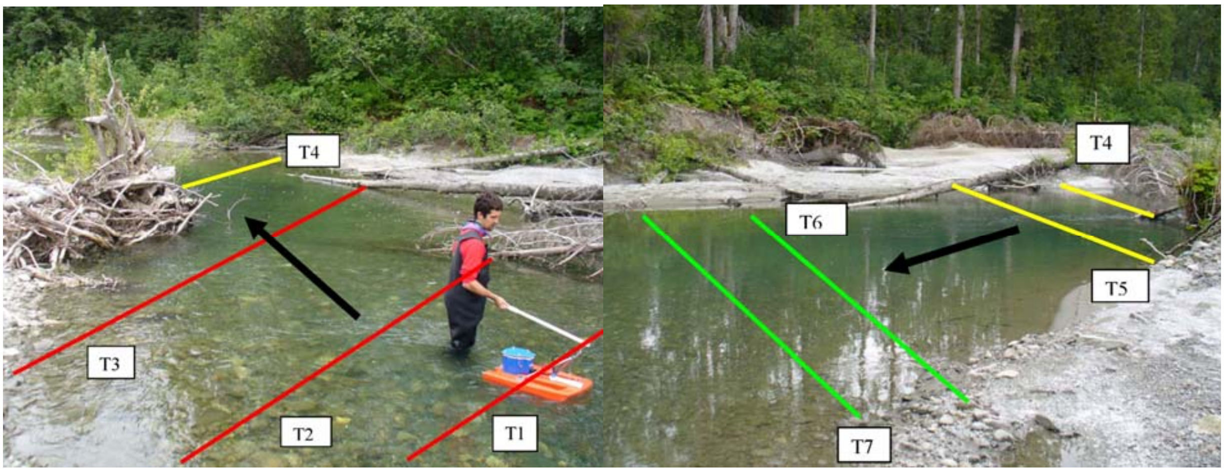


Figure 3.4: Berg Bay South field site. The black arrows indicate the direction of flow and the red, yellow and green lines indicate the location of transects upstream (T1- T3), at (T4- T5) and downstream (T6- T7) of the CWD cluster.

Scatter plots of fluid speed and depth-averaged velocity vectors at each of the transect locations at the study sites were created to illustrate the influence of CWD on the surrounding stream hydrology, and those differences in the degree of influence between the two streams.

Descriptive statistics were used to ascertain differences in stream averaged depth, velocity and shear stress between transects using the statistical package SPSS. Oneway ANOVAs were used to determine changes in mean depth, velocity and shear stress between consecutive transects taken at CWD structures, whilst error plots illustrating the mean velocity, depth and shear stress values and their associated error bars (95% confidence intervals) highlight those transects which are significantly different from one another.

3.3 Results

3.3.1 Sediment analysis

Sediment analysis revealed high bankfull shear stress within each of the streams, resulting in the entrainment of all except the largest sediment particle sizes being transported during bankfull flows (Table 3.2). Observed median particle size however, ranged from coarse gravel within BBS and RPC (39 and 50mm respectively) to small cobble within WPC, IVS and NFS (80, 80 and 90mm respectively; Figure 3.5).

Table 3.2: Sediment and hydraulic characteristics within the five study streams. The observed : expected ratio provides a measurement of textural fining (Buffington and Montgomery, 1999a). Low ratio values suggest the occurrence of a finer reach averaged surface grain size than would be otherwise expected given the calculated power of the stream.

	Bankfull shear stress (N/m^2)	Minimum stable particle size (mm)	Observed D_{50} (mm)	D_{50} Observed: expected
WPC	169	261	80	0.31
IVS	152	235	80	0.34
NFS	147	227	90	0.40
BBS	156	241	39	0.16
RPC	202	312	50	0.16

3.3.2 Physical characteristics of CWD

A summary of CWD characteristics within each of the streams is provided in Table 3.3. Wolf Point Creek, Berg Bay South and Rush Point Creek supported the largest number of structures, whilst analysis of CWD loading (number of CWD structures per 100m of mapped stream) within the surveyed areas of each of the streams reveals similar figures across the chronosequence.

The physical characteristics of CWD, however, were found to vary across stream age. CWD from WPC, the youngest stream, was characterised by small, transient debris predominantly consisting of young alder boles recruited from the adjacent river banks. As stream age increased however, the size of key members and associated debris dams increased. The majority of the debris was active within the channel, due to its location within or on the margin of the water channel. CWD within older streams, such as BBS and RPC, however, were typically more complex and covered a larger percentage of the channel than that found in the younger streams.

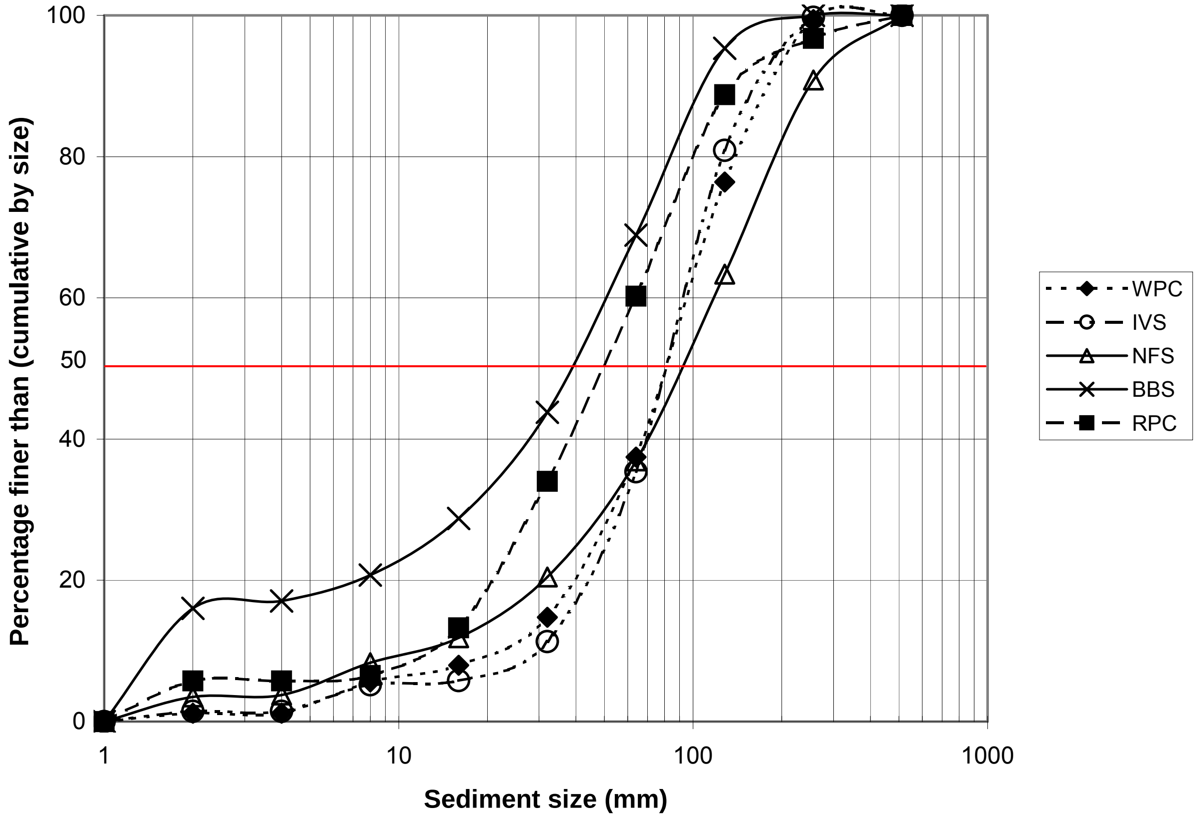


Figure 3.5: Bed material particle size distribution of pebble count data for the five study streams within Glacier Bay National Park.

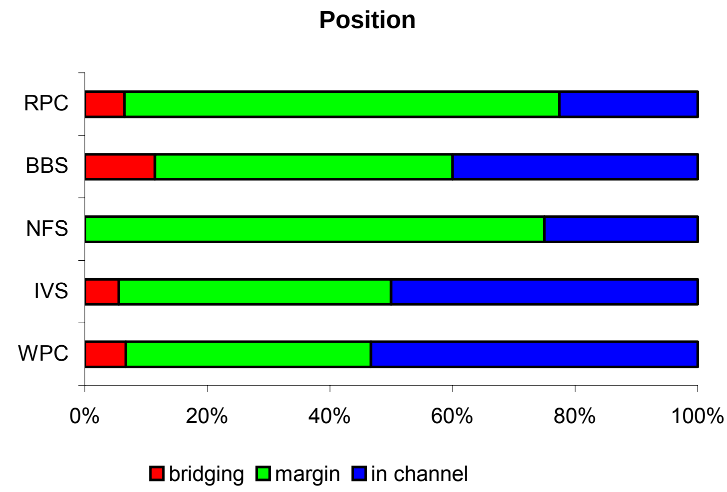
Table 3.3: Summary of observed CWD characteristics within the five study streams

CWD characteristic (stream age in years)		WPC (57)	IVS (133)	NFS (158)	BBS (173)	RPC (198)	Total/ average
No. new CWD pieces recorded	2006	11	10	6	24	20	**71**
	2007	16	7	7	9	10	**49***
	2008	4	1	3	2	1	**11**
	Total	**31**	**18**	**16**	**35**	**31**	**131**
No. of CWD structures not relocated	2007	2	1	0	1	0	**4**
	2008	1	1	0	0	1	**3**
	Total	**3**	**2**	**0**	**1**	**1**	**7**
CWD loading (No./ 100m)- 2008 figures		1.3	1.3	1.2	1.4	1.8	**1.4**
Average dam dimensions - length (m) x width (m)		5.3 x 1.1	10.6 x 2.7	17.9 x 1.2	13.8 x 3.2	15.7 x 3.6	**12.7 x 2.4**
Average diameter of key members (m)		0.12	0.18	0.23	0.29	0.40	**0.25**

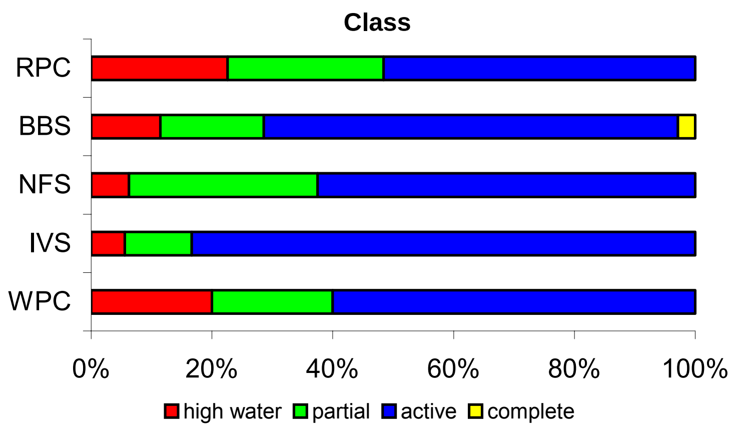
* The majority of these new structures are due to an increase in the length of surveyed area within each of the streams in 2007, which was subsequently re-surveyed in 2008.

Changes in the percentage contribution of CWD variables across the stream chronosequence are illustrated in Figure 3.7. These figures reveal that the position (Figure 3.6a) of CWD within older streams typically consisted of structures which either bridged the stream channel or occupied a position on the channel margin. Structures within younger streams such as Wolf Point Creek and Ice Valley Stream, however, were predominantly located within the stream channel. Comparison of the class and percent channel coverage of CWD structures (Figures 3.6b & 3.6c respectively) within the streams were similar across the chronosequence, with only small variations observed. The complexity of CWD structures (Figure 3.6d) within the streams, however, suggests a trend of increasing structural complexity of CWD structures as stream age increases, with the exception of Rush Point Creek, which had a lower percentage of complex structures (3 and 4 rankings) than Berg Bay South and North Fingers South Stream which are closest in age. The decay of CWD structures (Figure 3.6e) was similar in the two youngest (Ice Valley Stream and Wolf Point Creek) and the oldest stream (Rush Point Creek), whilst Berg Bay South had a large number of decaying structures, and North Fingers South Stream had few.

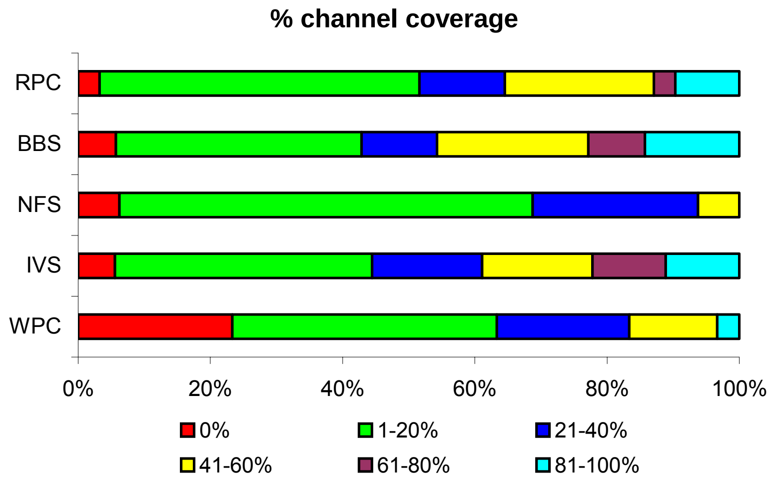
(a)



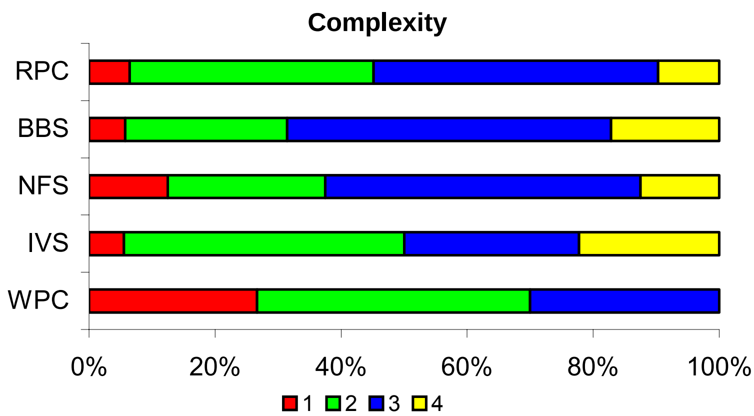
(b)



(c)



(d)



(e)

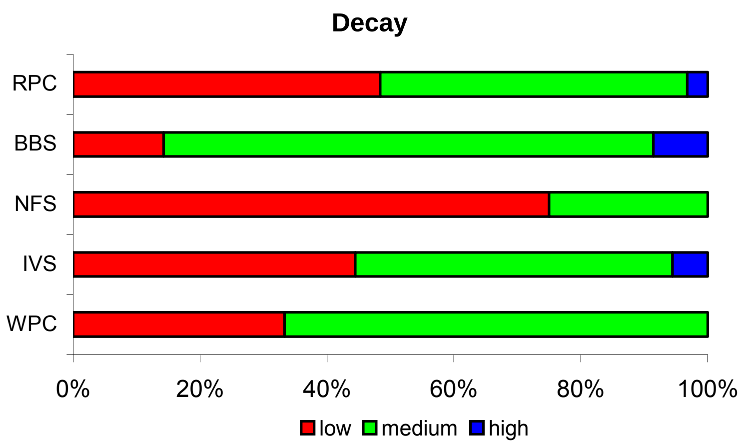
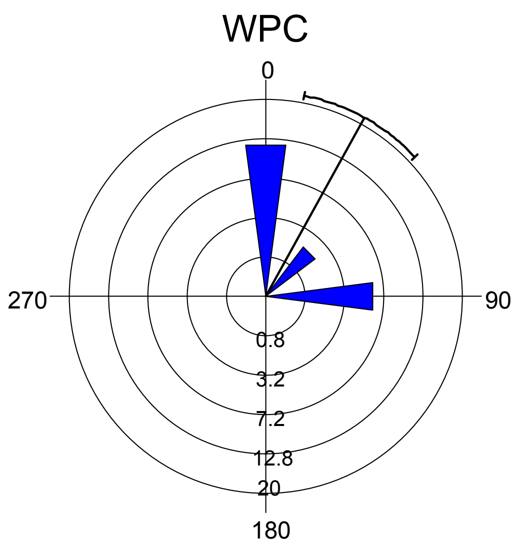
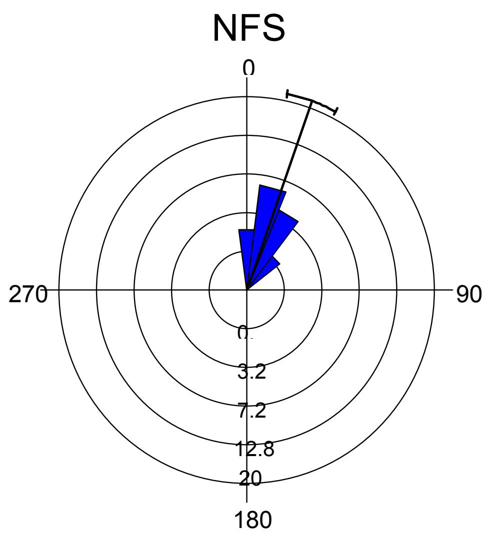


Figure 3.6: Bar graphs illustrating the percent contribution of CWD characteristics to the study streams within Glacier Bay National Park, Alaska. (a) Position of CWD within the stream channel; (b) CWD class, indicating the degree of influence the

structure has on the stream channel; (c) Percent channel coverage; (d) Degree of complexity of CWD structure, from 1 (lowest) to 4 (highest); (e) Decay state- low, medium and high. Used as a proxy of the retention time of CWD structures within the stream channel.

The orientation of CWD within the study streams (Figure 3.7) was found to vary among streams. Structures within WPC, IVS and BBS were typically orientated either parallel or obliquely to the flow, with very few structures orientated at a shallow angle (0-15°) to the flow. Structures within RPC were predominantly orientated parallel to water flow, whilst NFS contained debris typically occupying 15-30˚.





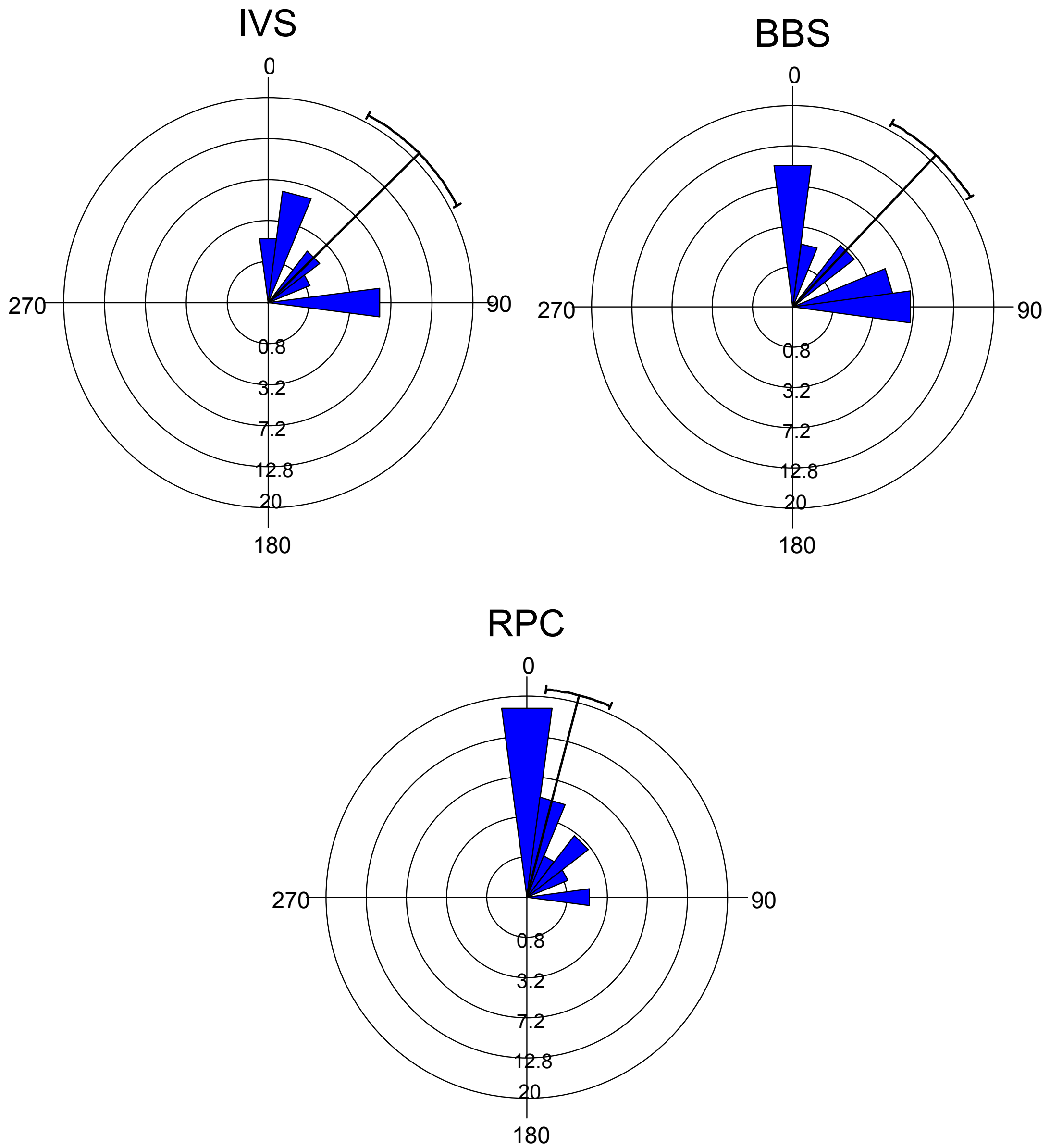


Figure 3.7: Orientation rose diagrams of CWD orientation to water flow. Note that orientation was only assessed looking downstream, from 0-90°, as assessment from 270-360° is only applicable due to changes in which bank the CWD structure is on, and not due to any real differences in orientation. Average angle of orientation and 95% C.I. are illustrated by the error bars.

3.3.3 Hydraulic complexity around CWD

A summary of the characteristics of the seven CWD structures used for ADCP transects are provided in Table 3.4 Oneway ANOVA results of the difference in velocity, depth and shear stress between transects at a single location (Table 3.5) reveal a significant difference in the depth of transects at all seven CWD structures, whilst the velocity and shear stress of transects at NFS, BBS1, BBS2 and RPC1 were also significantly different at transects above, adjacent to and downstream of the CWD structures. These results as shown in Figure 3.8, illustrate the changes in mean depth, velocity and shear stress across the transects surrounding CWD structures. Changes in velocity and shear stress surrounding CWD structures in the two youngest streams (WPC and IVS) and the second surveyed structure at the oldest stream (RPC2) did not change significantly between transects.

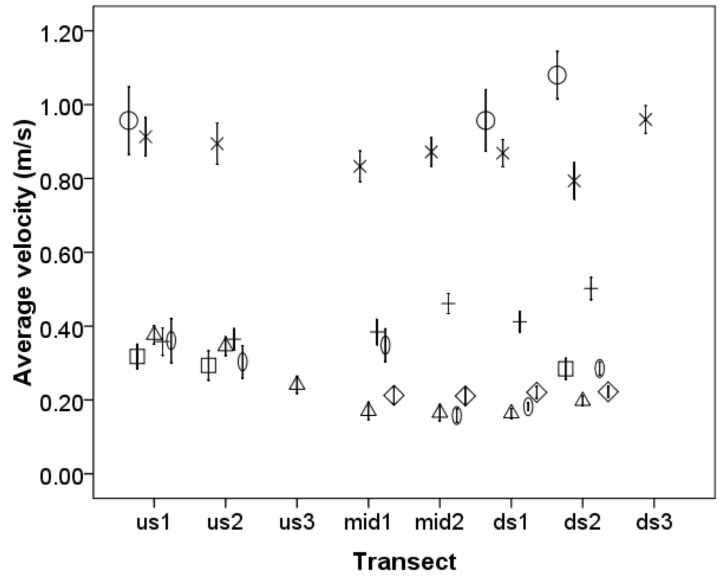
Scatter plots and depth-averaged velocity vectors of ADCP transects around CWD structures (Figures 3.9 & 3.10) illustrate the changes in stream depth and velocity which occur at the microscale.

Table 3.4: Summary of the characteristics of CWD complexes used for ADCP transects within the five study streams. U/S= upstream, adj= adjacent to, D/S= downstream.

	WPC	IVS	NFS	BBS 1	BBS 2	RPC 1	RPC 2
Description	Woody debris mass in centre of channel, forming downstream mid channel bar	Single cottonwood bole spanning entire channel, forming point bar on left bank	Complex mass of fallen spruce trees on channel margin,	Two cottonwood boles on either side of channel, constricting flow to the centre of the channel	Mass of debris anchored by two buried boles on left channel margin	Mass of CWD pieces on left bank of channel, anchored by large living spruce tree	Large spruce bole on channel right channel margin
Number of ADCP transects	1 U/S 2 D/S	2 U/S 1 D/S	2 U/S 2 adj 3 D/S	3 U/S 2 adj 2 D/S	2 U/S 2 adj 2 D/S	2 U/S 2 adj 2 D/S	2 adj 2 D/S
Position	In channel	Bridging	Margin	In channel	Margin	Margin	Margin
Class	Partial	Partial	Active	Active	Active	Active	Partial
% channel coverage	40	100	30	50	10	40	5
Horizontal orientation	45	90	15	75	15	0	60
Complexity	2	2	3	2	3	4	3
Decay state	Medium	Low	Low	Medium	Medium	Medium	Low

Table 3.5: One-way ANOVA results of the differences between ADCP transects at CWD structures within the five study streams. ** = significant at p <0.01; NS= not significant.

		Degrees Freedom	F value	Significance
	Velocity	2	3.09	NS
WPC	Depth	2	24.12	**
	Shear Stress	2	1.57	NS
	Velocity	2	1.17	NS
IVS	Depth	2	7.42	**
	Shear Stress	2	1.40	NS
	Velocity	6	6.07	**
NFS	Depth	6	15.53	**
	Shear Stress	6	5.66	**
	Velocity	6	67.07	**
BBS1	Depth	6	106.11	**
	Shear Stress	6	92.46	**
	Velocity	6	12.76	**
BBS2	Depth	6	52.57	**
	Shear Stress	6	15.52	**
	Velocity	5	19.21	**
RPC1	Depth	5	25.18	**
	Shear Stress	5	24.30	**
	Velocity	3	0.39	NS
RPC2	Depth	3	39.03	**
	Shear Stress	3	0.16	NS


1.20
1.00
0.80
0.60
0.40
0.20
0.00
Average velocity (m/s)
us1
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mid1
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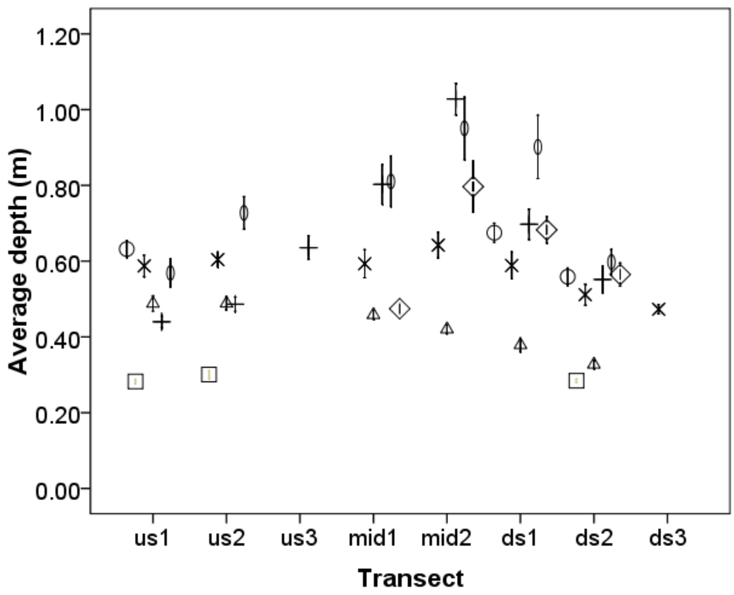
ds2
ds3
Transect


1.20
1.00
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0.60
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Average depth (m)
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ds2
ds3
Transect

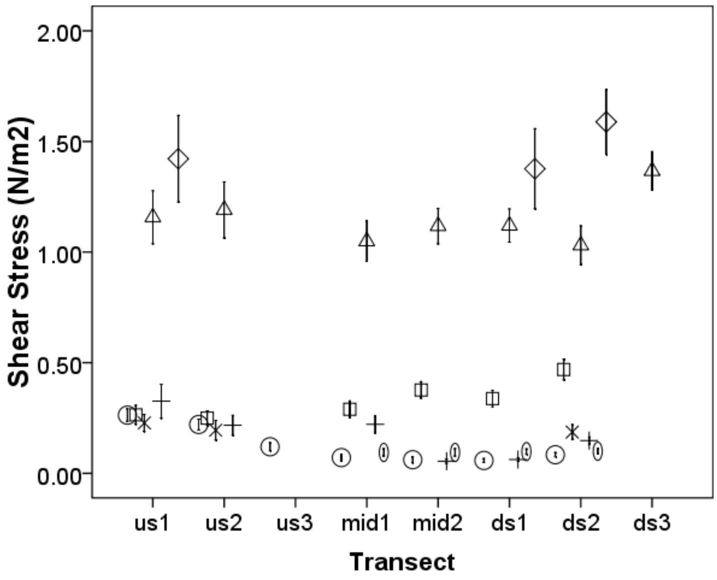
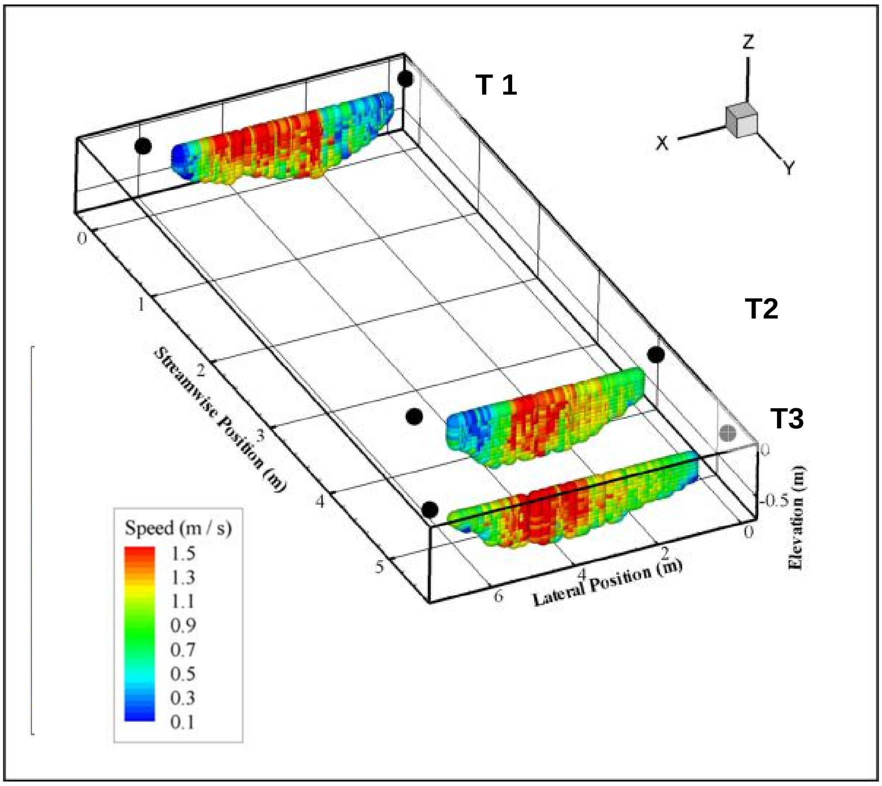


Figure 3.8: Average depth, velocity and shear stress of ADCP transects from the seven surveyed CWD structures within each of the study streams. Bars represent the 95% C.I. ○ WPC; □ IVS; X NFS; △ BBS1, + BBS2, ⬯ RPC1, ◇ RPC2.



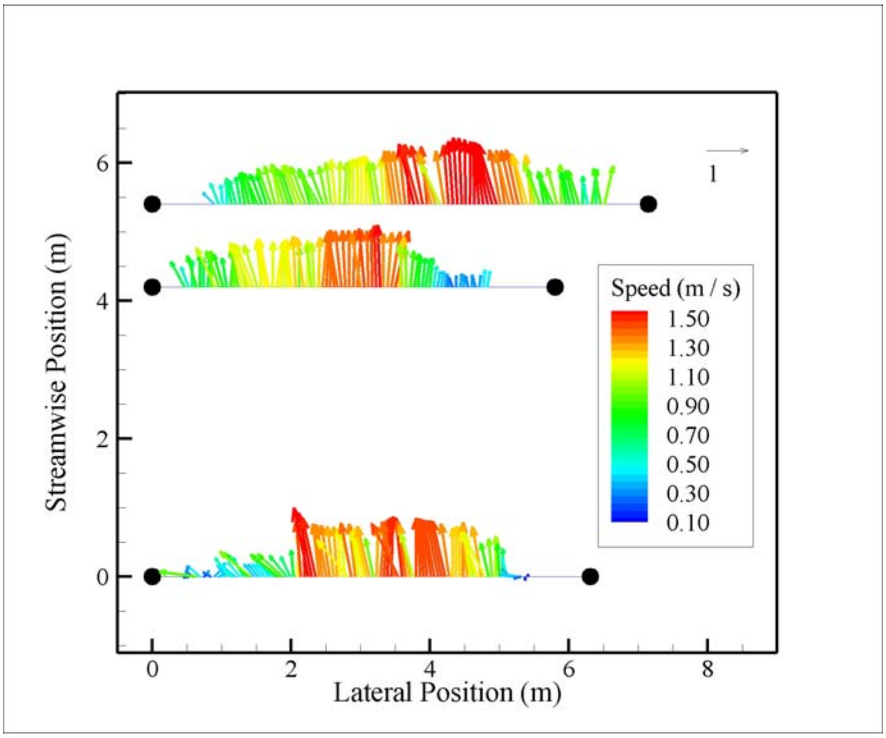
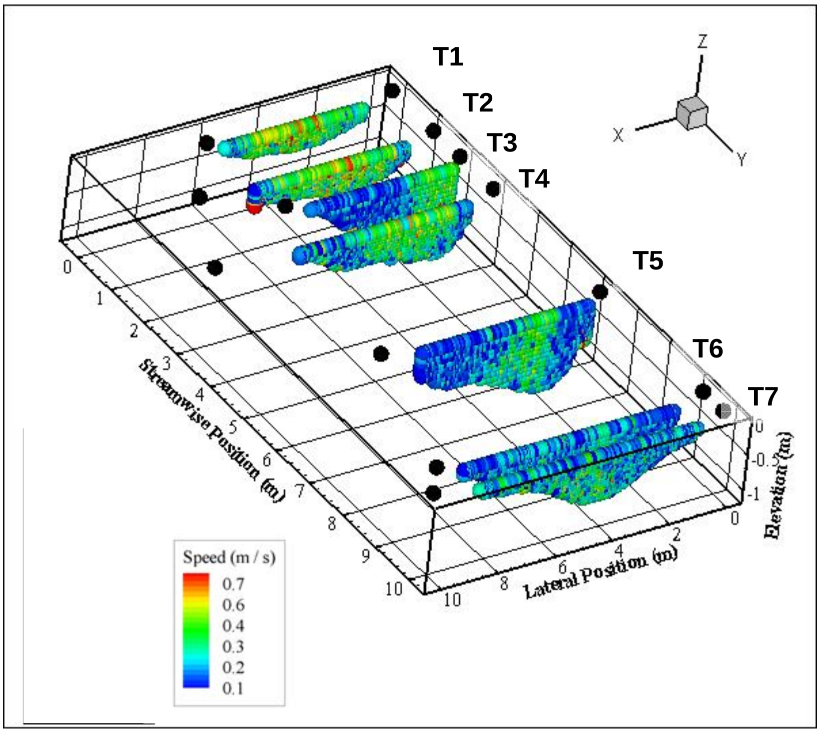


Figure 3.9: Scatterplot of fluid speed (top) and depth- averaged velocity vectors (bottom) for the three transects at the WPC site. The back dots indicate the bank locations. The coloured beads represent a single depth/ velocity cell detected by the

ADCP. The colour represents the water velocity, as illustrated by the key. In the scatter plot, flow is from top to bottom.

Figure 3.9 shows two different views of the ADCP data for the three transects at Wolf Point Creek. Note that the black dots indicate the locations of the banks. In most cases, it was not possible to obtain ADCP data right up to the banks, due to vegetation along the banks and / or the fact that the ADCP cannot obtain data in water less than 15 cm in depth. The distances between transects were measured allowing the transects to be properly spaced in Figure 3.9. However, transects were not surveyed relative to a common datum, so it was not possible to determine the exact lateral positioning of the transects. Therefore, in Figure 3.9, the three transects are simply left-justified.

The scatter plot of water velocity shows the complex vertical and lateral structure of velocity. As expected, the peak velocities are found near the centre of the channel in the upstream transect. Additionally, a clear boundary layer structure is observed with low velocities near the bed and high velocities near the free surface. Transect 2, which lies just downstream of the CWD, shows a narrower ‘core’ of high speed water, due to the constriction of the channel. Additionally, a region of completely slack water is observed on the right, due to the sheltering provided by the CWD. As velocity is a proxy for shear stress, it can be concluded that this region will experience low bed shear and greater sediment deposition.



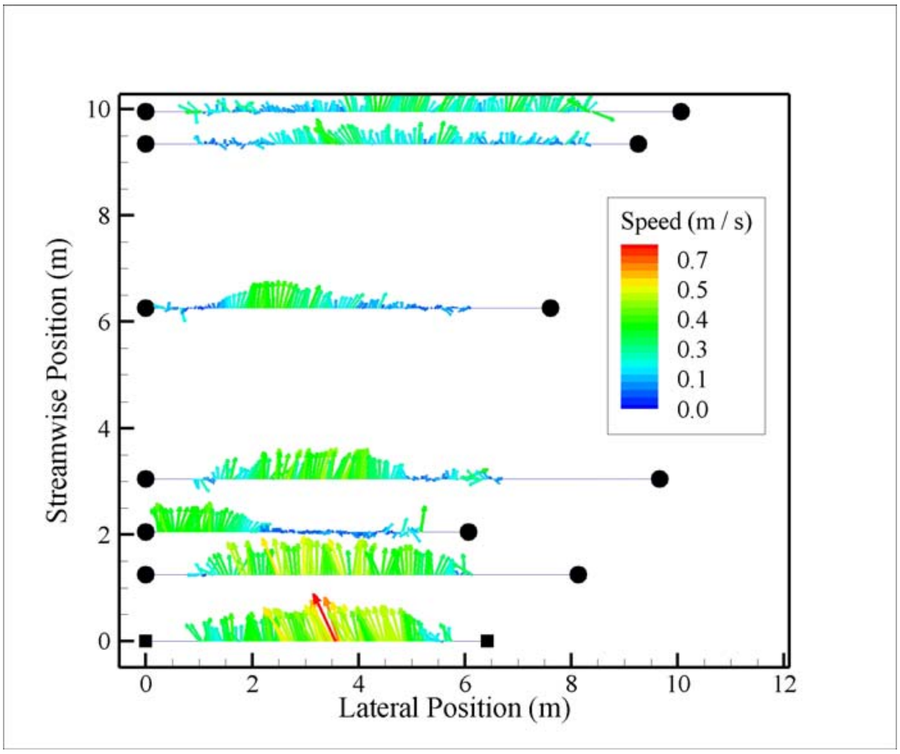


Figure 3.10: Scatterplot of fluid speed/ velocity (top) and depth-averaged velocity vectors (bottom) for the seven transects surrounding the CWD structure within BBS. The black dots indicate bank locations, whilst the coloured beads represent a single

depth/ velocity cell detected by the ADCP. The colour represents the water velocity, as illustrated by the key.

Figure 3.10 shows different views of the ADCP data for the seven transects at the BBS site. As before, the transects are left justified to give them a common origin for the lateral coordinate. Comparing Figures 3.9 and 3.10, it is clear that the study location at BBS is characterized by shallower, much slower flow. This is evidenced by the relative lack of ripples on the water surface when compared to the Wolf Point Creek site. The large CWD on the right bank (close to T2) of the Berg Bay South site creates a significant dead zone at T3. There is then a large CWD on the left bank, at the location of T4. As indicated by the velocity data at T5, there is again a large dead zone (this time on the left) just downstream of this CWD. Transects 6 and 7, markedly downstream of the CWD, reveal a very broad, shallow, and quiescent flow.

Comparison of ADCP transects surrounding CWD structures within the youngest (Wolf Point Creek- 57 years) and the second oldest (Berg Bay South- 173 years) streams illustrate the difference in the degree of influence CWD within the respective streams has on the surrounding environment. Transects upstream and downstream of debris within WPC shows very little difference in stream depth or velocity within the five metre area surveyed. The CWD structure within BBS, however, appears to have a much larger effect on the surrounding stream hydromorphology; resulting in an increase in stream depth and velocity adjacent to and up to several metres downstream of the structure.

3.4 Discussion

3.4.1 The role of coarse woody debris in the development of geomorphic and hydraulic complexity

Analysis of coarse woody debris characteristics and the degree of influence these structures have on surrounding channel hydraulics reveal differences between the five streams of different ages. Although woody debris loading (number of structures per 100m) across the stream chronosequence was similar, and hence had a similar potential influence, assessment of CWD characteristics and their influence on stream hydraulics using the ADCP has suggested that there are significant differences in the degree of influence the structures within each of the streams have on the surrounding stream system. Such differences may be due to differences observed in the characteristics of floodplain vegetation (e.g.- size and complexity), which comprises the woody debris structures within the streams. CWD within the youngest stream studied (Wolf Point Creek) was dominated by small, transient alder boles, which occupy a smaller percentage of the stream channel than structures found in older streams. Decay of these structures was low, due to the ability of alder boles to re-root within the streambed, resulting in the creation of some stable structures within the middle of the channel. CWD structures within older study streams, such as Rush Point Creek and Berg Bay South, were dominated by large, complex accumulations, which typically covered a much larger percentage of the stream channel, creating increased flow resistance around the structure.

Debris must be of a sufficient size (generally at a length greater than the stream width (Montgomery et al., 2003; Piégay and Gurnell, 1997)) and complexity in order to override geomorphic processes acting at the reach scale, and hence influence the geomorphic composition of a stream (Inoue and Nakano, 1998). CWD within the older streams, such as North Fingers South Stream, Berg Bay South and Rush Point Creek, are of sufficient size and complexity to elicit morphological and hydraulic changes as detailed above. Complex debris jams have been shown to be more hydraulically efficient in causing morphological change than simpler, single member structures (Richmond and Fausch, 1995). Due to the small size and complexity of

CWD within the youngest stream surveyed (Wolf Point Creek), the structures only weakly influence the geomorphology and hydraulic structure of these streams.

Changes to CWD characteristics are the result of changes to the adjacent riparian vegetation. The growth and gradual establishment of large, complex vegetation (e.g.- cottonwoods and Sitka spruce) along the stream banks and their eventual introduction into the stream environment as a result of channel migration and erosion appears to drive the changes in CWD characteristics observed across the stream chronosequence and ultimately, those changes in hydraulic and geomorphic diversity which were observed.

Assessment of the changes in stream morphology and hydraulics surrounding CWD within each of the streams has shown that average velocity and shear stress is lower upstream of debris within older streams, with a corresponding increase in stream depth adjacent to CWD accumulations. These changes are most pronounced in the oldest streams (North Fingers South Stream, Berg Bay South and Rush Point Creek), which is likely to be due to wood forced patterns of scour and deposition surrounding the structure, creating a high diversity of geomorphic units at the reach scale (Brooks et al., 2004; Wondzell and Bisson, 2003).

CWD structures have been shown to create a diversity of hydraulic gradients which increase microhabitat complexity (Forward, 1984, as cited in Hicks et al., (1991)), and geomorphic variability (Faustini and Jones, 2003), both of which contribute to the creation of hydraulic diversity at the meso- and micro- scale. CWD has also been shown to produce a localised influence on flow complexity, as a result of changes in helicity and velocity gradients surrounding the debris, resulting in an increase in hydraulic variation at the microscale (Shen and Diplas, 2008). This has been observed in the scatter plots created from the ADCP transects which illustrate how changes in stream hydromorphology resulting from the presence of CWD differ between Wolf Point Creek and Berg Bay South. CWD within the youngest stream, Wolf Point Creek, did not appear to alter instream geomorphology or hydraulics, whilst stream depth increased substantially and water velocity decreased adjacent to and downstream of CWD within Berg Bay South.

Previous studies have reported a decline in fast water habitats, such as rapids and riffles, and an increase in pool habitat following the addition of complex CWD (Cederholm et al., 1997; Robison and Beschta, 1990), thus contributing to the overall diversity and complexity of stream habitat (Floyd et al., 2009). Comparison of differences in geomorphic composition across the stream chronosequence (as outlined in Klaar et al., (2009) / Chapter 2) has shown that younger streams were dominated by large, fast flowing CGUs, with little hydraulic variation. Older streams, however, tended to contain a greater diversity of CGUs, dominated by slower flowing, deeper units such as runs and glides which provided an increase in hydraulic variation at the mesoscale. The addition of complex CWD structures into the study streams, appear to result in the creation of smaller channel geomorphic units due to forced scour and deposition surrounding the structures. Such alteration leads to an increase in geomorphic and hydraulic diversity as observed across the chronosequence.

Changes in meso and microscale hydraulics and geomorphology resulting from the recruitment of CWD benefits instream biota by providing a number of habitats which may otherwise be limited or absent within the streams. Increased frequencies of pool habitat has been found to provide a greater volume of suitable habitat, particularly at periods of low flow, and typically contain a more complex trophic structure, supporting a larger number of species than that found within shallow pools (Dolloff and Warren, 2003). In addition to the geomorphic and hydraulic changes induced by CWD, it is also important to note the secondary benefits of increased overhead cover, visual isolation and increased substrate surface area which are also introduced following the introduction of CWD into the stream environment, and are also of importance to the aquatic community (Crook and Robertson, 1999; Dolinsek et al., 2007; Entrekin et al., 2009).

3.4.2 Coarse woody debris, sediment transport and habitat complexity

Zones of reduced shear stress resulting from the presence of CWD allow the deposition of sediment (Wallerstein, 2003) which may then be reworked, contributing to habitat heterogeneity (Yarnell et al., 2006). CWD has been shown to influence the amount of gravel habitat within low gradient, alluvial channels, such as those found within southeast Alaska, by creating sediment traps that increase the frequency of gravel storage sites (Martin, 2001). Analysis of sediment characteristics across the stream chronosequence suggests that older streams such as Berg Bay South and Rush Point Creek typically contain finer sediment, such as gravel, whilst younger streams (i.e.- Wolf Point Creek, Ice Valley Stream and North Fingers South Stream) were dominated by larger, coarser sediment such as cobbles.

Retention of fine sediment within older streams is most likely due to the increase in hydraulic roughness within these streams as a result of large, complex woody debris. This result is consistent with other studies, (e.g.- Buffington and Montgomery, (1999a) and Montgomery et al., (2003)) which have found that streams with greater hydraulic roughness as a result of the occurrence of CWD have reduced bed shear stress and hence a decreased competence for sediment transport which results in the occurrence of finer reach averaged surface grain sizes than would otherwise be expected. All streams displayed evidence of textural fining (with ratios of observed vs expected D_{50} sizes <1), however, the oldest demonstrated a higher degree of textural fining than younger streams (Table 3.2).

These observed differences in textural fining may be due to differences in sediment supply, as laboratory experiments have shown that bed surface grain size varies inversely with sediment supply rate (Buffington and Montgomery, 1999b), or the presence of a sediment rich tributary upstream of the study reach (Knighton, 1980) which may account for the differences observed between streams. Although the quantification of sediment supply was not explicitly assessed within this study, younger streams are likely to have higher sediment inputs than older streams due to inherent channel instability and sparser vegetation on the floodplain within these streams which continue to alter course during high flow events (Sidle and Milner, 1989). Higher sediment supply relative to sediment trapping potential within the youngest streams may account for the lower degree of textural fining (observed: expected D_{50}) observed, however, it does not account for the occurrence of finer sediment within the oldest streams despite similar bankfull shear stress values (Table 3.2).

The retention of finer sediment within the streams (in particular, North Fingers South Stream, Berg Bay South Stream and Rush Point Creek) is most likely the result of increased sediment storage resulting from the occurrence of complex debris structures. Complex debris jams have been found to be less porous than simpler structures (Manners and Doyle, 2008) thus affecting the degree of sediment storage CWD structures may exert upon the stream. This increase in sediment storage may also be the cause of increased habitat heterogeneity (measured in terms of geomorphic and hydraulic diversity) observed within older streams, as geomorphic diversity has been found to be highest when sediment supply relative to transport capacity (e.g.- sediment storage as a result of CWD) is moderate and the flow regime is varied (Yarnell et al., 2006). Under such conditions, it has been shown that differential scour and deposition under varying flow regimes result in a high degree of geomorphic complexity characterised by varied sorted surface textures (Yarnell et al., 2006), and thus increased habitat complexity for instream biota.

The combination of a moderate sediment supply and the presence of mature riparian vegetation and complex CWD may account for the high geomorphic diversity found within NFS. Such local conditions may be working in tangent to maximise habitat availability, as hypothesised by Yarnell et al. (2006). As the stream age increases, however, sediment supply begins to decline and channel stability increases as riparian vegetation continues to develop. Increased CWD input continues to 'force' habitat heterogeneity as flow is diverted around the structures, increasing scour and deposition in a manner similar to intermediate sediment supply. Increased sediment storage within complex CWD structures within the older streams however, may prevent the mobilisation of sediment, and hence prevent maximum geomorphic heterogeneity, resulting in a decline in habitat diversity within these streams as observed within Berg Bay South and Rush Point Creek. The introduction of complex woody debris habitat within the older streams may offset this decline in terms of the provision of fish habitat as cover and hydraulic complexity provided by the presence of CWD may be more important to resident salmonids than geomorphic diversity associated with intermediate sediment supplies. Chapter 4 investigates this possibility in further detail.

A theoretical relationship between physical habitat heterogeneity, stream development and relative sediment supply within Glacier Bay is illustrated in Figure 3.11. This relationship expands that of Yarnell et al. (2006), to include those processes, such as channel stability, CWD loading and recruitment, which influence sediment supply.

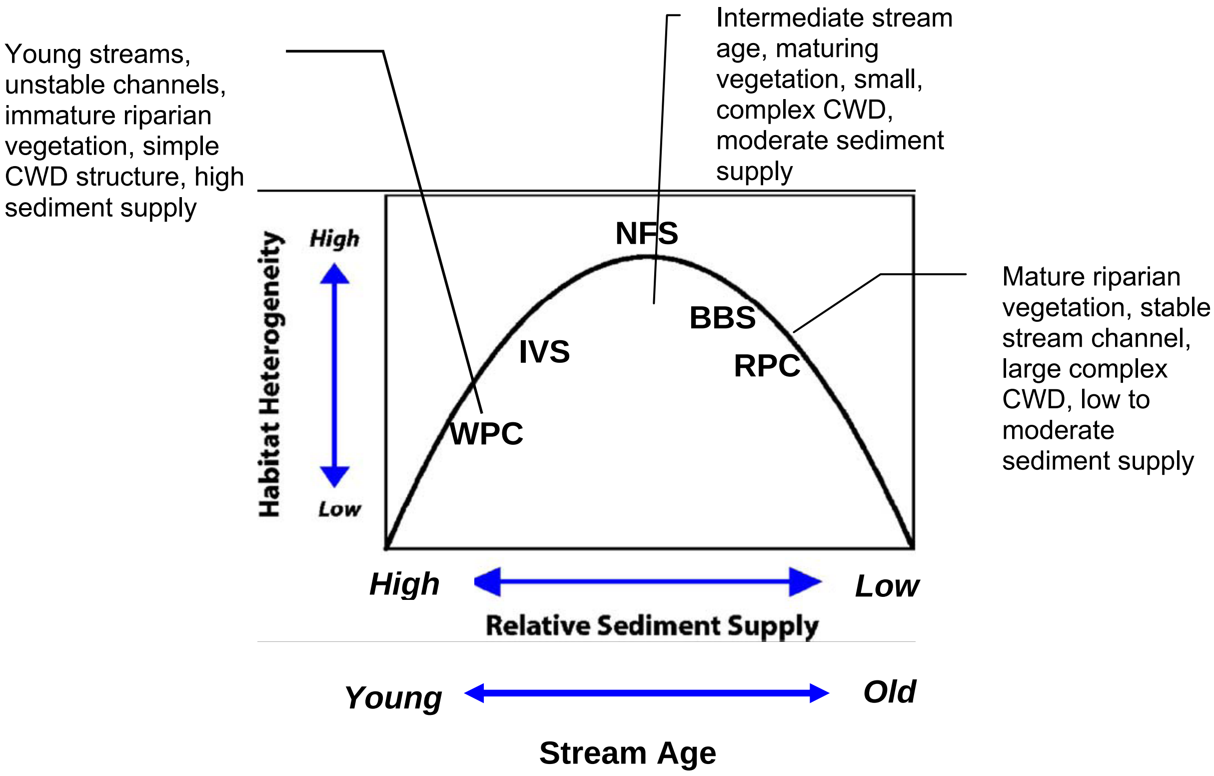


Figure 3.11: Theoretical relationship between physical habitat heterogeneity, stream development and relative sediment supply. The probable location of the five study streams within the schematic is also denoted. Modified from Yarnell et al., 2006.

3.5 Conclusions

Within low gradient gravel bed rivers such as those found within GBNP, CWD is often the only pool forming element within the streams (Dolloff and Warren, 2003). The introduction of woody debris and its subsequent development in size and complexity over time represent a significant habitat-forming element. Changes in CWD characteristics as a result of adjacent terrestrial landscape development result in significant changes in the geomorphic and hydraulic complexity of the developing streams. These changes are of significant benefit to instream biota, not only due to the creation of favourable instream habitat, but also in the retention of detritus and salmon carcasses which contribute to increased nutrient cycling and subsequent community production and biomass (Naiman et al., 2002).

Further research in the next two chapters seek to examine the linkages between terrestrial and aquatic habitat development (Chapter 5), including the role of CWD in the continued colonisation of these habitats by Pacific salmon (Chapter 4). Such information will contribute to our knowledge of how CWD jams alter the complexity of instream habitats, which in turn, will assist in wood- based restoration techniques.

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4

The response of juvenile Pacific salmon to changes in geomorphic and hydraulic complexity caused by the recruitment of coarse woody debris

Populations of juvenile coho salmon and Dolly Varden were monitored within five streams representing 200 years of stream development within Glacier Bay National Park, Alaska. Differences in coarse woody debris characteristics resulting from variations in adjacent terrestrial succession were found to result in a gradual increase in hydraulic, geomorphic and structural complexity at the reach and micro scale. The frequency of occurrence of preferred depth and velocity habitats were found to alter over time. Optimal water velocity increased with time, whilst optimal depth peaked at streams of intermediate age. Young-of-the-year salmonids and 1+ coho salmon were found to show a preference for the combined occurrence of suitable depth, velocity and overhead cover provided by complex woody debris within older streams. Increasing interactions between riverine and terrestrial ecosystems during landscape development were found to create beneficial conditions which resident salmonids could utilise.

4.1 Introduction

The abundance, distribution and utilisation of habitat by salmonid fish remains a widely researched area, as knowledge of habitat selection and the processes which drive the creation of preferred habitat underpin the science of habitat restoration (Roni et al., 2002). Research has shown that the availability of instream habitat within rivers is determined by the interaction of channel geomorphology and hydrology (Maddock, 1999). Changes in the diversity and complexity of geomorphic and hydraulic features therefore influence habitat and species diversity (Bartley and Rutherford, 2005; Maddock, 1999; Sullivan et al., 2006) and resultant stream biodiversity.

Habitat manipulation, through the addition of coarse woody debris (CWD) into river systems is often used as a restoration technique to enhance the availability and quality of instream habitat for biota (Brooks et al., 2001; Brooks et al., 2004; Floyd et al., 2009; Gippel et al., 1996; Manners and Doyle, 2008). Scour and deposition around debris structures creates geomorphic and hydraulic complexity, which may be utilised by fish. For example, the addition of CWD has been shown to result in an increase in salmonid fish abundance due to the formation of favourable conditions at a number of habitat scales. The amount of pool habitat at the reach scale has been found to be positively correlated with CWD abundance (Cederholm et al., 1997; Lisle, 1986; Richmond and Fausch, 1995), resulting in increased salmonid abundance (Cederholm et al., 1997), whilst studies at the channel unit scale have also found that juvenile salmonids prefer habitat units associated with CWD (Beechie et al., 2005; Horan et al., 2000). Changes to the microhabitat surrounding CWD structures, through the creation of hydraulic (Crook and Robertson, 1999; Hughes et al., 2007) and structural (McMahon and Hartman, 1989; Sweka and Hartman, 2006) cover which shelter fish from predators and high flow events, are particularly beneficial to juvenile salmonids (Crook and Robertson, 1999; Inoue and Nakano, 1998), while the retention and accumulation of gravel within the channel as a result of CWD accumulations also benefit adult salmonids by increasing the number of suitable spawning areas available within the streams (Floyd et al., 2009).

Debris dams have also been found to play an important role in the trophic structuring of the riverine environment through the retention of organic matter (Bilby and Likens, 1980) which may be utilised at a number of levels including macroinvertebrates (Smock et al., 1989). Debris dams are also important in the retention of salmon carcasses in late summer following the migration of adult spawners (Milner et al., 2007). The subsequent release of marine derived nutrients (MDN) into the stream environment after spawning has been shown to play an important role in the productivity of riverine communities (Naiman et al., 2002), for example juvenile salmon production and biomass and the abundance of some macroinvertebrates (Lessard and Merritt, 2006) within oligotrophic streams (Bilby et al., 1998; Williams et al., 2009) have been observed in streams with MDN input. This has led to the practice of addition of salmon carcasses to nutrient poor streams to increase stream productivity (Bilby et al., 1998; Williams et al., 2009; Wipfli et al., 1998).

Earlier chapters have focused on the development of hydraulic and geomorphic complexity within streams spanning 200 years of stream development within Glacier Bay National Park (GBNP). Such development was found to be the result of differences in the characteristics of riparian vegetation, which is subsequently recruited into the stream as a result of channel migration. Terrestrial succession follows a known series of stages, starting with a pioneer community of blue-green algae, lichens and liverworts, *Dryas drummondii* and scattered willows for the first 15-25 years following glacial recession. Woody species such as alder begin to dominate approximately 50 years following deglaciation, followed by cottonwood and scattered Sitka spruce which form a mixed forest approximately 100 years following glacial retreat, leading to a climax community of western hemlock forest, and later *Sphagnum* dominated muskeg over a period of thousands of years (Chapin et al., 1994; Milner et al., 2000). This process of terrestrial succession results in differences in CWD characteristics within the streams of different ages, as CWD is recruited directly from the adjacent floodplain when streams migrate across them during flood events, and hence alters with stream age.

The aim of this study was to assess how juvenile salmonids respond to the changes in geomorphic and hydraulic complexity observed across the stream chronosequence, and determine whether or not these changes assist in the continued success of Pacific salmon within these newly created streams.

Knowledge of the process of natural CWD recruitment and the formation of complex jams within undisturbed streams, twinned with an assessment of the response of juvenile salmonids to the hydromorphic changes resulting from the introduction of CWD underpin the successful use of wood in habitat restoration (Brooks et al., 2001; Manners and Doyle, 2008). An understanding of the natural behaviour of ecosystems to changes in CWD characteristics will provide river managers with information on the inherent variation and response of ecosystems, thus contributing to long- term success of wood based restoration projects.

4.2 Methods

4.2.1 Study area

The process of salmonid colonisation following deglaciation within GBNP has been previously studied. Milner and Bailey (1989) reported that the primary factors governing the successful establishment of salmonids within GBNP streams were water temperature, sediment loading and stream discharge. The influence of these factors in salmonid colonisation were found to slowly decline over time as the streams undergo a transition from highly turbid, glacier fed meltwater streams to stable, clear water systems which are able to support diverse macroinvertebrate and salmonid populations (Milner, 1987). After this time, streams may be subject to unstable discharges, channel instability and marked fluctuations in flow following spring snowmelt and autumn storms. Such streams are often characterised by fast flowing channel geomorphic units (CGUs) such as rapids and riffles and low fish populations of primary colonisers such as pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon as the fry of these species migrate directly to the sea, thereby eliminating the need for suitable rearing habitat (Quinn, 2005). Dolly Varden (*Salvelinus malma*), coho (*O. kisutch*) and sockeye (*O. nerka*) salmon are later colonisers to clear water streams within Glacier Bay, appearing approximately 20-40 years following deglaciation. Resident Dolly Varden and juvenile coho populations were monitored within this study as they are the only species which reside in the streams year-round, and thus provide an indication of the suitability of stream habitat in both summer and winter.

4.2.2 Assessment of geomorphic and hydraulic diversity

Fieldwork in the summer of 2007 focused on the assessment of the quantity and hydraulic variation of CGUs within the five study streams. This research, detailed in Chapter 2, provided information on the process of hydraulic and geomorphic development of streams within GBNP following deglaciation. Initial identification and mapping of CGUs over a minimum distance of 1.3 km allowed representative reaches, a minimum of 300m in length, to be identified and assessed in greater detail. CGUs were identified using a modified version of the Hawkins et al., (1993) classification which identified units based on morphology and flow type, and mapped using a mapping grade GPS unit (Trimble GeoXT; accurate to the sub metre level).

The hydraulic characteristics of each CGU were assessed by measurement of a total of thirty randomly located total water depth and velocity measurements (at 0.6 depth, averaged over 30 seconds, using a Model 201D flow meter, Marsh-McBirnley Inc., Frederick, MD, U.S.A.) within each CGU to provide an indication of the hydraulic characteristics of that CGU. These data were then categorised into one of four categories (0 - 4), according to their habitat suitability for fish; with 0 indicating an unsuitable or actively avoided velocity or depth range, and 4 indicating optimum depth or velocity range for Dolly Varden and coho salmon in the summer months (Table 4.1). These values were based on published depth and velocity preferences of 0+ fish, and 1+ coho and Dolly Varden within the Pacific Northwest (Beecher et al., 2002; Bugert et al., 1991; WDFW, 2002). Young-of-the-year (0+) from both species were amalgamated as the requirements of 0+ fish at this time of development are remarkably similar, occupying stream margins associated with shallow, slow flowing habitat, thus negating the need to calculate separate depth and velocity preferences for 0+ coho and Dolly Varden. By separately categorising the thirty depth and velocity measurements by salmonid life stage, it is possible to ascertain the overall suitability of each stream for resident juvenile salmonids. The percentage occurrence of each of the habitat preference categories within the streams was calculated to provide an indication of the overall suitability of the study reach for the fish lifestages under investigation.

Table 4.1: Values used to calculate depth and velocity preferences of 0+ and 1+ coho salmon and Dolly Varden. Values were obtained from published habitat preference curves (Beecher et al., 2002; Bugert et al., 1991; WDFW, 2002) and represent a sliding scale of habitat suitability/ preferences. 0 = v poor habitat/ habitat avoided; 4 = ideal habitat condition

		0	**1**	**2**	**3**	**4**
Water depth (m)	0+ fish	< 0.30 >1.23	0.30- 0.33 1.22	0.34- 0.37 1.11- 1.21	0.38- 0.51 0.82- 1.10	0.61- 0.81
	1+ coho	≤ 0.06	0.07- 0.27	0.28- 0.37 ≥ 1.22	0.38- 0.76 0.99- 1.22	0.77- 0.98
	1+ Dolly Varden	< 0.26	0.26- 0.27	0.28- 0.29	0.30- 0.31	≥ 0.31
Water velocity (m / s)	0+ fish	≤ 0.045 ≥ 0.306	0.046- 0.060 0.245- 0.305	0.070- 0.075 0.199- 0.244	0.076- 0.121 0.184- 0.198	0.122- 0.183
	1+ coho	≥ 0.184	0.153- 0.183	0.138- 0.152	0.137- 0.151 < 0.005	0.005- 0.061
	1+ Dolly Varden	≥ 0.970	≤ 0.106 0.915- 0.960	0.107- 0.151 0.885- 0.914	0.152- 0.395 0.672- 0.884	0.396-0.671

Pebble counts were conducted in representative reaches to assess substrate composition. Substrate particles were randomly selected for measurement using a modified version of the Wolman walk (Wolman, 1954), as described by Bevenger and King (1995). A minimum of 30 substrate particles were measured along the intermediate, or ‘b’ axis within each CGU and subsequently grouped by stream to provide a reach wide percentage contribution of each substrate class. These data were then arcsine transformed for inclusion in statistical analysis.

An Acoustic Doppler Current Profiler (ADCP; RDI StreamPro, RDI Instruments, San Diego, CA, U.S.A.) was used to assess the influence of coarse woody debris structures (CWD) in altering the geomorphic and hydraulic complexity within the study streams. A number of transects using the ADCP upstream, adjacent to and downstream of debris structures provided information on the three-dimensional flow structure at these positions, as detailed in Chapter 3.

4.2.3 Fish sampling and associated data analysis

Sampling of juvenile fish populations was undertaken between July and September 2008, when small boat travel and access to streams is feasible, and water temperatures are conducive to minnow trapping. Juvenile fish were collected using minnow traps baited with salmon eggs soaked in Betadyne solution to limit the potential spread of infectious diseases. Traps were placed within distinct CGUs previously identified and mapped as detailed above. Effort was made to distribute the traps throughout the CGU, but was predominantly limited to those areas likely to support juvenile salmonids, such as undercut banks, river margins (excluding undercut banks), and areas associated with CWD. Those traps placed adjacent to or within CWD structures were noted for subsequent analysis to compare catch rates with and without CWD association. Traps fished for 1.5 hours (±10 minutes) within each stream. Captured fish were anaesthetised using MS222 and subsequently weighed (to a maximum of 30 individuals per species per river to the nearest 0.1g) and measured using fork length.

Length frequency histograms of fish length were constructed to ascertain the probable age structure of juvenile coho and Dolly Varden populations within each of the streams. Using this information, age breaks were identified within the population, allowing captured fish to be classified into 0+ or 1+ (and >1+ where appropriate) for subsequent analysis.

Catch per unit effort (CPUE) was calculated using the following equation:

$$CPUE = \frac{\text{total number of fish captured}}{\text{number of traps deployed}}$$

Mean CPUE for each river was calculated for each species and lifestage (0+ / 1+; coho salmon/ Dolly Varden) and analysed using second order polynomial regression to ascertain the relationship between fish condition and stream age. Mann Whitney U tests of CPUE of traps with and without CWD association were calculated at each of the streams to ascertain whether there are significant differences in fish densities between minnow traps at these locations.

The condition factor of those fish that were weighed and measured was calculated using Fulton's Condition Factor, based on Hile, (1936), using the equation below;

$$\text{Condition Factor (K)} = 10^7 (W / L^n)$$

Where W = wet weight (g), L = fork length (mm), n = the growth exponent. The growth exponent is typically a value between 2.5 and 3.5 which represents the type of growth the fish undergoes, with n= 3 when growth is isometric (i.e.- even), n<3 where growth is negatively allometric, and n> 3 when growth is positively allometric. A value of 3 was chosen in this instance as it has been shown in practice that n is normally very close to 3 (Hart and Reynolds, 2002), and as the population studied in this instance is of a very small age range (typically 1+ to 3+ fish), it was considered an appropriate choice.

This relationship provides an index to quantifying the state of well being of a fish (Samat et al., 2008). Fish with a high condition factor are considered heavy for their length, and hence in better condition than fish with a lower condition factor. Condition factor may also reflect the welfare of a fish within its habitat (Ribeiro et al., 2004; Robinson et al., 2008). Due to the small number of sampled fish, it was not possible to compare the condition factor of fish associated with and without CWD. The mean condition factor of 1+ coho salmon and Dolly Varden were compared across the stream chronosequence using linear regression to ascertain the strength of the relationship. The condition factor of 0+ fish was not calculated due to the small sample size of weighed 0+ fish.

Tiny Tag (Gemini Data Loggers (UK) Ltd, Chichester, U.K.) temperature monitors were installed within each of the streams to monitor daily temperature fluctuations for the course of an entire year. These data were then averaged over a month to provide an indication of the differences in annual temperature, which may affect over wintering survival and summer growth of juvenile salmonids and eggs.

Ordination and regression analyses were conducted to assess the relationships between environmental variables and fish catches across the chronosequence. A correlation matrix (Spearman Rank; SPSS v 17.0, SPSS, Chicago, IL, U.S.A.) was initially used to identify any cross-correlation between the initial 17 environmental variables (Table 4.2) measured within the streams. These variables were subsequently reduced to seven variables which included the CWD loading (number of structures/ 100m of mapped stream), number of CGUs per 100m, Shannon's Diversity Index (SHDI), stream length, Pfankuch stability index, percent cobble and percent pool. The correlation between these variables and 0+ and 1+ Dolly Varden and coho were then assessed using principal component analysis (PCA; Pisces Community Analysis Package v 3.0, Pisces Conservation Ltd, Lymington, U.K.). Previous analysis has shown that the response of environmental variables across the stream chronosequence may often be best described in a non-linear manner, and hence the strength and shape of the relationships between environmental variables and fish catch were identified using curve estimate models (SPSS v. 17.0) which identified the best fit model (linear or quadratic) applicable to all three categories. The large number of quadratic relationships between fish catches and environmental variables prevented further linear multiple regression from being used.

Table 4.2: Environmental variables initially calculated for use in ordination and regression analysis. A Spearman Rank test was used to identify any cross correlation between variables. Those variables which were retained for subsequent analysis are highlighted in bold

Variable	Description
CWD loading	**Number of structures/ 100m of mapped stream**
CGU/ 100m	**Number of CGUs/ 100 m of mapped stream**
SHDI	**Shannon's Diversity Index**
SIDI	Simpson's Diversity Index
SHEI	Shannon's Evenness Index
SIEI	Simpson's Evenness Index
Gradient	Study reach gradient (%)
Stream length	**Total stream length (km)**
Drainage area	Drainage area (km^2)- (Hill et al., 2009)
Sand	% sand within study reach (arcsin transformed)
Gravel	% gravel within study reach (arcsin transformed)
Pebble	% pebble within study reach (arcsin transformed)
Cobble	**% cobble within study reach (arcsin transformed)**
Pool	**% pools within study reach (arcsin transformed)**
Glide	% glides within study reach (arcsin transformed)
Pfankuch	**Pfankuch stability index (Milner et al., 2000)**
Discharge	Average discharge (m^3/s)

4.3 Results

4.3.1 Depth and velocity preferences

Table 4.3 outlines the number of fish from each life stage which were captured within each of the study streams. Assessment of depth and velocity categories within the study streams reveals a change in the frequency of occurrence of optimal habitat for fish over time. Favourable velocities (measured by the frequency of velocity categories classed as 3 and 4 values) tended to increase over time, peaking in the oldest streams (Berg Bay South and Rush Point Creek; Figure 4.1), whilst optimal depth for all life stages was found to occur in streams of intermediate age (i.e.- North Fingers South Stream, 158 years).

Of particular note is the dominance of unsuitable flow velocities across the stream chronosequence. Optimal flow velocities for 1+ coho salmon were found within the oldest stream, Rush Point Creek, which was composed of just over 20% optimal flow velocities (3 and 4 categories), whilst the remaining four streams appear to be relatively unsuitable for 1+ coho (Figure 4.1e). 1+ Dolly Varden, on the other hand, benefited from an increase in their preferred velocity habitats as stream age increased, whilst optimal occurrence of depth habitat was present within North Fingers South Stream, and decreased as stream age increased in the two oldest streams. The occurrence of suitable habitat for 0+ fish remained relatively low, which may be a reflection of the low sampling effort of shallow channel margins, due to the inability of minnow traps to operate in these areas in which 0+ fish are likely to prefer.

Table 4.3: Summary of the total number and life stage of fish caught using minnow traps, summer 2008

	0+	1+ coho	1+ Dolly Varden
Wolf Point Creek	67	66	23
Ice Valley Stream	22	3	3
North Fingers South	0	6	37
Berg Bay South	68	27	62
Rush Point Creek	70	88	98

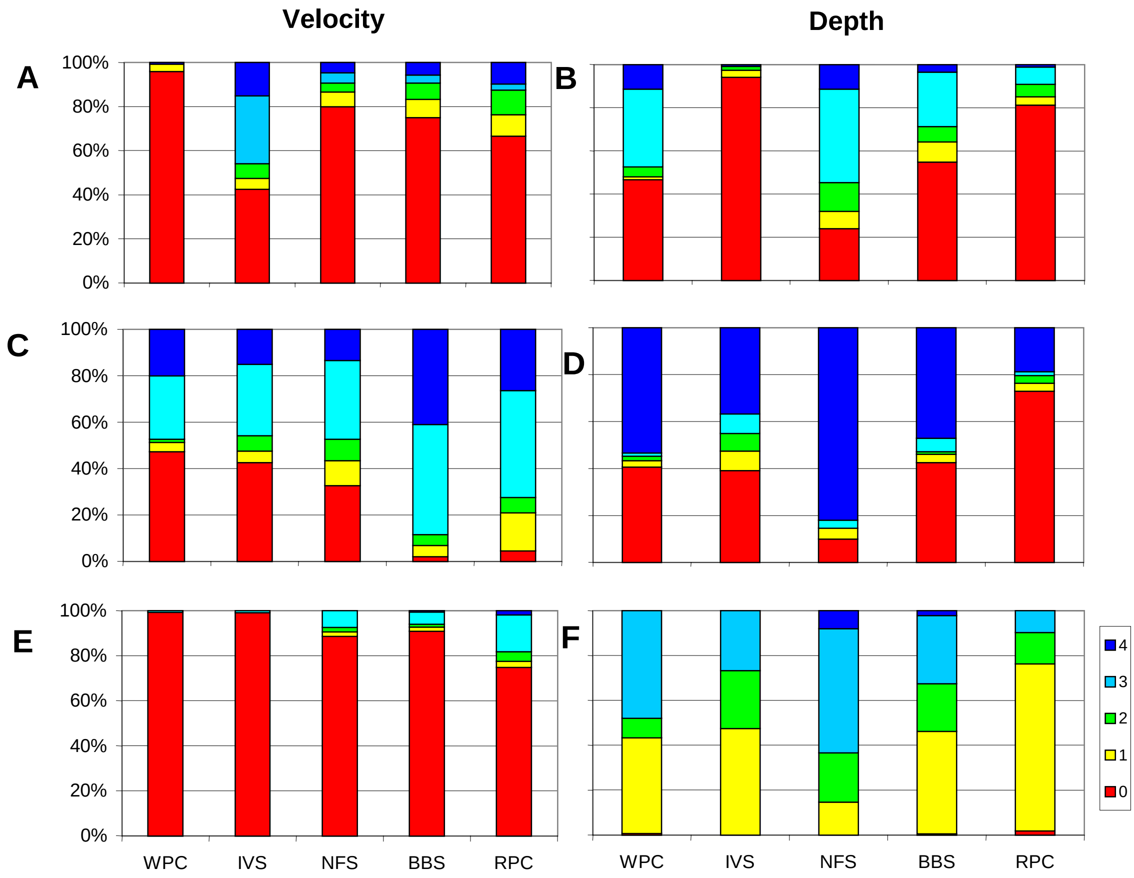

Figure 4.1: Occurrence of velocity and depth preferences of coho and Dolly Varden life stages within the five study streams. Preferences were calculated using published values and range from 0 (no preference/ active avoidance to 4 (optimal velocity/ depth). A) 0+ fish velocity preference B) 0+ fish depth preference; C) 1+ Dolly Varden velocity preference; D) 1+ Dolly Varden depth preference; E) 1+ coho salmon velocity preference; F) 1+ coho salmon depth preference.

4.3.2 Relationship between fish catch and environmental variables

Determination of fish densities across the stream chronosequence, using catch per unit effort analysis shows that Wolf Point Creek supported the highest fish densities. CPUE tended to decrease over time, reaching the lowest levels at North Fingers South, before increasing again in the two older streams (Figure 4.2). Examination of the fish catches using length frequency histograms (Figure 4.3) reveals the presence of a number of Dolly Varden age groups within the streams, ranging in length from 42-143mm. The exact age of these fish was not ascertained, but is likely to include fish ≥

4+. Few 0+ coho were caught within the sampled reaches at Berg Bay South and North Fingers South; these reaches appeared to have been more suitable for 1+ coho salmon. It is interesting to note that a few larger, possibly 2+ coho salmon were captured within Wolf Point Creek, Ice Valley Stream and Rush Point Creek. These fish may have remained in the streams for a further year rather than migrating to sea as smolts.

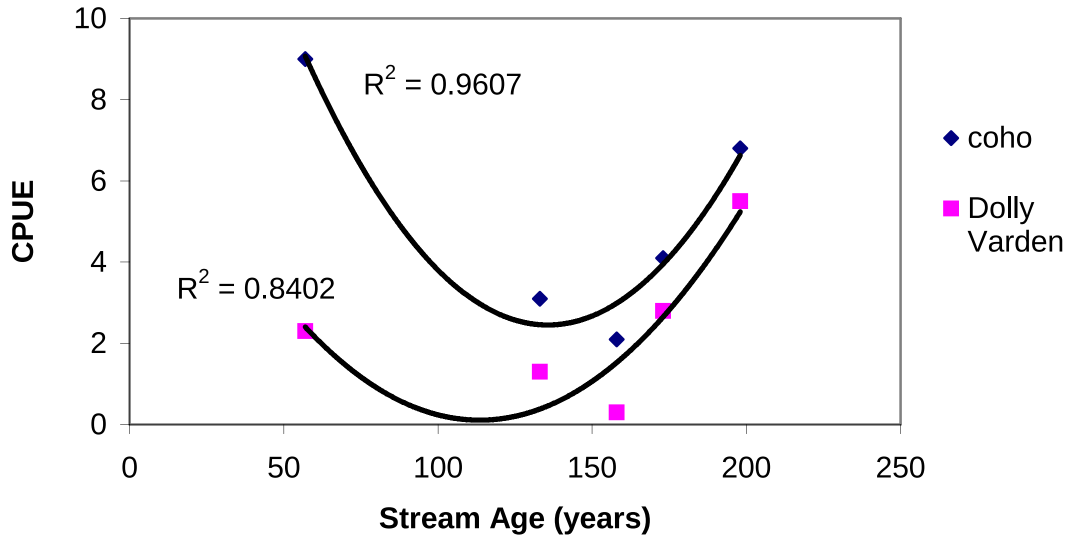

Figure 4.2: Changes in catch per unit effort (CPUE) across the stream chronosequence.

Investigation of average monthly temperature fluctuations within the streams (Table 4.4) shows that winter and summer monthly temperatures vary significantly within all of the streams. Winter temperatures are generally just above freezing, whilst summer temperatures range from 2.5 to 13.8°C. WPC appears to be the warmest stream in both the summer and winter months, whilst NFS is the coldest stream over the course of the year. Water temperatures within BBS appear to fall dramatically in the winter months, but rises quickly in the summer.

Table 4.4: Mean monthly temperature (°C) of the streams, summer 2006- 2007. * IVS water temperature; summer 2007- 2008.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
WPC	0.9	0.8	0.5	0.7	3.5	8.0	11.3	13.8	10.2	6.5	3.7	1.7
IVS*	0.3	0.4	1.1	1.8	2.4	4.0	6.7	11.1	7.7	4.7	2.6	0.4
NFS	0.3	0.1	1.3	2.3	3.6	3.6	6.2	8.7	7.6	5.4	0.1	0.6
BBS	-0.1	-0.2	-0.3	-0.5	1.4	2.5	5.1	9.8	7.9	5.3	0.15	-0.1
RPC	1.0	0.8	1.4	2.0	2.5	4.3	6.4	8.8	8.1	5.2	3.2	1.4

Ordination of the environmental data across the stream chronosequence with fish catch data using PCA produced a biplot (Figure 4.4) in which Axis 1 explained 57.2% of the fish catch / environmental variable correlation, whilst Axis 2 explained 31.0% of the data correlation. Axis 1 separates Wolf Point Creek from the other streams on the basis of the number of CGUs/ 100m, percent pools and habitat diversity (measured using SHDI). Axis 2 further separated the streams using the CWD loading and percent cobble variables. The ordination suggests that Rush Point Creek is closely associated with 0+ and 1+ coho and Dolly Varden catches, whilst Berg Bay South and Wolf Point Creek are both loosely associated with fish catch. Wolf Point Creek appears to be dissimilar from the other streams, and not particularly governed by any environmental variable, although more closely associated with fish catches than North Fingers South Stream and Ice Valley. North Fingers South appears to be very closely associated with stream length, although it is not clear how this variable affects this stream, as stream discharge, gradient and drainage area, all possible factors associated with stream length, were previously discounted from the analysis due to a lack of correlation with the streams. It is possible that some other factor associated with stream length may be driving this correlation.

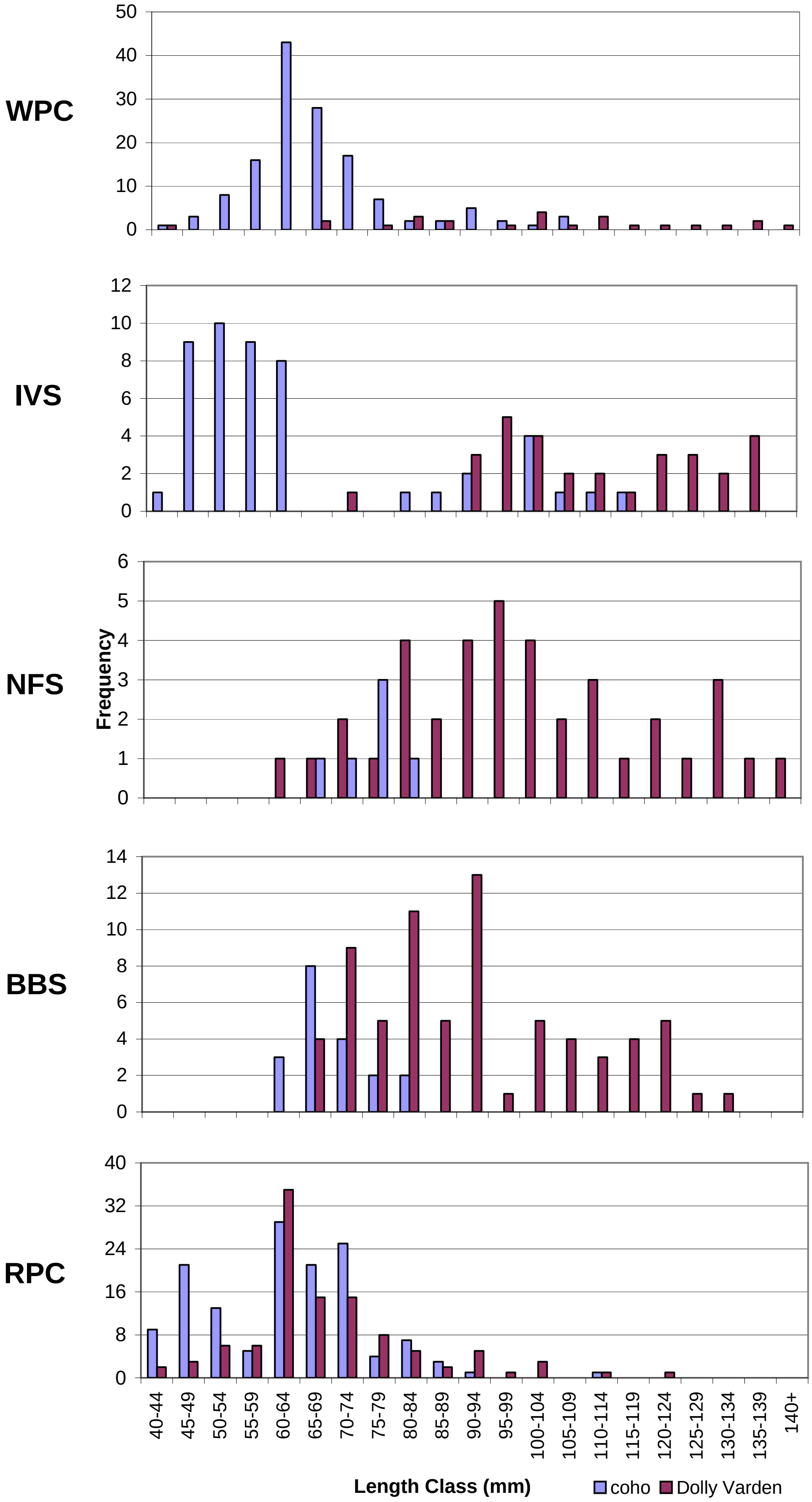

Figure 4.3: Length frequency histograms of fish catch, Summer 2008. Note the differences in the y- axis scale.

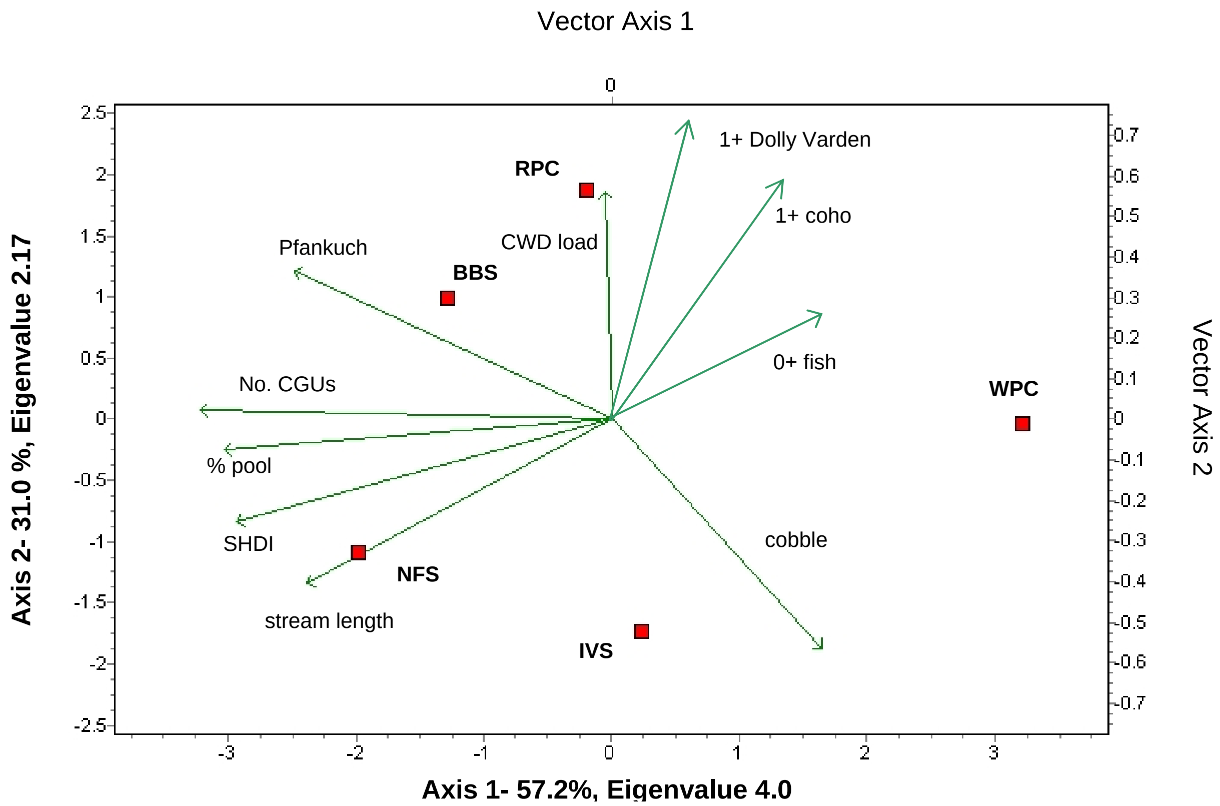

Figure 4.4: Ordination biplot of the PCA on fish catches and environmental variables within five Glacier Bay streams.

Closer examination of the relationship between environmental variables and fish catches (Table 4.5) reveals significant relationships between CPUE of 0+ fish and 1+ coho with the Shannon's Diversity Index, stream length and percent pool, all of which (with the exception of percent pool) display a quadratic relationship with fish catch. CPUE of 0+ fish was also significantly related to the number of CGUs per 100m of mapped stream. It is interesting to note that the majority of these relationships are negatively correlated to one another, and there was no relationship observed between woody debris loading at the reach scale with fish densities. 1+ Dolly Varden did not show a relationship with any of the measured environmental variables.

Table 4.5: Regression coefficients describing the relationship between environmental variables and fish catches within the study streams. The model column refers to the regression curve model used (linear vs quadratic), which provided the best fit across the three lifestages. *regression significant at the 0.05 level; **regression significant at the 0.01 level.

	Fry	Coho	Dolly Varden	Model
CWD loading	0.10	0.02	0.51	Quadratic
No CGU/ 100m	0.84*	0.70	0.01	Linear
SHDI	0.93*	0.99**	0.27	Quadratic
Stream length	0.96*	0.99**	0.80	Quadratic
Pfankuch	0.34	0.35	0.34	Quadratic
% cobble	0.17	0.07	0.51	Quadratic
% pool	0.96**	0.92**	0.11	Linear

4.3.3 Fish catch and occurrence of CWD

Although the amount of woody debris loading at the reach level was not found to be related to fish catch, statistical analysis of the differences in CPUE in traps associated with CWD vs those without CWD association using Mann Whitney U tests reveals 1+ coho catch was significantly higher at traps associated with CWD within the older streams, namely BBS and RPC (Table 4.6). CPUE of 0+ fish was also found to be significantly higher at minnow traps associated with CWD within WPC and BBS and RPC. 1+ Dolly Varden did not shown any preference for traps associated with or without CWD.

Table 4.6: Mean catch per unit effort of coho and Dolly Varden within traps associated with and without coarse woody debris. * significant at $p < 0.05$; ** significant at $p < 0.01$

Stream	Species/ Life Stage	CPUE (±1 SD)		P Value
		+CWD	-CWD	
	0+	1.67 (1.241)	0.24 (0.308)	0.03*
WPC	1+ coho	1.58 (1.829)	0.20 (0.199)	0.19
	1+ Dolly Varden	0.42 (0.292)	0.22 (0.437)	0.41
	0+	0.07 (0.074)	0.05 (0.100)	0.08
IVS	1+ coho	0.02 (0.027)	0.004 (0.01)	0.12
	1+ Dolly Varden	0.01 (0.011)	0.01 (0.014)	0.94
	0+	-	-	-
NFS	1+ coho	0.02 (0.039)	0.02 (0.056)	0.80
	1+ Dolly Varden	0.12 (0.110)	0.10 (0.152)	0.34
	0+	0.07 (0.072)	0.03 (0.058)	0.003**
BBS	1+ coho	0.03 (0.043)	0.002 (0.007)	0.02*
	1+ Dolly Varden	0.08 (0.111)	0.04 (0.066)	0.50
	0+	0.13 (0.107)	0.05 (0.078)	0.01*
RPC	1+ coho	0.16 (0.174)	0.02 (0.046)	0.03**
	1+ Dolly Varden	0.17 (0.239)	0.06 (0.132)	0.09

The condition of coho salmon and Dolly Varden, as measured using Fulton's Condition Index, reveals a peak in 1+ coho condition at the youngest stream, Wolf Point Creek, which decreases as stream age increases (Figure 4.5). The condition factor of 1+ Dolly Varden is also highest in the youngest streams, peaking at IVS. Regression analysis of changes in fish condition over the stream chronosequence shows a highly significant correlation for 1+ coho salmon ($R^2 = 1$), whilst Dolly Varden displayed a poor correlation ($R^2 = 0.31$; Figure 4.5). It should be noted, however, that the low number of values (or streams) used within the regression warrant the use of caution when interpreting these results.

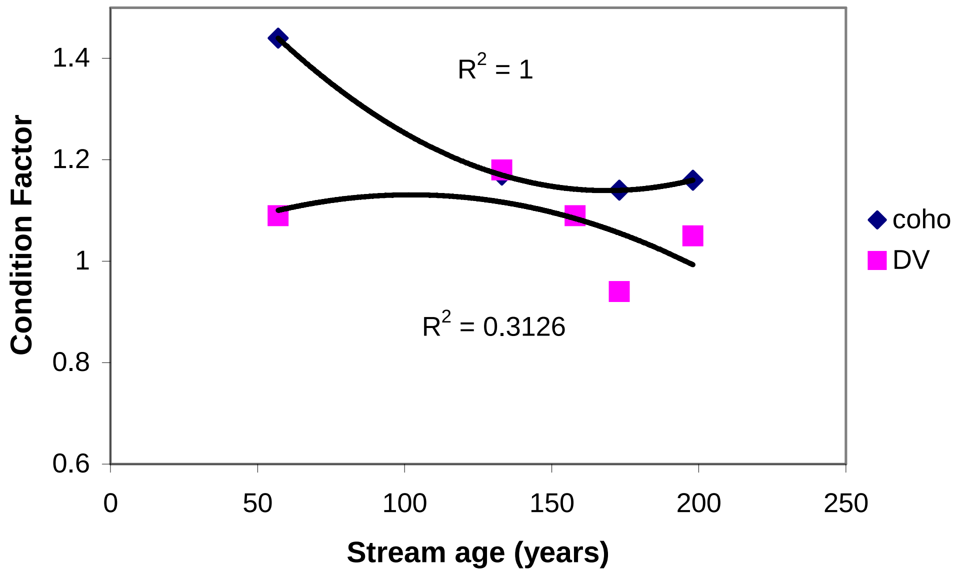

Figure 4.5: Mean condition factor and regression coefficients of 1+ coho salmon and Dolly Varden captured within the study streams, Summer 2008.

4.4 Discussion

Geomorphic and hydraulic diversity have been found to increase within GBNP streams as age increases. Such changes have been shown (in Chapter 2) to result in an increase in habitat diversity. Analysis of the occurrence of suitable depth and velocity habitat for 0+ fish and 1+ coho and Dolly Varden has found that the frequency of suitable velocity at the reach scale increases with stream age, whilst optimal depth tended to peak at streams of intermediate age (158 years). Simultaneous with such changes, the influence of CWD on channel hydraulics and geomorphology at the microscale increases over time, creating localised patches of both low velocity and increased scour (and hence, increased depth). These changes create suitable hydromorphic habitat which otherwise appear to be limited within the stream. 0+ fish and 1+ coho were found to actively seek out these habitats, showing a positive association with CWD structures within the older streams, as supported by previous studies (Beechie et al., 2005; Roni and Quinn, 2001).

The combined occurrence of both suitable depth and velocity surrounding CWD structures within the oldest streams may be the cause of increased usage by fish of these structures within BBS and RPC. Chapter 3 has shown that CWD does not have a strong influence on channel hydraulics and geomorphology within the youngest streams, predominantly due to the small size and complexity of recruited riparian vegetation within these streams. The introduction of large, complex CWD within the oldest streams, however, provides suitable microhabitat, which juvenile salmonids may utilise, which may also contribute to lower velocities observed at the reach scale. The creation of hydraulic conditions favourable to 0+ and coho salmon may be the reason for the increase in CPUE catches of these fish within older streams, as current velocity has been shown to be the primary variable in determining microhabitat selection by salmonids in summer (McMahon and Hartman, 1989). The observed increase in deep water habitat as stream age increased is also likely to benefit juvenile salmonids in the winter months. In winter, resident salmonids seek out deep water habitats with complex overhead cover, such as that provided by CWD (McMahon and Hartman, 1989; Nickelson et al., 1992). The creation of these conditions by complex CWD structures within older streams therefore provides favourable conditions which may otherwise be limited within the streams.

In addition to the provision of suitable microhabitat and pool habitats which resident salmonids can utilise, CWD has been found to offer a measure of visual isolation between juveniles and a degree of cover from overhead predators. Studies of the use of CWD by juvenile salmonids in a small Alaskan stream by Bugert et al., (1991) found that intraspecific aggression between juvenile salmonids, and in particular, aggression between yearling and sub-yearling coho was lower in areas with CWD, as a result of the provision of visual isolation between resident fish which subsequently reduces the number of aggressive interactions. Such a reduction in aggressive interactions may result in an increase in the resultant population density of the stream, due to a decrease in territory size of resident salmonids (Dolinsek et al., 2007). This may also be the cause for the increase in fish densities within older streams following the decline at streams of intermediate age. It is important to note, however, that excessive CWD loading may have a negative impact on the foraging efficiency of resident salmonids, as too many underwater structures limit the foraging success of visual feeders, such as coho and Dolly Varden (Giannico, 2000). Optimal summer coho habitat is therefore when there are open foraging areas interspersed with woody debris.

Chapter 2 has shown that the number of CGUs within the streams increases with stream age, resulting in the occurrence of a greater number of habitat patches, or ecotones. Research has shown that juvenile salmonids prefer to hold positions in areas such as the heads of pools which are typically characterised by areas of lower velocity adjacent to fast flowing habitat units (Dolloff and Reeves, 1990; Inoue and Nakano, 1999). These areas have been found to allow the fish to maximise their access to macroinvertebrate drift, whilst limiting their energy expenditure, resulting in a maximum food intake (Nielsen, 1992). The creation of areas of reduced velocity combined with an increased number of ecotones resulting from the recruitment of complex CWD structures within older streams therefore results in beneficial conditions for resident salmonids and increased stream productivity.

Analysis of juvenile fish density (using CPUE), however, shows that the youngest stream (Wolf Point Creek) contains the highest number and condition of juvenile salmonids, despite having the lowest hydromorphic complexity. This result is likely to be due to the presence of a large lake, which directly feeds the stream. Upstream lakes have been shown to provide a measure of stability to downstream watercourses by limiting peak flows, which in turn provide a degree of channel stability (Milner, 1987; Milner et al., 2000; Sidle and Milner, 1989) and warmer water temperatures than those streams without feeder lakes. Such thermal protection and channel stability may account for the higher CPUE and condition factor of juvenile salmonids within Wolf Point Creek. Evidence of thermal protection due to the presence of an upstream lake was evident from the monthly mean water temperatures. Wolf Point Creek consistently had the highest average water temperatures in both summer and winter. High winter/ spring temperatures result in a faster rate of development of incubating eggs, leading to earlier emergence of alevins and summer growth of juvenile fish (Bjornn and Reiser, 1991) and hence greater survival rates and condition factor. Higher summer water temperatures in some streams may also increase fish activity and movement, making it more likely that fish in these streams are captured by minnow traps. It should be noted, however, that trapping took place over a series of events over a two month period, and hence, such trapping bias is unlikely. The limiting of peak flows due to snow melt in the spring is also likely to improve egg and juvenile survival in comparison to those streams which lack upstream lake systems. Previous research by Milner and Bailey (1989) had found that the densities of juvenile coho salmon were six times higher in streams connected to lake systems than streams of a similar age which were not influenced by lake systems. The presence of a lake system at WPC therefore greatly influences the success and survival of juvenile salmonids, resulting in the higher fish densities and fish condition observed.

The colonisation and establishment of salmonids within stream environments has been shown to result in a major nutrient influx, which can influence stream and riparian food webs and stream productivity (Naiman et al., 2002). Research by (Milner et al., 2007) has shown that uptake of marine derived nitrogen (MDN) within young GBNP streams is low due to the lack of habitat features such as CWD and pools which are important for carcass retention. These streams therefore do not benefit from an increase in nutrients which may increase stream and terrestrial production. Older streams, however, are characterised as having higher MDN utilisation (Milner et al., 2007), due in part to the interaction between Pacific salmon and bear populations which widely distribute carcasses throughout the terrestrial ecosystem (Helfield and Naiman, 2006). The introduction of these nutrients has been found to accelerate the growth of riparian vegetation, in particular, spruce, so that trees may be come large enough to form complex CWD accumulations, which in turn enhance stream complexity (Naiman and Latterell, 2005) and salmonid productivity; a theme further investigated in Chapter 5.

The response of fish catches to environmental and physical variables is likely to be complex; a reflection the biocomplexity of river systems in which there are a number of interconnected relationships at a variety of levels which result in a non-linear dynamic (Cadenasso et al., 2006). The interplay between hydromorphology, CWD and biota is complex and multifaceted, interacting over a variety of temporal and spatial scales, which are often unknown, making current and future management priorities difficult to formulate. Quantification of the developmental processes which occur within Glacier Bay streams over a 200 year period provides an indication of the current and future landscape evolution within GBNP. Evidence of increased interaction between riverine and terrestrial ecosystems over time supports recent calls within the scientific community for the consideration of the condition and connectivity of the entire landscape in the management and restoration of riparian ecosystems (Naiman and Latterell, 2005). Further research into the creation and maintenance of such interactions is required to further enhance our understanding and usage of habitat restoration (Roni et al., 2002).

4.5 Conclusions

The recruitment of complex CWD into the stream environment as a result of continued terrestrial development was shown to produce favourable habitat for juvenile salmonids within GBNP. Changes in the characteristics of CWD resulting from the development of riparian vegetation through primary successional processes result in the creation of hydraulic and geomorphic variation and complex cover which fish may utilise, resulting in an increase in fish densities. Identification of the differences in CWD characteristics over time within Chapter 3 twinned with information on changes in fish densities across the stream chronosequence is likely to assist in the identification of those CWD features which produce hydraulic, geomorphic and structural complexity which may be reproduced within wood-based restoration projects. Knowledge of the functioning of natural wood jams in this manner will provide guidance on the installation and design of restoration programs, which continue to be used to improve degraded ecosystems.

4.6 Acknowledgements

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5

The role of coarse woody debris in the development of stream and floodplain complexity within a recently deglaciated environment

Previous chapters have highlighted the role of coarse woody debris (CWD) in creating geomorphic and hydraulic diversity, which benefits instream biota. This chapter focuses on the role of riparian vegetation and instream CWD as 'ecosystem engineers' which create and maintain biocomplexity within stream, terrestrial and floodplain environments. By extending the conceptual model of Milner et al. (2007) of the alteration of major linkages among stream, lake, terrestrial and marine intertidal environments within Glacier Bay over time, it is possible to highlight the role of CWD in creating and maintaining a number of these linkages. The development of complex interactions resulting from the introduction of complex CWD structures highlights the importance of the natural recruitment of riparian vegetation into the stream environment, and the value of CWD as a restoration technique within degraded systems.

5.1 Introduction

5.1.1 Riparian vegetation as an ecosystem engineer

The use of pristine river systems as a benchmark for investigations into the linkages between terrestrial and riverine ecosystems has received increasing attention (Bertoldi et al., 2009; Brooks and Brierley, 2002; Francis et al., 2008b; Gurnell et al., 2005; Tockner et al., 2003). Knowledge of the functioning, creation and maintenance of reference processes and process- form interactions within these systems greatly assists in the development of monitoring protocol for identifying deviations from reference conditions and the subsequent design of restoration practices to remedy degradation. Natural river systems are typically characterised as diverse, multi-channelled systems, with morphologically intact river corridors and floodplains which allow the interaction of aquatic, wetland and terrestrial landscapes over a large temporal and spatial scale (Tockner et al., 2003).

Investigations within a near- pristine river system in southeastern Australia by Brooks and Brierley (2002) suggested that instream CWD is an important element in the evolution of river character and behaviour. Current and historical practices of instream debris removal and loss of riparian vegetation has prevented the natural process of river development to occur, leading to suggestions that the continued investigation of the behaviour of contemporary rivers has led to a bias in the current theories of alluvial channel dynamics and development towards disturbed river systems in which riparian vegetation has only a negligible role (Brooks and Brierley, 2002; Francis et al., 2008a). The omission of the natural role of CWD in the development and maintenance of riverine processes prevents rivers from reaching their full ecological potential, and ensures that current restoration techniques continue to prevent natural functioning of these systems.

Research has therefore begun to focus on the relationships between riparian vegetation, geomorphological processes, instream flow and sediment dynamics (e.g.- Bertoldi et al., 2009; Corenblit et al., 2009; Gurnell and Petts, 2006; Gurnell et al., 2005). This research has shown that riparian vegetation acts as an ‘ecosystem engineer’ in connecting the hydrogeomorphic and biological components of river systems in a reciprocal relationship, rather than the traditional uni-directional process in which fluvial landforms and hydrogeomorphic processes determine the development of riparian plant communities (Corenblit et al., 2009; Corenblit et al., 2007).

Gurnell et al. (2005), for example, showed that the recruitment of riparian vegetation, and in particular, species which are capable of re-rooting within the stream bed result in the creation of braided river sections which produce an increased number of aquatic-terrestrial habitat linkages and increased biocomplexity within river and floodplain ecosystems. Fetherston et al. (1995) illustrated that riparian forest is an important link between riparian and terrestrial ecosystems within montane river systems of the Pacific northwest. Contributions of shade, bank stability, retention of organic matter, sediment and water provided by riparian forests as well as the provision of coarse woody debris (CWD) and particulate organic matter have been found to greatly influence channel form and stream functioning (Fetherston et al., 1995).

An assessment of the differences in CWD characteristics, hydromorphology and landscape development across the GBNP stream chronosequence provides the ideal opportunity to observe the changing role of CWD in the continued development of the riverine ecosystem. Such observations allow the linkages between terrestrial and aquatic ecosystem interactions with CWD to be further elucidated, culminating in the expansion of the Milner et al. (2007) conceptual model of landscape evolution within Glacier Bay (Figure 5.1).

Although the streams within GBNP are smaller than those studied by previous researchers, the preceding chapters have shown that the development of hydraulic and geomorphic complexity, and links between terrestrial and riparian ecosystems may be effectively studied using the space-for-time substitution present across the stream chronosequence within GBNP. Milner et al. (2007) have shown that the number and complexity of linkages between terrestrial, lake, stream and marine intertidal zone ecosystems increase over time, with linkages between stream and terrestrial environments becoming particularly strong as stream age increases (Figure

5.1). The previous chapters have highlighted the complex interactions between riverine and terrestrial ecosystems which create a diverse and complex environment in which a number of species may interact within a recently deglaciated environment. The maturation over time of both terrestrial and aquatic ecosystems within GBNP result in an increasing interaction between these systems (Milner et al., 2007), which in turn, creates a more complex and dynamic landscape.

The aim of this chapter is to highlight the importance of riparian vegetation and CWD as a key driver in landscape development within a recently deglaciated sub-arctic landscape such as GBNP. Determination of the role of riparian vegetation in the formation and development of floodplain and aquatic biocomplexity will help to identify those processes responsible for the formation of habitat complexity within natural systems, which may be used in the design of wood-based restoration programs within rivers.

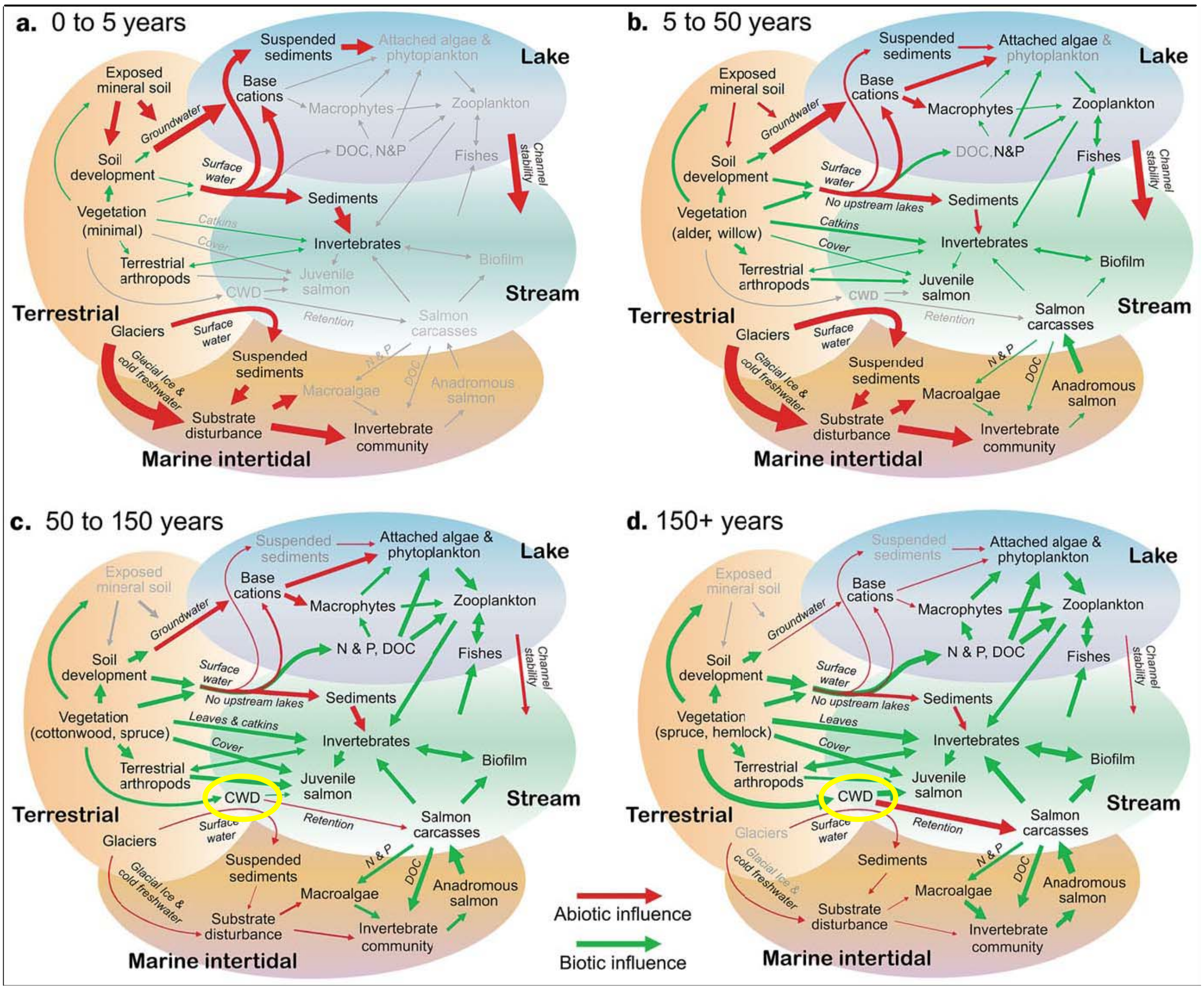

Figure 5.1: Major linkages among and within stream, lake, terrestrial and marine intertidal environments at Glacier Bay during four selected time periods following glacial retreat. The thickness of the arrows indicates the strength of the influence, which may be positive or negative. Grey components have little or no importance in the time period shown. The interaction of CWD within the ecosystem in streams 150+ years is highlighted by a yellow oval. This chapter seeks to further elucidate the role of CWD in driving those linkages shown here. Adapted from Milner et al. (2007).

5.1.2 Terrestrial and aquatic development within GBNP

As detailed in Chapter 3, previous research within GBNP on CWD recruitment indicates that woody riparian vegetation does not play an important role within the stream environment until at least 100 years following deglaciation in stream systems lacking lakes (Sidle and Milner, 1989), and often does not become a key component until more than 130 years following deglaciation (Milner and Gloyne-Philips, 2005).

The floodplains of streams downstream of lakes, however (such as the youngest stream in this study; Wolf Point Creek) are typically colonised by riparian vegetation at an earlier stage, due to the buffering effect of lake systems. This limits downstream peak flows, creating a more stable riparian environment, which allows the rapid development of bankside vegetation, including species of alder and willow.

CWD characteristics within GBNP change as stream age increases as a result of the continued development of adjacent riparian vegetation. Successional processes of terrestrial habitats within GBNP have been well documented (Chapin et al., 1994; Crocker and Major, 1955; Reiners et al., 1971), revealing a pioneer community of blue-green algae, lichens and liverworts, *Dryas drummondii* and scattered willows for the first 15-25 years following glacial recession. Woody species such as alder begin to dominate approximately 50 years following deglaciation, followed by cottonwood (*Populus trichocarpa*) and scattered Sitka spruce (*Picea sitchensis*) which form a mixed forest approximately 100 years after deglaciation, leading to a climax community of western hemlock (*Tsuga heterophylla*) forest, and later *Sphagnum* dominated muskeg over a period of thousands of years (Chapin et al., 1994; Milner et al., 2000). This process of terrestrial succession results in differences in CWD characteristics within the streams of different ages, as CWD is recruited directly from the adjacent floodplain when streams migrate across them during flooding events, and hence alters across stream age. Illustrations of these changes are included in Chapter 3.

The previous chapters have shown that hydraulic and geomorphic complexity increase as stream age increases, due to the introduction of slower flowing CGUs such as glides and pools as streams developed. Such changes were found to be driven by the recruitment and structural complexity of coarse woody debris (CWD) from adjacent terrestrial vegetation, which continues to evolve as a result of primary successional processes. Large, complex woody debris (in terms of its size, structural complexity and stream coverage), such as that found within the older streams, is more efficient in promoting forced scour and deposition to areas surrounding the structures. Such geomorphic changes result in the creation of smaller, more diverse channel units at the reach scale and hydraulic variation at the microscale. Juvenile salmonids are able to utilise the hydromorphic and structural complexity created by complex CWD structures, as a result of the increase in the occurrence of their preferred habitat.

These changes are the result of biotic- abiotic linkages which are created and maintained as a result of landscape development, which promote an increase in ecosystem complexity through an increase in the number and complexity of such interactions.

5.2 The role of complex woody debris in driving biocomplexity within the riverine ecosystem

Ecosystem engineers have been described as organisms which directly or indirectly modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials (Jones et al., 1994). Research within near-pristine river systems such as the Tagliamento River, Italy (Francis et al., 2008a; Gurnell and Petts, 2006) have highlighted the role of woody debris accumulations in driving a number of ecosystem processes including landscape evolution through the acceleration of landscape development and the formation of island-braided rivers (Gurnell et al., 2005). Island formation was found to influence biocomplexity within the river system by increasing the variety and arrangement of terrestrial and aquatic habitats, and the diversity and distribution of species which they support.

Cadenasso et al. (2006) have suggested a structural framework of biocomplexity which identifies three dimensions of complexity; namely heterogeneity, connectivity and contingency (Figure 5.2). Within this framework, biocomplexity was considered to increase along each axis to a maximum in which an ecosystem displays a shifting mosaic of habitat units with maximum connectivity resulting in a range of functional patch dynamics over a large temporal scale (Cadenasso et al., 2006; Ward et al., 1999).

It is within this framework of biocomplexity and landscape evolution that the role of CWD in landscape development within GBNP streams is assessed. Using examples from the scientific literature and experimentation and observations detailed below, the function of CWD in the creation and maintenance of biotic and abiotic interactions within and between terrestrial and aquatic ecosystems within GBNP are assessed.

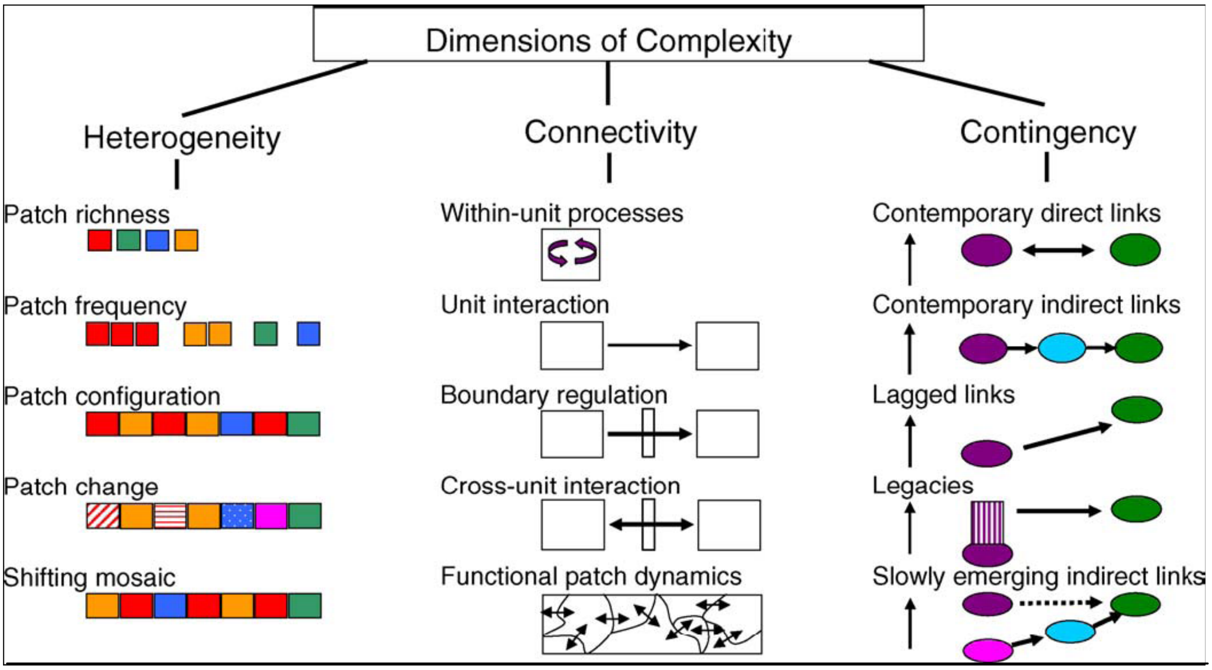

Figure 5.2: Framework for biocomplexity proposed by Cadenasso et al., (2006), which utilises three dimensions of biocomplexity. Components of the framework increase in complexity along each axis.

5.2.1 CWD and habitat complexity

The role of CWD in the creation of hydromorphic complexity has been discussed in Chapter 3. Wood forced patterns of scour and deposition within older streams resulted in an increased richness, frequency and configuration of geomorphic and hydraulic units at the reach and micro scales. Juvenile salmonids were found to utilise this complexity, resulting in increased fish density due in part to the addition of structural complexity provided by complex CWD, as reported within other river ecosystems, e.g.- Roni and Quinn (2001) and Brooks et al., (2004). Structural complexity has been found to provide suitable habitat for macroinvertebrates (O'Connor, 1991; Schneider and Winemiller, 2008) and plants (Harmon et al., 1986), which in turn, result in an increase in stream productivity (Entrekin et al., 2009). It should be noted, however, that only one obligate xylophage macroinvertebrate, *Polypedilium fallax* was found to rely on the presence of CWD within GBNP (Milner and Gloyne-Philips, 2005); other GBNP macroinvertebrate species were found to utilise CWD as a preferred habitat for access to high quality biofilm which typically develops on dead wood (Milner and Gloyne-Philips, 2005).

Increased habitat complexity such as that found within older streams has been found to influence ecosystem stability. The resilience of ecosystems to disturbances such as floods and droughts has been shown to be greater in those systems which contain a greater habitat and species diversity (Pearsons et al., 1992). For example, Brown, (2003) found that macroinvertebrate community variability at the reach scale decreased with increasing spatial heterogeneity, thereby suggesting that structurally diverse habitats support temporally stable and diverse macroinvertebrate communities. Similarly, those ecosystems which contain a high species and habitat diversity are thought to display a higher resilience to disturbance due to the provision of a number of avenues for both rapid and slow recovery (Pettit and Naiman, 2005). Increased habitat complexity therefore creates a more stable ecosystem in which a greater number of species may interact, thereby increasing biodiversity. Increased habitat complexity resulting from the recruitment of CWD therefore promotes the creation of a stable ecosystem in which a number of species and processes may interact.

5.2.2 CWD and the retention of organic matter

In addition to influencing geomorphic and hydraulic complexity as a result of forced scour and deposition, complex CWD is also important in retaining nutrients and organic matter which may be broken down and released to provide a temporally and spatially regulated food source for aquatic biota (Bilby and Likens, 1980; Piégay and Gurnell, 1997). CWD assists in increasing nutrient cycling (Smock et al., 1989), and connections and interactions within vertical and lateral ecosystems such as groundwater and floodplain ecosystems (Francis et al., 2008b; Pettit and Naiman, 2005).

The introduction of coarse particulate organic matter (CPOM) from adjacent riparian vegetation has been found to play an important role in the structuring and productivity of stream communities within GBNP. The addition of CPOM was found to result in a marked increase in meiofaunal (Robertson and Milner, 2001) and macroinvertebrate communities (Flory and Milner, 1999) via the provision of suitable habitat and increased food supply. The continued development of riparian vegetation and the subsequent recruitment of leaves and other CPOM into the stream channel are therefore likely to benefit instream biota and further strengthen biotic / abiotic interactions.

The retention of anadromous salmon carcasses within CWD structures has been found to contribute significant amounts of marine derived nutrients (MDN) to riparian vegetation, resulting in higher growth rates at sites with MDN enrichment than similar vegetation with no access to salmon carcasses (Helfield and Naiman, 2001). Growth rates of Sitka spruce adjacent to salmon streams in southeast Alaska were found to be significantly enhanced by MDN introduced from salmon carcasses to such an extent that the length of time for a tree to reach a diameter at breast height of 50 cm fell from ~307 years at control sites to less than 86 years where MDN were available (Helfield and Naiman, 2001), indicating a yearly growth rate of Sitka spruce three times higher than in reference conditions. The fertilisation effect of MDN on the growth of riparian vegetation has even been used to estimate the historical abundance of salmon runs within southeast Alaska (Drake et al., 2002).

As illustrated in Chapter 3, the size and complexity of CWD is important in determining the extent of interaction that the structure has on stream hydromorphology within GBNP. The recruitment of large complex riparian vegetation into the stream channel and the subsequent formation of complex debris structures that are capable of retaining salmon carcasses can have a profound effect on the subsequent development of the riparian ecosystem. This increased growth of riparian vegetation as a result of the retention of salmon carcasses appears to have a reciprocal arrangement in which the addition of MDN leads to an acceleration in the rate of primary successional processes. Previous studies by Milner et al. (2000), however, have found that uptake of MDN within GBNP streams varies. None of the five streams studied here have previously shown evidence of MDN enrichment, however, some of the older, more stable streams present within GBNP have shown evidence of MDN enrichment (e.g. Berg Bay North Stream). It is likely, therefore, that retention of salmon carcasses within the streams studied here is not sufficient enough to allow the eventual uptake of MDN (Monaghan and Milner, 2008). Continued colonisation of these streams by anadromous salmonids and further riparian and CWD accumulation development may facilitate the retention of salmon carcasses at a later date. For example, investigations within old growth forests of the Pacific northwest which are typically characterised by high CWD loading have found that complex CWD structures are highly efficient at retaining salmon carcasses (Cederholm and Peterson, 1985) which may then be broken down and utilised within the riparian ecosystem.

5.2.3 Sediment supply and CWD

Research by Yarnell et al. (2006) has shown that relative sediment supply drives geomorphic diversity at the reach scale within natural river systems. Maximum geomorphic diversity was found to occur when sediment supply relative to transport capacity is moderate and the flow regime is varied. Such conditions provide optimal habitat diversity by maximising the interaction between sediment supply and transport capacity within the river system. The addition of instream structures such as boulders and CWD within streams of varying sediment supply were found to 'force' habitat heterogeneity as flow is diverted, altering scour and deposition in a similar manner to that seen in streams with an intermediate sediment supply. The addition of CWD may therefore create high structural diversity, particularly in those streams with a low number of additional instream structures, which benefits a range of biota including fish (Inoue and Nakano, 1999; Walters et al., 2003) and macroinvertebrates (Beisel et al., 2000), and therefore increases stream diversity and productivity.

Similar results were found across the GBNP stream chronosequence, where the addition of complex woody debris was shown to create geomorphic and hydraulic complexity at the reach and micro scale. Such hydromorphic complexity was shown within Chapter 4 to benefit juvenile salmonids in the provision of preferred habitats, thus strengthening the interaction between CWD, physical processes and instream biota.

5.2.4 CWD and land / water interfaces

Floodplains provide a range of habitat needs for both aquatic and terrestrial species. The diversity of both aquatic and terrestrial floodplain habitats is controlled by the magnitude and frequency of the hydrologic regime which in turn influences habitat distribution and turnover (Whited et al., 2007). Seasonal inundation of the floodplain results in the re-distribution of resources such as sediment and nutrients between the terrestrial and aquatic habitat, the addition of which often results in an increase in stream productivity and biodiversity (*sensu* the Flood Pulse Concept of Junk et al., (1989); (Naiman et al., 2008; Pettit and Naiman, 2005) and biogeochemical hotspots (McClain et al., 2003)). The recruitment of complex CWD into the stream channel has been found to facilitate the duration and frequency of floodplain inundation and thus increases the occurrence of land / water interfaces by increasing the occurrence of localised overbank flows (Jeffries et al., 2003).

Recruitment of stable, complex CWD into the stream channel also results in the creation of a number of floodplain and instream islands and bars within the stream (Fetherston et al., 1995) which increase the occurrence of terrestrial / aquatic interactions. These accumulations and are often sites of initial plant colonisation within the developing floodplain. For example, accumulations of CWD deposited on river floodplains following large floods have been found to substantially influence the development of riparian vegetation within South African rivers severely affected by large floods (Pettit and Naiman, 2005). CWD accumulations formed after the flood were found to act as resource nodes due to the accumulation of fine sediments and soil nutrients and moisture, which facilitate the regeneration of vegetation within the disturbed area. Flood deposited CWD may later interact with developing vegetation to influence terrestrial patterns and processes as the decomposition of CWD has been shown to facilitate the development of biogeochemical hotspots (McClain et al., 2003), which contribute to the spatial heterogeneity of the landscape (Pettit and Naiman, 2005).

Such interactions of terrestrial- aquatic ecosystems mediated by the recruitment, movement and function of CWD have been observed at GBNP. The recruitment of CWD into the stream channel has been found to result in the creation of a number of stable structures in which sediment may accumulate, creating islands and bars on which vegetation and terrestrial invertebrates may colonise. These terrestrial habitats contribute new food sources (e.g. terrestrial beetles, flies and spiders; Charlotte Willis, *pers.comm.*) and habitat complexity to instream biota, thus reinforcing terrestrial-aquatic linkages.

5.3 A conceptual model of the role of CWD in the development of a recently deglaciated landscape within Glacier Bay

Research detailed above and observations made during fieldwork within GBNP has assisted in the formation of a conceptual model of the role of CWD in the development of biocomplexity and linkages between terrestrial and aquatic ecosystems within GBNP, as detailed in Figure 5.3. The model builds upon the work of Milner et al., (2007), which highlighted the major patterns of landscape change which occur over time within Glacier Bay. The model highlights the importance of CWD in driving and maintaining a number of biotic and abiotic linkages between terrestrial and aquatic ecosystems. A conceptual model of the changes in streams within Glacier Bay over time is summarised in Figure 5.4. This diagram illustrates how varying physical and biological factors alter in their relative importance and influence over 250 years of stream development within Glacier Bay.

Additional linkages and interactions are likely to be operating between and within stream, terrestrial, lake, and marine intertidal ecosystems within GBNP over time. Further investigations may provide information on the linkages between CWD and soil development, floodplain sediments and nutrient cycling for example.

The framework for biocomplexity proposed by Cadenasso et al. (2006) identified three dimensions of biocomplexity; heterogeneity, connectivity and contingency. Heterogeneity refers to the spatial heterogeneity of a landscape, beginning with simple measures of spatial heterogeneity, including the number and richness of habitat patches up to the assessment of habitat configuration and the change in the mosaic over time. Connectivity refers to the organisation interaction of habitat units within the landscape. At the lowest level, interaction between units is low and the necessary structures required for habitat function is available within that unit. With increasing interaction and connectivity, habitat units interact over a range of processes including nutrient and energy fluxes, resulting in the structure and dynamics of the landscape to be altered by changes in these fluxes. Cadenasso et al., (2006) identified contingency to represent the gradual change from temporal relationships being defined by direct contemporary interactions to the indirect relationships which may develop as a result of legacies and lagged effects.

When using this framework of complexity with reference to those interactions observed across the stream chronosequence within GBNP, it is possible to observe a gradual increase in all three dimensions of complexity over time. Habitat richness, frequency and configuration were all found to increase with stream age, as habitat units became smaller and more diverse as a result of the influence of CWD. The connectivity within and between terrestrial and stream environments was found to increase with time as interactions such as terrestrial development, retention of MDN and CWD characteristics began to develop, resulting in increased biotic and abiotic linkages. Observations of stream development over the 200 year GBNP chronosequence have provided the timescale in which interactions and linkages have developed, creating a complex riverine ecosystem.

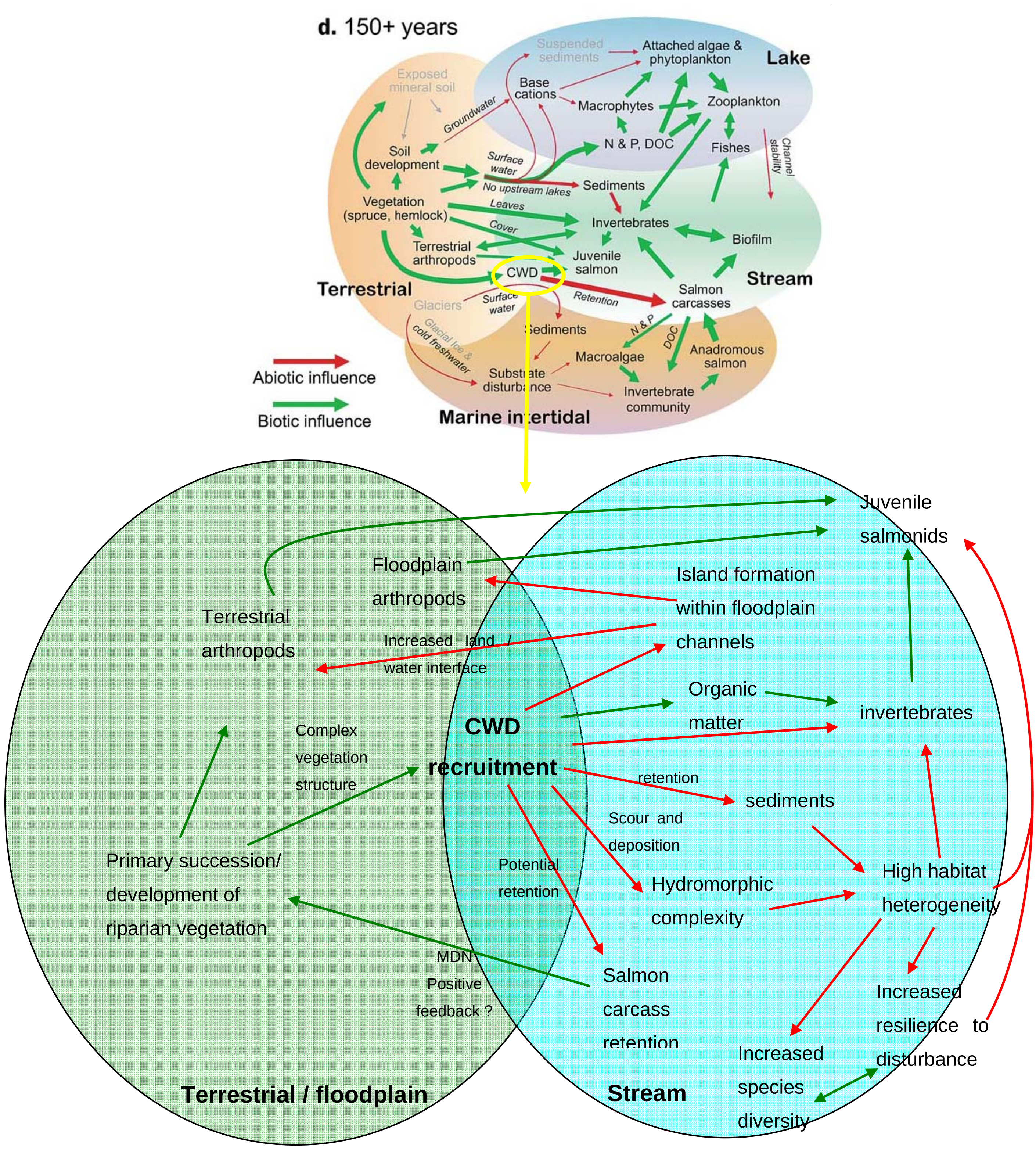

Figure 5.3: Extension of the conceptual model of Milner et al. (2007) of the major linkages among and within stream, lake, terrestrial and marine intertidal environments at Glacier Bay, highlighting the importance of coarse woody debris (CWD) in the

connection of terrestrial, floodplain and stream ecosystems within streams ≥ 150 years.

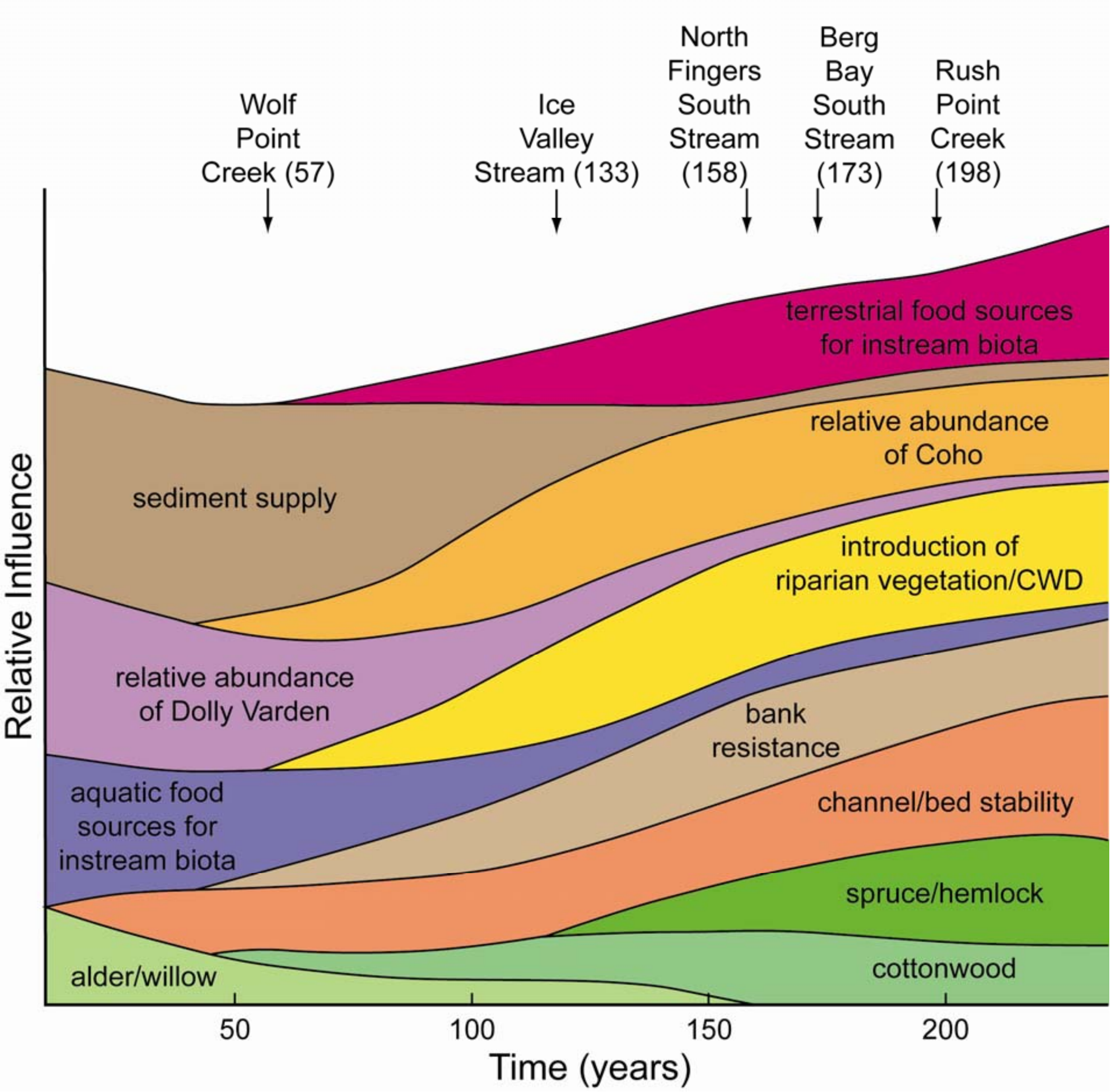

Figure 5.4: A conceptual model of the changes in importance of varying physical and biological factors across the chronosequence within Glacier Bay streams. The scale is relative, and only indicates the varying influence of each factor over time. The approximate location of the five study streams along the time sequence is indicated at the top of the diagram.

5.4 The role of CWD in landscape evolution and ecosystem functioning

A loss of natural processes through years of past management in which riparian vegetation is removed, preventing it from playing an active role has been identified as a probable cause of current 'non-equilibrium' behaviour of current river regimes (Brooks and Brierley, 2002). The presence of instream vegetation and debris has been purported to mediate flow and sediment transport to acceptable levels, allowing for 'equilibrium' channel conditions in which bank erosion, channel capacity, hydraulics and bedload transport rates are in equilibrium, resulting in a stable fluvial dynamic. Removal of riparian vegetation and instream debris results in a loss of such equilibrium, and may be the cause of some contemporary river management problems including flooding and erosion, which may be a direct consequence of system readjustments following vegetation removal (Brooks and Brierley, 2002).

It has been noted that river islands created from the input of riparian vegetation are often among the first natural features to be lost following river management, highlighting their importance in maintaining riverine geomorphic diversity (Francis et al., 2009; Tockner et al., 2003). Maintenance of such diversity is achieved by a number of biotic- abiotic feedback mechanisms (Pettit and Naiman, 2005), which operate within natural ecosystems highlights the importance of investigations within near-pristine ecosystems (Bertoldi et al., 2009).

CWD has been shown to form a central function in creating and maintaining a number of the linkages and interactions between terrestrial and aquatic ecosystems within GBNP. This increased interaction between ecosystems creates a complex, resilient system which is able to respond to a number of stressors. Loss of this natural functioning within contemporary rivers may be the cause of non-equilibrium behaviour often observed within degraded systems. Current restoration programs fail to address the creation and maintenance of reciprocal adjustments between living organisms and abiotic environment dynamics (Corenblit et al., 2008). Identification of the role of CWD in the development of stream and floodplain complexity within Glacier Bay provides further knowledge of the importance of biotic- abiotic interactions in the optimal functioning of these ecosystems.

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6

Synopsis

The overall conclusions of this thesis are summarised, highlighting the importance of hydromorphic complexity in determining river habitat. Suggestions for further research and a discussion of possible research limitations are included to provide the reader with a synopsis of this research.

6.1 Hydromorphic complexity within river systems

Following the inclusion of hydromorphic condition as a component in the determination of the ecological status of river systems within the EU Water Framework Directive, investigations into the role of hydromorphic complexity in determining the availability and condition of instream habitat has received increasing attention (Clarke et al., 2003; Orr et al., 2008; Petts et al., 2006; Thorp et al., 2006; Vaughan et al., 2009) Questions have remained, however, regarding the processes involved in creating and maintaining hydromorphic complexity. Lack of such information has hindered the quantification and classification of hydromorphic condition due to difficulties in establishing what constitutes ‘reference’ conditions, thus delaying the application of hydraulic and geomorphic condition as a component of ecological status.

Studies of landscape development within pristine environments, such as Glacier Bay, provide the opportunity to study how landscapes evolve and develop into stable, diverse ecosystems, typical of reference systems. By assessing the development of hydraulic and geomorphic complexity within streams spanning 200 years of development following deglaciation, it has been possible to identify how geomorphic and hydraulic complexity develop, and indicate the rates at which such components are created. Chapter 2 has shown that channel geomorphology and hydrology altered as stream age increased, with fast flowing units such as rapids and riffles being replaced by slow flowing units as streams developed, resulting in increased geomorphic, hydraulic and landscape diversity within older streams. Coarse woody debris and the development of riparian vegetation was shown within Chapter 3 to contribute to these changes, as the size, complexity and orientation of recruited vegetation tends to alter with stream age and development.

The importance of interactions between terrestrial and stream habitats in influencing the role of CWD on hydromorphic diversity and complexity was documented in Chapter 5, whilst the response of instream biota (predominantly juvenile Pacific salmonids) to these changes was discussed in Chapter 4.

This research has helped identify how biotic and abiotic interactions alter in strength and complexity over time, resulting in increased biocomplexity as a result of strengthened linkages between fluvial geomorphology, hydrology and ecology. Knowledge of the natural functioning of stream ecosystems in this manner is likely to help inform restoration programs which seek to restore geomorphic and hydraulic complexity and diversity to degraded systems. Such an understanding will also assist in determining the composition and functioning of reference habitats to which degraded systems may be compared. Prior to such application, however, a number of research questions must be addressed, an outline of which is included below.

6.2 Perspectives and future research

The present thesis has highlighted the complexity present within riverine and terrestrial ecosystems, and identified those processes and components, which contribute to such complexity. It is important to note, however, that a number of limitations were experienced during the course of this study. Such potential limitations and suggestions for future research are outlined below.

6.2.1 Limitations

- Due to difficulties in accessing sites in the winter months, this research has failed to assess the behaviour of stream systems and instream biota during these times. Variable flows, low water temperature and changes to the relative sediment supply during the winter months may play an important role in the structure and functioning of the river and terrestrial systems observed during the time of survey. Assessment of the impact of winter conditions on the structure and functioning of the river environment and instream biota may assist in determining whether or not additional investigation is required to ascertain the role of these conditions on stream development.

- It should be noted that a large precipitation event in the winter of 2005, just prior to the commencement of this study, in which over 650mm of rain fell on the Glacier Bay area in a period of less than 72 hours (Dan Lawson, *pers.*

comm.) may have affected stream habitat and biotic communities. A NERC grant awarded to Prof. A. Milner has shown that although streams throughout the area had undergone differing degrees of disturbance as a result of the 1 in 50 year event, the streams appear to have recovered to pre-flood condition by 2008. The impact of this event on fish populations remains unknown, but is likely to have resulted in lower juvenile survival due to the loss of incubating eggs. Juvenile fish abundance observed within this study may therefore be lower than would otherwise be expected.

- Initial experimental design of this research included a sixth stream, Nunatak Creek, aged 68 years, which was chosen to provide a more detailed coverage of the development of younger streams within Glacier Bay. High bear activity in 2006 and preliminary surveys of the stream in 2007 however, highlighted the unsuitability of this stream in subsequent analysis. A large ponded area (50m x 150m) approximately 2.5 kilometres from the river's mouth was found to alter the downstream nature of the river due to the buffering of the downstream flow regime. Exclusion of this river and a lack of alternative study streams have resulted in a 76 year gap between the two youngest streams. Such a large difference in age is not ideal, but could not be avoided.

6.2.2 Further research

- Only a small number of streams were surveyed within this study. The inclusion of a larger number of streams of differing ages would greatly improve the resolution and applicability of this research, as well as assess the accuracy of the research conclusions. Such investigations may provide answers to such questions as 'Does stream development reach a plateau in the absence of external disturbances (such as the flood of 2005)? And if so, at what age? Do all streams within Glacier Bay undergo the same process of development?' The inclusion of a larger number of streams of differing ages may also provide further insights into the rate and process of landscape development, identifying critical timescales and / or pathways of development.

- Elucidation of the rate and mechanism of the development and maintenance of linkages between stream, terrestrial, lake and marine intertidal environments through the observation of landscape development within systems such as Glacier Bay would greatly benefit the wider ecological community. For example, experimental simulation of large and small scale disturbance within a number of streams of differing ages within GBNP may help to test the theory that complex habitats tend to have a higher degree of resilience to outside stressors, and are hence better able to recover from ecosystem disturbance.

- This research has shown that the interaction between CWD, hydromorphology and instream biota is very complex, with small alterations in the placement and characteristics of CWD accumulations resulting in significant changes to the degree of influence such structures have on the surrounding stream. Successful application of wood-based restoration techniques will require further investigations into the optimal placement and installation of wood structures. Further use of an ADCP at transects surrounding CWD structures would aid in identification of those features which create hydraulic and geomorphic diversity which benefit instream biota and may be recreated in restoration techniques.

- Attempts were made to assess the usage of identified habitat units by juvenile salmonids using snorkel surveys. Due to high flow conditions, and poor water clarity, however, such surveys were abandoned at a number of sites, preventing analysis of habitat usage in three out of the five study streams. Initial results had suggested that juvenile salmonids utilised CGU types differently within the two streams which were assessed. It was not possible to determine whether or not differences in hydromorphic complexity within the streams were the cause of these differences, however, it would be interesting to re-attempt snorkel surveys within all five of the streams to determine fish habitat preferences across the chronosequence.

- Investigations by a fellow researcher were undertaken in 2008 to assess the contribution of terrestrial vs. aquatic food items in the diets of juvenile salmonids across the stream chronosequence. Using stomach flushing techniques, samples were obtained from a minimum of thirty coho and Dolly Varden from each stream which allowed dietary analysis to be obtained. Unfortunately, this work was not completed, however such information, possibly combined with isotope analysis, would provide an indication of the importance and development of aquatic- terrestrial linkages over time, and contribute a great deal of information on the development of ecosystem interaction and complexity which may be used in habitat restoration and management techniques.

- Further investigation into the applicability of the theoretical relationship between physical habitat heterogeneity, stream development and sediment supply proposed within this research would help to clarify the possible linkages between these components. Application of this theory may help to explain and predict the amount of habitat heterogeneity which may be expected within streams given a known relative sediment supply. Comparison of observed vs. expected heterogeneity, particularly following disturbances which may alter the relative sediment supply of the stream system may help to form management objectives which seek to maximise habitat heterogeneity. Investigations of newly created stream environments following flood events or restoration efforts may provide such study opportunities.

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7

Appendices

Appendix 1

Details of stream flow, channel morphology and CWD characteristics used in the classification of CGU types, CWD dam types and the degree of complexity of CWD structures.

Table 7.1: Surface flow type classification system used to identify CGUs within the study streams, from Environment Agency River Habitat Survey Guidance Manual, 2003.

Flow Type	Description
Free fall (FF)	Where vertically falling water clearly separates from the 'back-wall' of a distinct vertical rock face. Generally associated with waterfalls
Chute (CH)	Low, curving flow with substantial water contact 'hugging' the substrate. Where multiple chutes occur over individual boulders or bedrock outcrops, and 'stepped' profile is created. Mostly associated with cascades
Broken standing waves (BW)	Occur on a localised scale where water appears to trying to flow upstream. A white water tumbling wave must be present for the wave to be described as broken. Mostly associated with riffles, but may also occur within a rapid
Unbroken standing waves (UW)	'Babbling' water with a disturbed 'dragon's back' surface, which has upstream facing wavelets that have not broken. White water may occur as crest waves, but not as breaking waves. Mostly associated with riffles, but may also occur within a rapid.
Chaotic flow (CF)	A chaotic mixture of several faster flow types (e.g.- FF, CH, BW, UW) in no organised pattern. Should only be used where there are three of these fast flow types at a spot-check, and where no one of them is clearly dominant.
Rippled (Rp)	Water surface with distinct, symmetrical, small ripples that are generally only a centimetre high and moving downstream. Do not confuse with wind induced ripples.
Upwelling (Up)	Found where strong upward flow movements disturb the surface, creating the appearance of bubbling or boiling water. Typically found on the outside of tight meander bends, behind in-channel structures or below waterfalls.
Smooth (Sm)	Laminar flow where water movement does not produce a disturbed surface. A stick placed vertically in the flow will produce an upward facing 'V'.
No perceptible flow (NP)	As found in ponded reaches and pools. No disturbance in water when stick placed in the flow

Table 7.2: CGU Classification which utilises surface flow types and channel morphology to classify habitat units within the study streams, from Environment Agency River Habitat Survey Guidance Manual, 2003.

Mesohabitat	**Turbulence**	**Description**
Fall (Fa)	Turbulent & very fast	Vertical drops of water over the full span of the channel, commonly found in bedrock and step-pool stream reaches. Chaotic, free fall and upwelling flow.
Cascade (Ca)	Turbulent & very fast	Stepped rapids with very small pools behind boulders and small waterfalls. Chaotic SFT, with some standing waves.
Rapid (Ra)	Turbulent & fast	Higher gradient reach than a riffle, with faster current velocity, coarser substrate, and more surface turbulence. Convex streambed shape. SFT typically dominated by broken and unbroken standing waves
Riffle (Ri)	Turbulent & moderately fast	Shallow stream reach with moderate current velocity, some surface turbulence, with some substrate breaking the surface. SFT typically dominated by unbroken standing waves, and some rippled flow
Run (Ru)	Non- turbulent & moderately fast	Moderately fast and shallow gradient with ripples on the water surface. Laterally concave streambed, laminar flow. SFT typically rippled with some smooth areas
Glide (Gl)	Non-turbulent & moderately slow	Smooth, 'glass-like' surface, with visible flow movement along the surface, moderately shallow. SFT typically smooth, with occasional rippled flow.
Backwater pool (Bw)	Non-turbulent & slow	Associated with an obstruction; water flow diverges from the axis of the channel. SFT dominated by no perceptible flow.
Drawdown pool (Dd)	Non-turbulent & slow	Associated with thalweg; flow rapid at entrance, slow in middle, and accelerates at the exit. Mixed SFT.
Other (O)		To be used in unusual circumstance where feature does not fit any recognised feature

Table 7.3: Dam type characterisation, after Abbe and Montgomery, 2003, as detailed in Chapter 3.

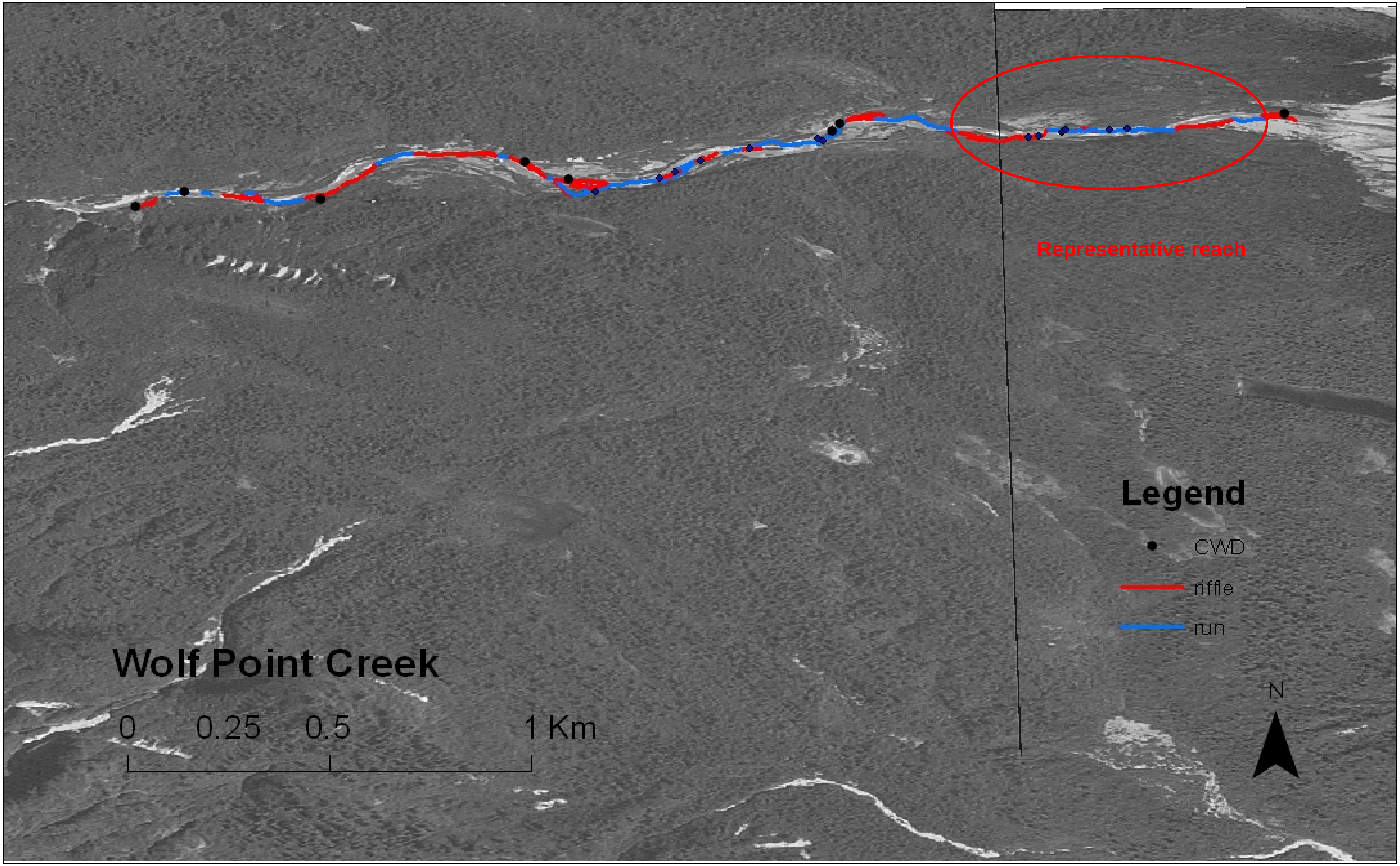
Origin	Type	Distinguishing characteristics
In-situ Key member has not moved down the channel	Bank Input	In-situ. Some or all of key members in the channel. Consists of tree boles fallen in the channel from their growth locations
	Log step	In-situ, key member forming step in channel bed. Forms when a tree bole spans the channel, partially blocking the channel so that water flows over the top.
Combination In-situ key members with additional racked WD	Valley jam	Jam width exceeds channel width and influences valley bottom. Form when large trees fall into the channel and constrict much of the channel cross-section.
	Flow deflection	Key members may be rotated, jam deflects channel course. Don't completely span the channel, unlike valley jam.
Transport Key members moved some distance downstream	Debris flow/ flood	Chaotic WD accumulation, key members uncommon or absent, catastrophically emplaced. Result from episodic deposition of WD entrained in debris flows.
	Bench	Key members along channel edge forming bench-like surface. Key members orientated oblique or parallel to the flow and wedged into the margins or in bedrock etc
	Bar apex	One or more distinct key members downstream of jam, often associated with development of bar and island. Typically occur at the upstream end of mid-channel bars.
	Meander	Several key members buttressing large accumulation of racked WD upstream. Occur along the outer margins of meander bends, often unstable.
	Raft	Large stable accumulation of WD capable of plugging even large channels and causing significant backwater. Extensive floating accumulations of WD
	Unstable	Unstable accumulations composed of racked WD upon bar tops or pre-existing banks. Typically left in flood events, and out of channel.

Table 7.4: Measurement of dam structure complexity, after Hughes et al., 2007, as detailed in Chapter 3.

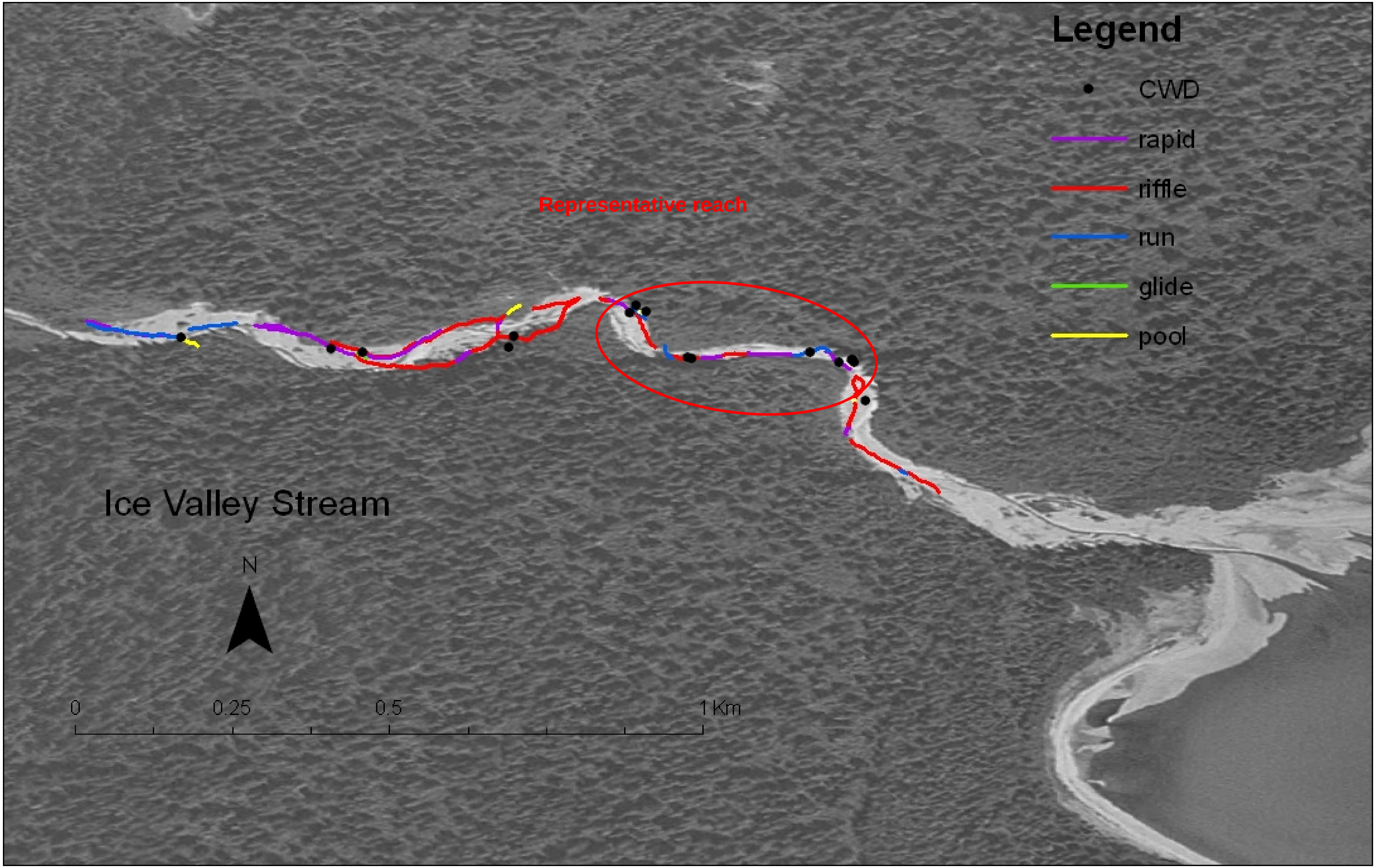
Description	**Class**
A single trunk or branch- a root mass or small part of a branch may be present	1
Double trunk or branch; or a single trunk with one level of branching for most its length	2
Trunks with multiple branches for most of its length, with second level of branching present	3
Complete tree with extensive branching OR an accumulation of large wood in which individual pieces could not be resolved	4

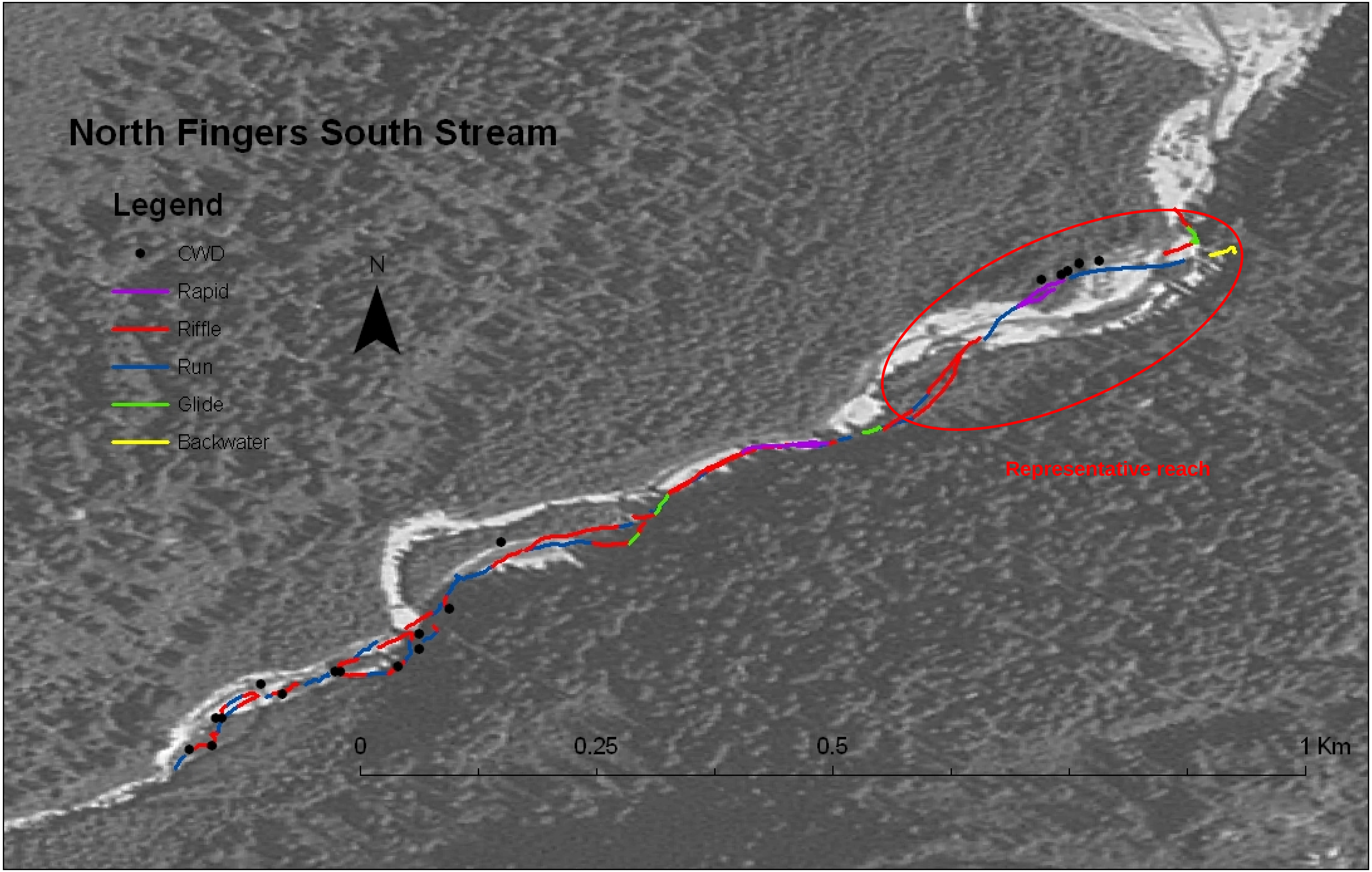
Appendix 2

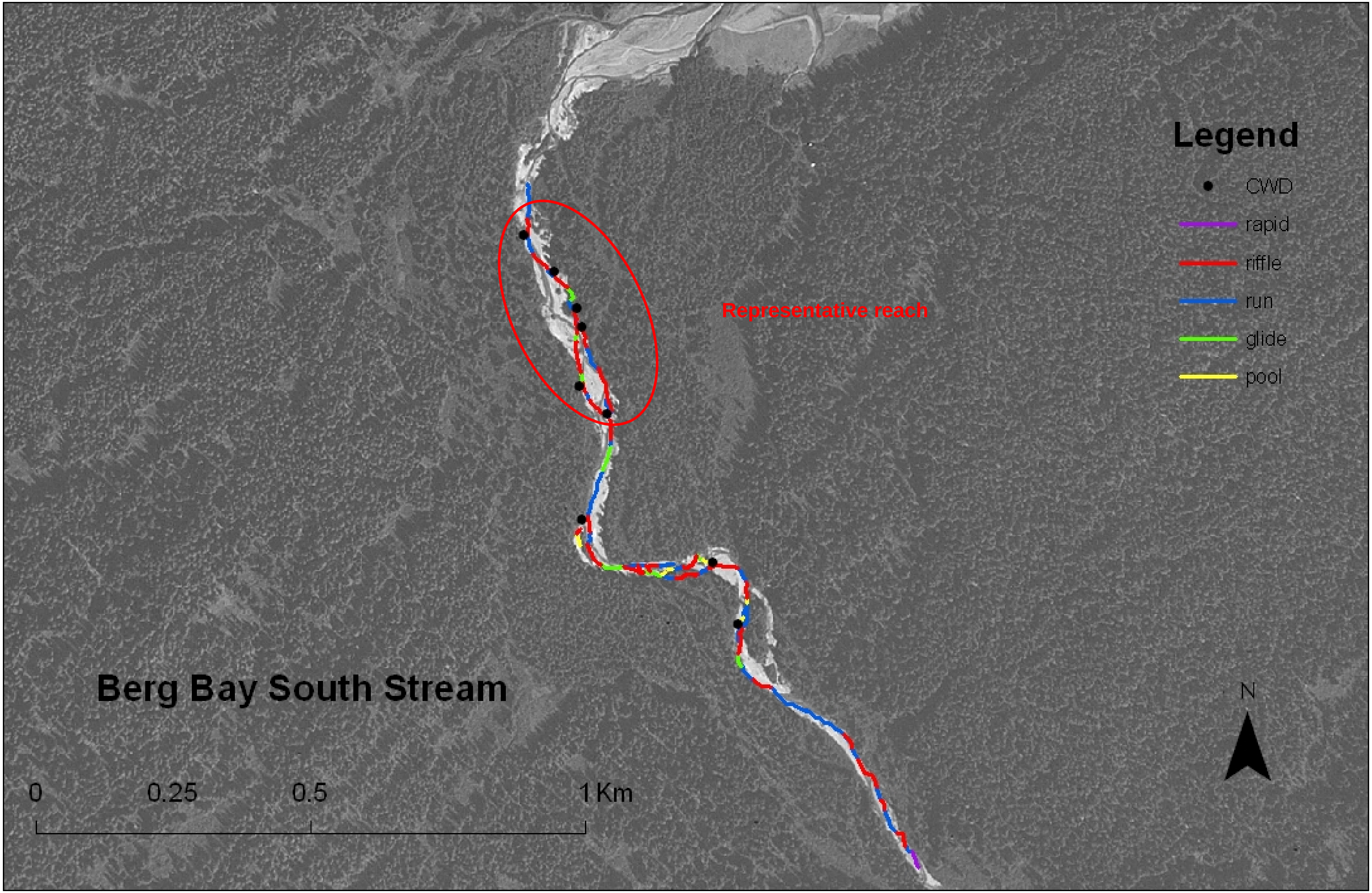
Aerial photos (circa 1995) of the study streams, highlighting mesoscale mapping of CGU types, Summer 2007.

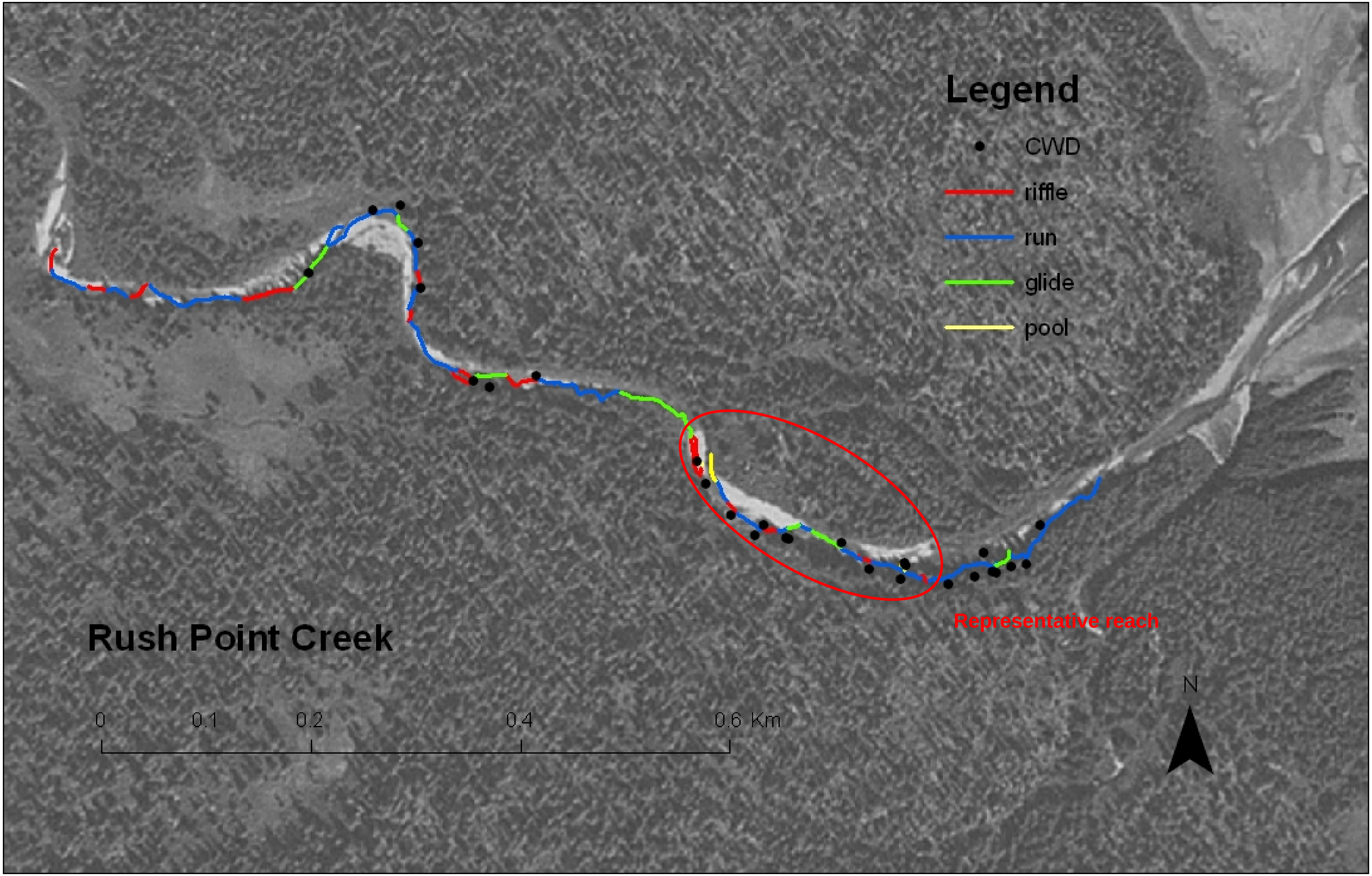


Representative reach
Legend
CWD
riffle
run
Wolf Point Creek
0
0.25
0.5
1 Km
N


Legend
CWD
rapid
riffle
run
glide
pool
Representative reach
Ice Valley Stream
N
0
0.25
0.5
1 Km


North Fingers South Stream
Legend
CWD
Rapid
Riffle
Run
Glide
Backwater
N
Representative reach
0
0.25
0.5
1 Km


Legend
CWD
rapid
riffle
run
glide
pool
Representative reach
Berg Bay South Stream
0
0.25
0.5
1 Km
N


Legend
CWD
riffle
run
glide
pool
Representative reach
Rush Point Creek
0
0.1
0.2
0.4
0.6 Km
N

Appendix 3

Published paper within River Research and Applications, based on Chapter 2 of this thesis.

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SHORT COMMUNICATION

THE DEVELOPMENT OF HYDRAULIC AND GEOMORPHIC COMPLEXITY IN RECENTLY FORMED STREAMS IN GLACIER BAY NATIONAL PARK, ALASKA

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ABSTRACT

Geomorphic and hydraulic complexity within five streams representing 200 years of stream development were examined in Glacier Bay National Park, Alaska. Channel geomorphic units (CGUs) were mapped using a hierarchical approach, which defined stream habitat according to morphological and hydraulic characteristics. Detailed hydraulic assessment within the geomorphic units allowed differences in hydraulic characteristics across the 200-year chronosequence to be documented. Channel geomorphology and hydrology changed as stream age increased. Younger streams were dominated by fast flowing geomorphic units such as rapids and riffles with little hydraulic or landscape diversity. As stream age increased, slower flowing habitat units such as glides and pools became more dominant, resulting in increased geomorphic, hydraulic and landscape diversity. These results suggest that geomorphic and hydraulic complexity develop over time, creating habitat features likely to be favoured by instream biota, enhancing biodiversity and abundance. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS: geomorphology; habitat heterogeneity; hydraulic diversity; stream age; HydroSignature

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INTRODUCTION

The availability of instream habitat within rivers is determined by the interaction of channel geomorphology and hydrology (Maddock, 1999). Changes in the diversity and complexity of hydraulic features have been found to influence habitat and species diversity (Maddock, 1999; Bartley and Rutherford, 2005; Sullivan *et al*., 2006), contributing to increased biodiversity within the stream environment (Stalnaker and Waddle, 1996; Crowder and Diplas, 2006; Dyer and Thoms, 2006; Principe *et al*., 2007). In comparison, little research has focussed on how changes in geomorphic diversity and complexity influence habitat availability within the aquatic environment (Yarnell *et al*., 2006).

Geomorphological complexity may be defined as the complexity in both composition and configuration of geomorphological elements within a river channel. Changes in the geomorphic composition of a river influence community diversity, productivity and condition (Beisel *et al*., 2000; Sullivan *et al*., 2006) as geomorphic complexity creates spatial heterogeneity which can be utlized by instream biota, such as macroinvertebrates (Beisel *et al*., 2000) and fish (Inoue and Nakano, 1999; Walters *et al*., 2003).

Previous work by Yarnell *et al*. (2006) suggests relative sediment supply influences stream habitat heterogeneity, with streams containing a moderate relative sediment supply supporting the highest habitat diversity due to an increase in geomorphic diversity within these streams as a result of variable deposition and scour at any given flow. Although research has alluded to the importance of geomorphic complexity in creating habitat and hydraulic diversity, our knowledge of how geomorphological complexity develops, and the response of instream biota to these changes is negligible.

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We used the unique conditions found at Glacier Bay National Park, Alaska, to elucidate the development of geomorphic and hydraulic complexity within streams over time. Identification of channel geomorphic units (CGUs; e.g. riffle, run, pool etc.) using a hierarchical description of the morphological and hydraulic properties provides an ecologically meaningful measure of the geomorphic and physical diversity of the instream environment. Analysis of differences in the habitat and hydraulic environments within five streams representing a 200-year age chronosequence will assist in identifying changes in instream habitat which occur as streams develop. Assessment of these changes at the 'meso' scale will provide an assessment over the entire riverscape, allowing identification of landscape and hydraulic features at scales relevant to the entire lifecycle of instream biota such as fish (Fausch *et al*., 2002). Detailed mapping and assessment of smaller representative reaches identified from meso scale mapping is able to quantify the hydraulic (microscale) and habitat changes, which occur as the streams age.

Study site

Rapid glacial recession within Glacier Bay National Park, Alaska, has created a unique opportunity to document the geomorphological development of streams and associated physical and ecological responses over time. Within Glacier Bay, new stream systems have been formed within the last 250 years, following rapid glacial recession following the Neoglacial maxima (Soiseth and Milner, 1995). Detailed historical, geological and dendrochronological data allows glacial recession within Glacier Bay to be accurately dated, whilst extreme disturbance to the area resulting from glacial processes provides the opportunity to study habitat and community development via primary colonization processes (Crocker and Major, 1955; Reiners *et al*., 1971; Chapin *et al*., 1994). Stream age is related to the distance of a stream from the retreating glacier termini (Figure 1), and thus temporal changes in stream complexity can be studied on the basis of spatial differences (Milner *et al*., 2000). Five streams were chosen for study according to their similarity in catchment and geological characteristics (Table I), and together, represent the full range of stream ages and development present within Glacier Bay.

METHODS

Fieldwork conducted in 2006 and 2007 focussed on the identification and quantification of the geomorphic composition within study streams. CGUs were identified at base flow conditions, over a minimum distance of 1.3 km using a modified version of the (Hawkins *et al*. 1993) classification system, and mapped using a mapping grade GPS unit (Trimble GeoXT; accurate to the sub metre level). Representative reaches (minimum 300 m) were identified from mapping at the 'meso' scale carried out in 2006, and studied in greater detail in order to quantify hydraulic and habitat structure at the microscale within CGU types across the stream chronosequence.

Thirty random water velocity (at 0.6 depth, averaged over 30 s, using a Model 201D flow meter, Marsh-McBirnley Inc., Frederick, MD, U.S.A.) and total water depth measurements were taken from each CGU type. The data were then assessed using HydroSignature software (Le Coarer, 2005). HydroSignature is free-to-use software which classifies surface depth and velocity percentages into cross-classed grids, displaying the hydraulic diversity within a site as a velocity/ depth plane or hydraulic signature. Analysis of the data using HydroSignature allows the hydraulic diversity present within CGUs to be quantified, enabling a comparison of hydraulic composition between streams and CGU types to be assessed. Plotting hydraulic characteristics on two axes such as this provides a greater ability to differentiate between morphological units than standard statistical methods (Moir and Pasternack, 2008).

The data were input into HydroSignature as NOXY 2 (non-spatialized data; Scharl and Le Coarer, (2005)), using Froude number as the sorting factor. Surveyed CGUs were grouped together within each stream according to their CGU type, and analysed using HydroSignature's inbuilt 'HydroSignature Comparison Index' (HSC; Scharl and Le Coarer, 2005). The HSC utilizes a spatial analysis filter technique to construct a comparison matrix, which provides a relative scale of comparison of two hydraulic signatures. A single 'HSC general total' value is then output from HydroSignature, with values ranging from 0 to 100; 0 implies two hydraulic signatures are identical, or homogenous, whilst a value of 100 suggests that the hydraulic signatures have no similar properties, or are heterogeneous.

HSC was used to evaluate differences in hydraulic diversity in three instances; (1) the 'CGU total' constructed for each CGU within each of the five study streams was compared against itself in order to obtain an average value

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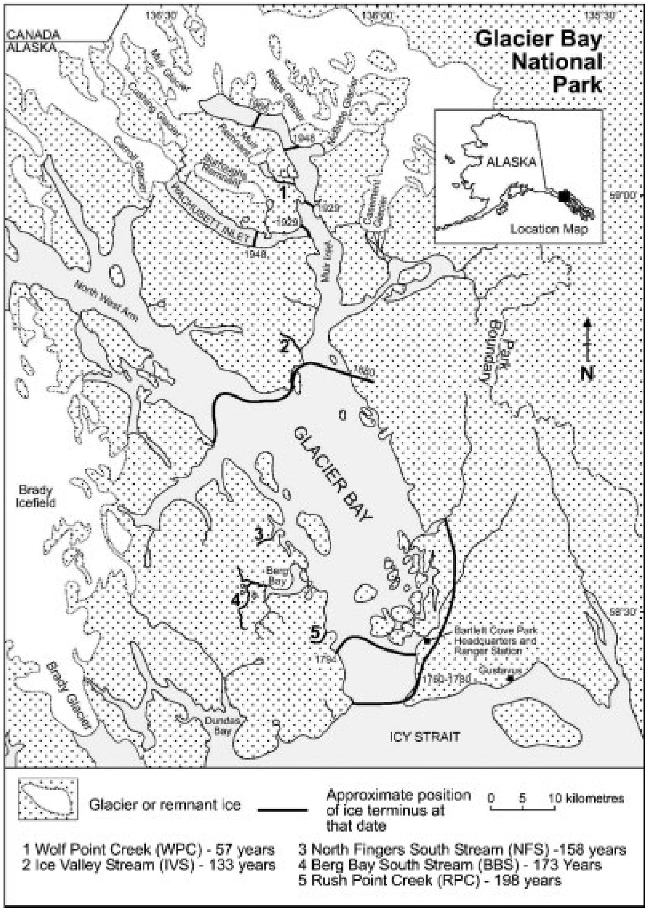

Figure 1. Map of Glacier Bay National Park, Alaska, including the study streams (and acronyms) and dates of glacial recession

of comparison index, which provides an indication of the amount of natural variation present within a CGU type over the study reach (i.e. hydraulic variation present between 'run' CGUs within Stream A; Y. Le Coarer, *pers.comm.*) (2) 'CGU total' hydraulic signatures were compared with their corresponding CGU type across the chronosequence to evaluate changes in hydraulic diversity which may occur as stream age increases (i.e. 'run total' from Stream A versus 'run total' from Stream B) and (3) a mean HSC value for each CGU type was calculated from point 2 above to assess the degree of change in hydraulic diversity within CGUs across the chronosequence.

Landscape evenness and diversity indices were calculated for each of the streams using the spatial analysis program FRAGSTATS v3.0 (McGarigal *et al*., 2002). FRAGSTATS is able to evaluate raster maps created within

Table I. Summary of physical characteristics of the five study streams

	Stream age	Reach gradient(%)	Stream length (km)*	Drainage area (km^2)**	Ave discharge (m^3/s)	Stream order *	Dom substrate	Geology
WPC	57	1.14	5.6	29.8	2.29	2	Bo	A/W
IVS	133	0.98	8.3	19.4	3.02	2	Co	A/W
NFS	158	1.14	8.0	16.8	5.65	2	Bo	A/W
BBS	173	0.80	7.2	33.1	4.95	3	Gr	A/W
RPC	198	0.88	6.6	23.3	7.51	2	Co	A/W

Bo, boulder; Co, cobble; Gr, gravel; A/W, Alexander/Wrangellia Terrane. Data sources- *Robertson and Milner (2006); ** Hill *et al*. (2009).

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ArcGIS and calculate a number of metrics at the landscape, patch and class level. For the purposes of this study, only landscape level diversity (Shannon's and Simpson's Diversity indices) and evenness (Shannon's and Simpson's Evenness indices) indices were calculated. The landscape diversity indices calculate the richness, or number of habitat units within the landscape, whilst the evenness indices provide information on how the different habitat units are distributed within the landscape (i.e. clumped or evenly spread). Both of these landscape measures provide information on landscape composition, and provide ecologically meaningful measures of geomorphic diversity (Yarnell *et al*., 2006).

RESULTS

Younger streams supported lower geomorphic and hydraulic diversity than older streams, and were characterized by faster flowing CGUs (rapids and riffles; Figure 2), with higher velocities and shallower depths, and thus higher Froude numbers (Figure 3). As stream age increased, however, slower flowing CGUs, (e.g. glides and pools) began to dominate, resulting in a decline in mean velocity and Froude number. Analysis of the amount of hydraulic variation in CGU types within a single stream (Table II) shows that glide CGUs within BBS had the highest dissimilarity from one another, followed by riffle and run CGUs, within WPC, BBS and RPC. CGUs within IVS and NFS were similar to one another, as suggested by the low HSC values.

Comparison of the hydraulic complexity across the chronosequence (Figure 4) reveals a gradual increase in HSC values as the difference in steam age increases, whilst the lowest HSC values occur when the difference in stream age are lowest (e.g. comparison of the two youngest or older two streams). It is interesting to note that riffle and pool CGUs in the two oldest streams (173 and 198 years respectively) have similar hydraulic signatures. Mean HSC in fast flowing CGUs was low (Table III), indicating little difference in hydraulic characteristics between streams, whilst the HSC values for slower flowing CGUs was high, suggesting a growing disparity in the hydraulic characteristics of these CGUs, in those streams which contained them (NFS, BBS and RPC).

Landscape diversity and number of CGUs per 100 m of mapped stream both increased with stream age, peaking at streams of intermediate age, whilst evenness decreased from the younger to older streams (Figure 5). These results indicate diversity is highest in the streams of intermediate age containing the greatest number of CGU types. As stream age increased, however, the habitat units became less evenly distributed, possibly due to habitat units becoming smaller and in greater number, resulting in the landscape becoming increasingly uneven.

DISCUSSION

Hydraulic and geomorphic composition differed between the streams. Differences in channel geomorphology may be due to inherent differences between the streams, such as catchment geology, sediment load, stream discharge and gradient, however, differences in these primary driving factors were taken into account when study streams were selected, and when identifying channel reaches in which hydraulic characteristics were assessed. The scouring action of glacial advance and retreat results in the removal of all previous biological and physical features from the

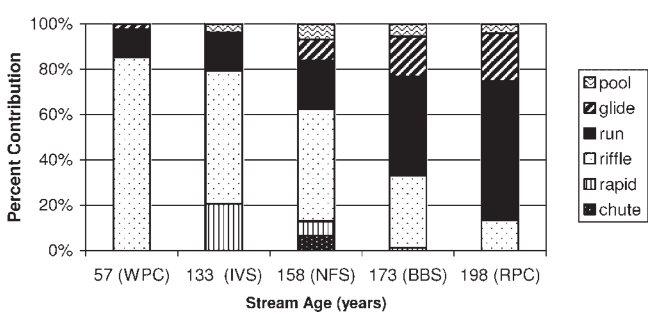

Figure 2. Percent contribution of CGU types within the study streams.

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Table II. Average value of comparison index of CGU types within the study streams, indicating the amount of natural variation within CGUs across the stream chronosequence

Stream and age (years)	WPC-57	IVS-133	NFS-158	BBS-173	RPC-198
Rapid	*	5	13	*	*
Riffle	29	0	4	24	16
Run	18	0	0	25	25
Glide	*	*	0	40	0
Pool	*	*	0	0	0

Zero values occur when only one example of a CGU occurred within the study reach; comparison of that Hydrosignature with itself will be identical, and hence have an HSC value of 0.
*denotes a lack of that CGU within the river.

stream catchments, effectively creating a 'clean slate' from which new stream habitats can evolve within a landscape driven by primary successional processes and current hydraulic regimes. Stream variables do not appear to vary substantially (Table I); stream size, gradient and geology are similar across the chronosequence, indicating that inherent differences between the study streams are unlikely. It is therefore proposed that the differences in geomorphic composition within the study streams were due to differences which have occurred as a result of changes in channel geomorphology which result from stream development over time.

Analysis of geomorphic composition at the 'meso scale' using diversity and connectivity measurements revealed that that the number and diversity of CGUs increased with age, whilst the size of the CGUs decreased. Geomorphic composition, size and diversity shift within older streams, changing the hydraulic characteristics of these streams at the microscale. Young streams typically consist of large, fast flowing CGUs with few velocity shelters. As stream age increases, however, slower flowing CGUs, such as glides and pools, become dominant, thereby decreasing flow velocities and increasing water depth. These changes produce velocity shelters which are likely to benefit instream biota, such as juvenile fish. Hydraulic signatures became more diverse (less similar to one another, as a result of increased diversity) in slower flowing CGUs such as glides and pools than faster flowing CGUs, suggesting that the addition of slower flowing CGUs in older streams results in increased hydraulic variation. Differences between hydraulic signatures were also found to increase as differences in stream age increase (i.e. the oldest stream vs. the youngest stream), indicating a significant change in stream hydraulics over time.

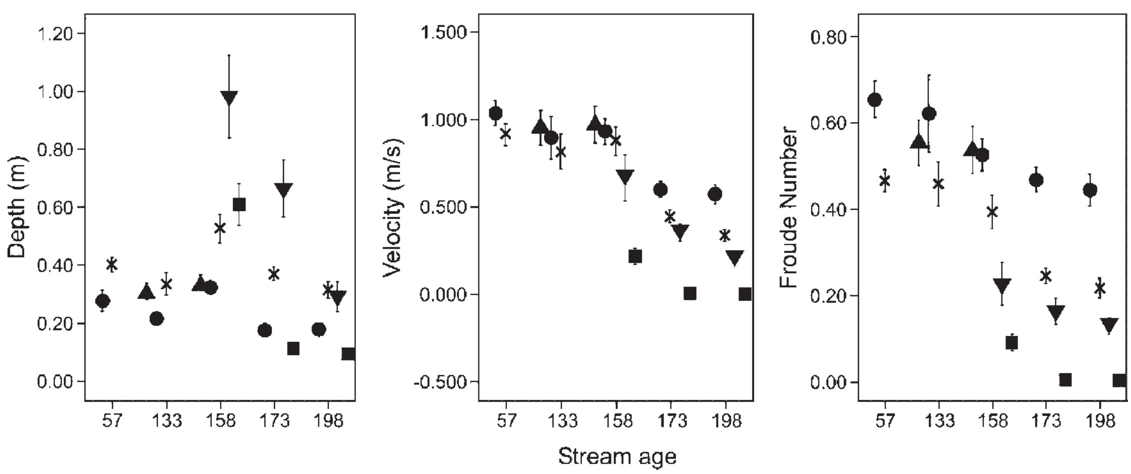

Figure 3. Average CGU depth, velocity and Froude number within CGUs across the stream chronosequence. Stream age is in years. ▲ Rapid; ● Riffle; X Run; ▼ Glide; ■ Pool. Bars represent 95% CI

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rapid	**57**	**133**	**158**	**173**	**198**
57					
133	*				
158	*	14			
173	*	*	*		
198	*	*	*	*	

riffle	**57**	**133**	**158**	**173**	**198**
57					
133	22				
158	20	18			
173	49	33	46		
198	48	33	45	9	

run	**57**	**133**	**158**	**173**	**198**
57					
133	26				
158	32	37			
173	56	48	60		
198	71	65	78	25	

glide	**57**	**133**	**158**	**173**	**198**
57					
133	*				
158	*	*			
173	*	*	69		
198	*	*	76	62	

pool	**57**	**133**	**158**	**173**	**198**
57					
133	*				
158	*	*			
173	*	*	82		
198	*	*	84	2	

Figure 4. Summary of the comparison of hydraulic signatures within CGUs across the 200 year chronosequence. Figures in bold indicate the stream age, whilst figures within the matrix signify the comparison index of the similarity between CGUs within those two streams. A low figure indicates that the hydraulic composition of CGUs within those rivers is similar, whilst a high value indicates that the hydraulic signatures are dissimilar.

The development of hydraulic complexity within older streams is likely to have important consequences for instream biota. Hydraulic complexity had been shown to be an important aspect in creating habitat diversity, yet few habitat assessments take hydraulic habitat into account (Crowder and Diplas, 2006; Shoffner and Royall, 2008). The geomorphic complexity of entire reaches has been studied to allow comparisons along the 200-year chronosequence to be assessed. Analysis of habitat availability allows assessment of habitat usage by instream biota across their range of behavioural functions (i.e. feeding vs. resting).

The changes in geomorphic composition observed across the chronosequence result in an increase in habitat diversity as stream age increases. This increased diversity benefits instream biota by allowing a greater number of species to co-exist within a stream reach, across a broad range of life stages. Smaller CGU size (and resultant increase in CGU numbers) within older streams (with the exception of NFS) also provide an increased number of ‘ecotones’, (Ward *et al*., 1999) such as pool heads and riffle tails, which many species, such as juvenile salmonids can utilize.

Differences in landscape diversity across the stream chronosequence revealed an increase in stream diversity as stream age increased, peaking at streams of an ‘intermediate’ age around 150 years, before declining slightly in the older streams surveyed. A similar trend can be observed in the number of CGUs per 100 m of mapped stream. Yarnell *et al*. (2006) found that streams with a moderate relative sediment supply displayed the highest habitat heterogeneity. Differences in landscape diversity within the streams studied in Glacier Bay may therefore be due to differences in relative sediment supply. The youngest streams potentially have a high sediment supply due to their unstable nature and general lack of riparian vegetation, resulting in increased channel erosion and elevated sediment supply. Older streams typically have lower sediment supplies due to the occurrence of established riparian

Table III. Summary of mean HSC values for each CGU type across the stream chronosequence. The mean HSC value indicates the degree of change in hydraulic diversity within CGUs across the chronosequence

CGU Type	Mean HSC value
Rapid	14
Riffle	34
Run	46
Glide	69
Pool	56

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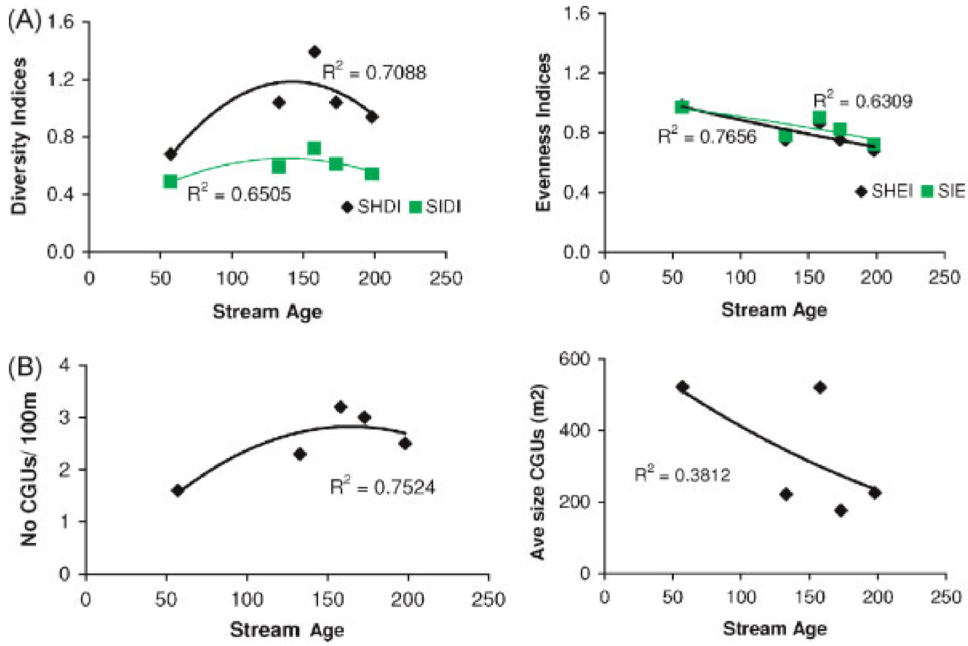

Figure 5. Changes in habitat and CGU variables within the study streams (A) Reach landscape and evenness indices within the study streams. SHDI = Shannon's Diversity Index; SIDI = Simpson's Diversity Index; SHEI = Shannon's Evenness Index; SIEI = Simpson's Evenness Index. (B) Number (per 100m) and size (m^2) of CGUs across the stream chronosequence. This figure is available in colour online at www.interscience.wiley.com/journal/rra

vegetation and increased channel stability. However, streams of intermediate age remain relatively unstable, with developing riparian vegetation and moderate sediment supplies, which may be utilized to create geomorphic complexity and diversity.

Ongoing investigations are currently underway to determine how biological (e.g. coarse woody debris; CWD) and physical (channel stability) features influence stream development. Initial results show that differences in CWD structure and orientation across the stream chronosequence may create the changes in hydraulic diversity seen at the microscale. Knowledge of how geomorphological and hydraulic diversity develop will assist in developing restoration techniques, which maintain habitat diversity and complexity.

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