Harlequin duck (*Histrionicus histrionicus*) density on rivers in southwestern British Columbia in relation to food availability and indirect interactions with fish

by

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ABSTRACT

I investigated factors affecting harlequin duck (Histrionicus histrionicus) prey availability on breeding streams in southwestern British Columbia. I measured flow variability, prey availability, harlequin duck breeding density, and quantified fish communities on eight rivers in 2003 and 2004. I found that prey availability was strongly and negatively associated with flow variability. Harlequin duck density was positively associated with prey availability in both years. I found a negative relationship between harlequin ducks breeding density and an index of fish abundance, supporting the existence of a Behaviourally Mediated Indirect Interaction between harlequin ducks and fish, in which prey availability is reduced in fish-bearing streams because insects alter behaviour to reduce vulnerability to fish. This supports the hypothesis that fish introductions into previously fishless rivers has negatively affected prey availability on breeding streams. Such widespread introductions may be contributing to the current low productivity measured in the western North American harlequin duck population.

KEYWORDS: Food availability, indirect interactions, Harlequin Duck, breeding habitat, fish introduction.

DEDICATION

For my family,

Mom for being my pillar of strength,

Dad for your unshakeable pride,

Aunty Norah for your relentless confidence,

Aunty Weetsie for your quiet dedication,

Grama for your wisdom,

Jana for being my lifelong friend,

Leslie for your humour and acceptance,

Andy for your encouragement,

and to my Burrito and Drewster for reminding

me what is important in life.

Mine is a life truly blessed, kukwstsétseme

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I was lucky enough to arrive at SFU in September 2003 when the Centre for Wildlife Ecology was celebrating its 10th anniversary. This is a fantastic organization that is made possible by all the extraordinary people that work there. Thank you to Connie

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Finally the biggest thanks of all goes to my friends and family. It is only because of you that I am here today. You have taught me to sit back, take a deep breath and just breathe. This is the end of many chapters of my life but as these doors close another is opening and now I am ready.

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CHAPTER 1:
GENERAL INTRODUCTION

Anthropogenic disturbances to freshwater systems have proliferated over the past century due to increasing human populations and demands. Many freshwater species are being confronted by introduced species, impoundment, water quality deterioration, and overexploitation (Cambray 2003). One of the important concerns shared by the fields of ecology and conservation biology is to understand, predict, and minimize human impacts on aquatic ecosystems, including the effects of introduced species on natural communities (Flecker and Townsend 1994; Elton 1958; Drake et al. 1989; Moyle and Light 1996). Fish invasions in freshwater systems have far-reaching results and consequences that are difficult to predict and document (Moyle and Light 1996). For example, the introduction of the Nile Perch (*Lates niloticus*) into Lake Victoria in the 1950's obliterated many endemic fish species of the family Cichlidae (Kaufman 1992). In this thesis I investigate whether the introduction of fish into previously fishless streams and rivers may be having a negative effect on food availability on harlequin duck (*Histrionicus histrionicus*) breeding streams.

The harlequin duck has a holarctic distribution with two populations in North America. The eastern population was reduced from an estimated 5-10,000 birds to less than 1,500 birds by 1990, and was consequently listed as an endangered species at that time by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). This was downgraded to a Species of Special Concern in 2001 due to population stability and a marginal increase in numbers (COSEWIC 2006). The western population is listed as a Species of Special Concern, and Sensitive Species throughout the northwestern United States, and is on the Yellow List in both British Columbia and Alberta (Robertson and Goudie 1999). Winter age ratios of the population wintering in the Strait of Georgia have detected low recruitment in this population (Rodway et al. 2003; Smith et al. 1999; Smith et al. 2001). The discrepancy between juvenile/adult ratios on breeding grounds versus the wintering grounds may be the result of an increase in non-breeding females and reduced productivity. This would render the population incapable of accounting for adult mortality, inevitably leading to population decline which may go unnoticed due to strong site fidelity on the breeding and wintering grounds (Smith et al. 1999).

In breeding streams, harlequin ducks feed opportunistically on a variety of benthic aquatic insects (Robertson and Goudie 1999). They have been known to feed almost exclusively on one group of aquatic insects (e.g. simuliids) (Rodway et al. 1998; Wright et al. 2000), while other studies document a diet composed of many different aquatic insect families (Robert and Cloutier 2001; Wallen 1987). Harlequins shifted from a diet composed of mainly trichopterans in June, to one primarily made up of simuliids in August in accordance with the local aquatic insect community (Rodway et al. 1998).

Aquatic insect communities are influenced by both abiotic and biotic factors. Abiotic factors that influence aquatic insect community composition and abundance include current, temperature, substrate composition, flood history, water source, and geomorphology (Holomuzki and Messier 1993). In large part due to flow variability, disturbance to the aquatic insect community plays a substantial role in community structure (Allan 1995; Giller and Malmqvist 1998; Hildrew and Giller 1994). Predation, competition, disease and parasitism are biotic factors that also may influence the aquatic insect community (Allan 1995; Hynes 1970). The relationship between abiotic and biotic factors results in the variability of the distribution and abundance of aquatic insects seen in differing stream reaches.

Predators like harlequin ducks are attracted to areas with high levels of food availability (Stenberg and Persson 2005). Measures of 'availability' must take into account not only the quantity of prey items, but also their vulnerability to predators (De Crespin De Billy et al. 2002). Food availability on harlequin duck breeding streams is the result of a complex series of abiotic and biotic factors that may affect both the density of aquatic insects and their susceptibility to predation (Figure 1.1). Food availability is an important aspect of ecology because it influences life history traits, population sizes, and community structure of both predators and their prey. There is extensive evidence that food limitation may affect both current and future avian reproductive success (Martin 1987; Nilsson and Svensson 1993; Robbins 1993). In birds (particularly waterfowl) adequate food availability prior to egg-laying is thought to be essential to breeding success due to the energetic demands of egg synthesis (Lack 1954; 1956; Perrins 1970). In K-selected bird species, such as harlequin ducks, low food availability in spring could result in the deferral of breeding because these long lived birds maximize lifetime reproductive output by reducing survival risks of parents (Goudie and Jones 2005; Lack 1968).

Predators may interact with one another indirectly through a shared prey base by means of a reduction in prey availability (Werner and Peacor 2003; Preisser et al. 2005). Traditionally interactions between species have been studied as a series of density-dependent relationships (Werner and Peacor 2003). Density Mediated Indirect Interactions (DMII) between predators result from an initiating species causing a density reduction in their prey (transmitter), which results in reduced foraging efficiency of another predator (receiver) using this resource (Dill et al. 2003; Werner and Peacor 2003). The importance of trait plasticity has initiated further investigation into indirect interactions, and their resulting Trait Mediated Indirect Interactions (TMII). A TMII results when the presence of a species (initiator) causes a phenotypic change in its prey (transmitter) which results in a per capita effect on another species (receiver) (Werner and Peacor 2003; Dill et al. 2003). Interactions due to phenotypic plasticity are widespread, a major component of predator-prey interactions, and may be stronger than impacts from direct consumption (Bolnick and Preisser 2005; Preisser et al. 2005). The contributions of both DMII and TMII should be considered when studying interactions between species (Werner and Peacor 2003; Bolker et al. 2003).

Competitive relationships have been documented between fish and birds. Goldeneyes (*Bucephala clangula*) prefer lakes without their competitive fish counterparts (Eriksson 1979; Eadie and Keast 1982) and Red-necked Grebes (*Podiceps grisegena*) utilise areas of lakes with low fish abundance where food biomass is consequently higher (Wagner and Hansson 1998). Competition between harlequin ducks and fish is plausible because they consume the same prey and overlap in their spatial and temporal distribution on streams. The hypothesized relationship between harlequin ducks and fish would be indirect, and could be density-mediated (fish reduce the density of prey by consuming them), and/or trait-mediated (predation risk posed by fish reduces the availability of insects for harlequin duck foraging).

The introduction of fish has been identified as a major threat to biodiversity, and conservation of native species (Cambray 2003; Horne and Goldman 1994). The effects of invasive fish species are exacerbated if they competitively exploit resources already being used by other species (Kohler and McPeek 1989; Townsend 1996). The introduction of fish into historically fishless harlequin duck breeding streams could result in a reduction in aquatic insect availability as a consequence of a density and/or trait mediated indirect interaction. The resulting degradation of harlequin duck breeding habitat might be a factor contributing to low productivity and recruitment documented in wintering populations.

1.1 Thesis Purpose and Outline

The purpose of this thesis was to investigate the relations between harlequin ducks and their food supply on breeding streams, with particular reference to exploring interactions among harlequin ducks, fish and their shared aquatic invertebrate prey. The thesis also provides information regarding the importance of abiotic and biotic factors on food availability. The Chapter 2 was written in order to be submitted as a manuscript for publication and therefore there was some repetition in the text.

In Chapter Two, I examine the importance of abiotic factors on aquatic insect availability, and how harlequin ducks distribute themselves with respect to food availability. In particular I investigate the importance of flow variability on aquatic insect availability. It is important to determine the significance of this factor in order to determine the impact of hydroelectric damming and flow regulation on harlequin duck breeding habitat.

Chapter Three investigates possible indirect interactions between harlequin ducks and fish. The widespread introduction of fish into historically fishless reaches may be reducing food availability to harlequin ducks, resulting in a broad scale decline in breeding habitat quality. This relationship may be the result of fish reducing the density and/or altering the behaviour of the aquatic insects.

Chapter Four draws conclusions regarding this research and how it may be used to inform future conservation decisions concerning harlequin duck breeding habitats. I identify specific concerns to harlequin duck breeding habitat in our study area, and propose areas for future research.

Two appendices have been added to this thesis. The first summarizes the data collected and methodology employed to determine the fish rating system for the stream reaches studied. The second documents a predator odour experiment conducted during the course of this study. I examined the behaviour of aquatic insects in the Order Ephemeroptera, family Ephemerellidae from a fishless reach to determine if they reduce their daytime activity and visibility under rainbow trout (*Oncorhynchus mykiss*) and harlequin duck predation risk.

1.2 Study Area

Data were collected from eight stream reaches in the Southern Coastal Mountains surrounding the communities of Lillooet and Pemberton BC, Canada (Figure 1.2).

1.2.1 Birkenhead River

The Birkenhead River flows southeast for 54 km from Sun God Mountain in the Coast Range to Lillooet Lake, draining an area of 596 km^2 (Cook 1983). This river is not regulated and experiences level fluctuations with local precipitation and weather conditions.

1.2.2 Bridge River

The Bridge River reach studied during this project flows from Carpenter Lake and the Terzaghi Dam to a point on the Fraser River approximately 5 km north of Lillooet, BC. The Terzaghi dam was completed in 1960 and facilitates the diversion of water from the Bridge River system to the Seton Lake power generating systems. The 4 km reach directly below the Terzaghi dam was dry until August, 2000 when a continuous water release of 3 m^3/s was initiated (Walton and Heinrich 2004). The reach upstream of the Yalakom River confluence is therefore highly regulated and experiences extremely low levels of flow variability.

1.2.3 Cayoosh Creek

The Cayoosh Creek reach extends from Duffey Lake to its confluence with the Lower Seton River about 4 km upstream from their confluence with the Fraser River. The Walden North Project is a privately owned dam and powerhouse owned by Aquila Networks Canada. This dam was built in the 1970's and is located about 2.6 km upstream from the confluence of Cayoosh Creek with the Lower Seton River (Uunila and Guy 2002). This river is surrounded by steep mountainous terrain and despite the presence of the dam, and Duffey Lake, river levels are highly influenced by local precipitation and run-off.

1.2.4 Cheakamus River

The Cheakamus River originates from Cheakamus Lake, which eventually empties into the Squamish River near Brackendale, BC. In 1957, the creation of the Daisy Lake dam caused alteration to the natural flow regime of the Cheakamus River. The lower reach located downstream of the Daisy Lake Dam is moderately regulated, but may experience flooding due to spill events from the dam. The upper reach is moderately buffered due to the presence of Cheakamus Lake, but the surrounding steep valleys augments variability from local precipitation and run-off.

1.2.5 Rutherford Creek

Rutherford Creek originates in the Pemberton Icefield area, and empties into the Green River next to Highway 99. There has been a recent hydroelectric development on this river and a dam with water diversion is now located about 10 km upstream of its confluence. This development provides some flow regulation to the reach below its construction, however the majority of this creek fluctuates with local precipitation and weather conditions.

1.2.6 Ryan River

The Ryan River originates in the Pemberton Icefields, and empties into the Lillooet River about 10 km North of Pemberton, BC. This river is not regulated and experiences fluctuations with local precipitation and weather conditions, however this river has been prospected as a site for hydroelectric generation through the formation of an Independent Power Project (IPP).

1.2.7 Seton River

The Lower Seton River receives its water from Seton Lake and empties into the Fraser River south of Lillooet, BC. Since 1956, a portion of Seton Lake has been diverted by BC Hydro's Seton River Project to a powerhouse near the Fraser River via a power canal that runs along the south side of the Lower Seton River. The Seton Dam at the outlet of Seton Lake regulates the flow of water into both the Seton Canal and the Lower Seton River, essentially buffering water level fluctuations (Uunila and Guy 2002).

1.2.8 Yalakom River

The Yalakom River begins at Yalakom Mountain and runs approximately 56 km down to its confluence with the Bridge River 13 km below the Terzaghi Dam at the Horseshoe Bend. The Yalakom River is not regulated, and river levels fluctuate regularly with precipitation. Peak discharges are usually in June/July as a result of snow melt, and the flows progressively decline as snow packs diminish (Griffith 1995).

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Figure 1.1 Aquatic insect availability as a function of abiotic and biotic factors.

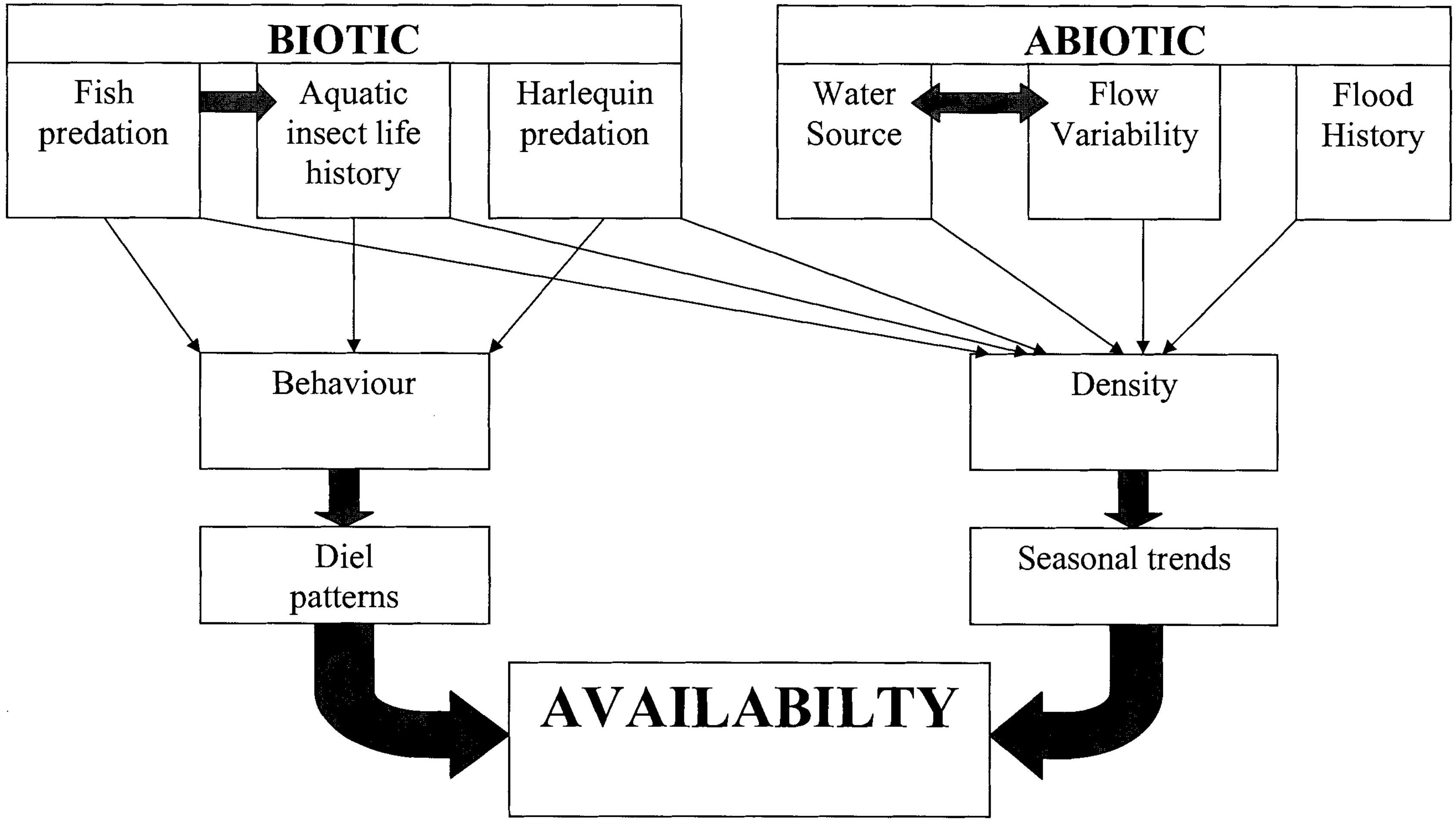
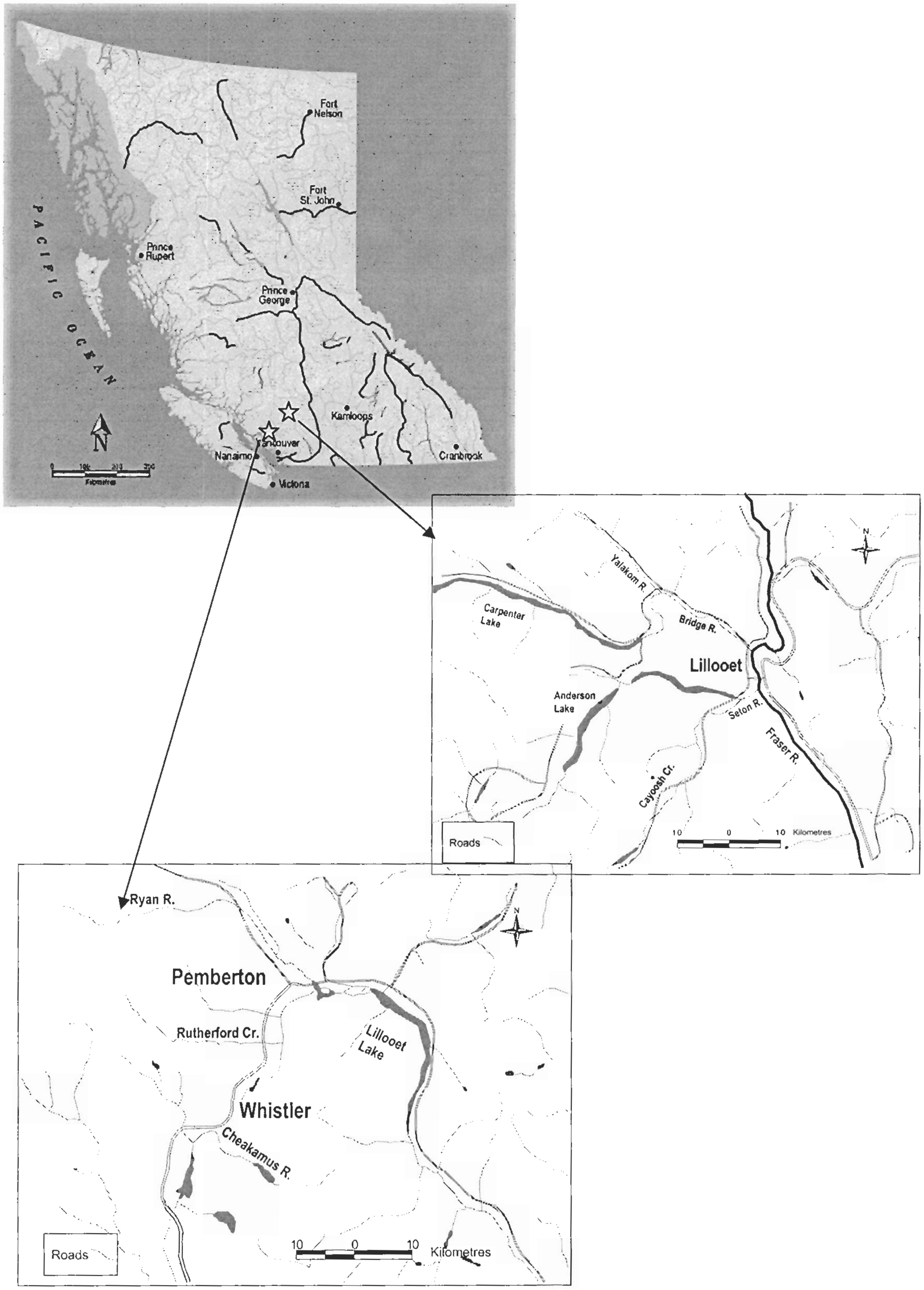


Figure 1.2 Map of British Columbia, Canada with inset maps of study rivers.



CHAPTER 2:
VARIATION IN AQUATIC INSECT COMMUNITIES AND RELATIONSHIPS WITH HARLEQUIN DUCK DISTRIBUTION.

2.1 Abstract

I measured the availability of stream benthic aquatic insect prey for breeding harlequin ducks (*Histrionicus histrionicus*) in eight rivers in the Southern Coast Mountain Range in British Columbia, Canada, in 2003 and 2004. Prey availability was measured using the 'five-rock' method. We found that flow variability had a strong effect on prey, with decreased flow variability resulting in higher availability of aquatic insects. Densities of harlequin ducks on the rivers were significantly and positively related to prey availability. Overall insect availability was greater in 2004, and data simultaneously collected in a companion project documented higher breeding propensity and earlier nest initiation dates in 2004 by harlequin ducks, both traits known to be affected by food limitation. These findings suggest that annual and environmentally-driven variation in prey availability can have important effects on harlequin duck reproductive performance.

2.2 Introduction

The heterogeneous distribution of food resources leads to the variable distribution of consumers as they attempt to maximize their foraging intake, ultimately congregating in or spending more time in areas with higher resource availability (Stenberg and Persson 2005). Food supply is of utmost importance to consumers in order to obtain the energy necessary for self maintenance and reproduction. These considerations affect organisms as different as small echinoderms and large vertebrates. The sea urchins *Lytechinus variegates* (Lamarck) and *Strongylocentrotus droebachiensis* (Mueller) actively aggregate and distribute themselves vertically in response to quality and quantity of food present in a specific area (Burdett-Coutts and Metaxas 2004). Humpback whale (*Megaptera novaeangliae*) distributions in New England waters are highly correlated with the distribution and abundance of their prey (Payne et al. 1990). The richness of breeding waterfowl species in boreal lakes in Finland and Sweden were best explained by the number of prey taxa encountered in the lake (Elmberg et al. 1994).

The harlequin duck (*Histrionicus histrionicus*) occupies an ecological niche virtually unique among birds in the northern hemisphere. Harlequin ducks spend the majority of their year on marine environments feeding on a variety of invertebrates in the intertidal zone including crabs, amphipods, and gastropods. In April individuals migrate inland, where they breed on clear, fast- flowing, turbulent rivers, diving to the bottom to pick aquatic insects from the substrate surface, even flipping over smaller cobbles with their bills (McCutchen 2001).

Two populations are recognized in North America. The eastern population winters along the coast of Greenland, and the central east coast of North America surrounding the Maritimes, and breeds inland on suitable rivers in Labrador, Newfoundland, Quebec, and the Maritimes. The western population winters along the Pacific coast from Alaska through Washington, moving inland to breed on streams throughout the western cordillera of Alaska, Yukon, Northwest Territories, British Columbia, Alberta, and the northwestern United States (Robertson and Goudie 1999).

Males provide no parental care, typically leaving the breeding grounds after mating early in June, followed by unsuccessful females. Successful females and their broods may not leave until September (Hunt 1997).

Harlequin ducks feed on a wide variety of aquatic insects from many different families (Robert and Cloutier 2001). In eastern North America trichopterans were the most commonly occurring food item (83.3%), followed by ephemeropterans (64.3%), dipterans (61.9%), and plecopterans (33.3%) (Robert and Cloutier 2001). Harlequins in a Montana stream consumed the full range of plecopterans, ephemeropterans, and trichopterans observed in stream samples (Wallen 1987) while in Oregon they fed heavily on the caddisfly *Dicosmoecus gilvipes* (12 of 16 fecal samples were 100% *D.gilvipes*) (Wright et al. 2000). In Iceland they fed on a diet consisting mainly of simuliids and chironomids which comprised up to 97% of the calculated aquatic insect standing crop (Bengston and Ulfstrand 1971).

Kuchel (1977) hypothesized that variation in size and distribution of consumed prey was explained by non-selective feeding, in which ducks scraped the benthic surfaces in order to dislodge any available food items. Studies do however indicate that harlequins exhibit selection at a higher level, as demonstrated by dietary shifts across a single breeding season. In Prince William Sound, Alaska, harlequin females subsisted on a diet of marine invertebrates until salmon began spawning in local streams, whereupon they moved to these reaches to feed on the roe (Crowley 1997). Rodway (1998) found in eastern North America that harlequin fecal samples in July were devoid of simuliids, but by August larvae of these insects dominated. Harlequins in Montana shifted from a diet of primarily trichopterans in May, to one of chironomids in June and July (Wallen 1987).

The structure of the aquatic insect community on which harlequin ducks feed is a function of the relationship between abiotic, environmental characteristics and biotic interactions between species residing in the stream reach. Many abiotic factors, including current, temperature, substrate composition, flood history, water source, and geomorphology are known to affect the distribution and abundance of stream-dwelling aquatic insects (Allan 1995; Giller and Malmqvist 1998; Holomuzki and Messier 1993). The source of water for a stream also affects the nature of the community. For example, water originating from a lake is loaded with suspended organic material, creating a highly productive stream community below lake outlets with large populations of aquatic insects that consume this material (Hynes 1970). Climate and geomorphology have important influences on local discharges and determine the rate at which precipitation from surrounding areas moves into the water channel (Minshall et al. 1985). Discharge and its associated physical influences represent the most important abiotic factor to aquatic insect communities because discharge variability determines substrate stability, particle size, and food delivery in the water column, also acting as a direct force on aquatic insects (Allan 1995; Hynes 1970).

It is widely held that the level of disturbance to the benthic community, mainly in the form of flow variation, plays a large role in community structure (Giller and Malmqvist 1998; Allan 1995; Hildrew and Giller 1994). The "harsh-benign" hypothesis suggests that local environments range from harsh to benign in their degree of environmental disturbance, and that the importance of abiotic and biotic factors vary across this continuum (Peckarsky 1983). For example, physical disturbances in a Montana stream prevented the competitive monopolization of substrate surfaces by the caddisfly *Leucotrichia pictipes* (McAuliffe 1984). Without this abiotic intervention this aggressive, territorial species dominates the substrate surface, and outcompetes other species such as *Parargyractis confusalis, Rheotanytarsus* sp., and *Eukiefferiella* sp. for space and periphyton resources (McAuliffe 1984). While the diversity and abundance of stream organisms tends to increase with increasing substrate stability (Giller and Malmqvist 1998), no single hypothesis or model can explain all the variation, and a combination of biotic and abiotic factors are influential (Allan 1995).

In addition to competition, disease, parasitism, and predation are biotic factors that affect the composition of the aquatic insect community. Allen (1951) advocated the importance of predation when he calculated that brown trout (*Salmo trutta*) could consume over 150 times the standing crop of aquatic insects. While this number has been refuted as an overestimate, studies have shown that fish are capable of reducing the density of aquatic insects (Feltmate and Williams 1989; Holomuzki and Stevenson 1992; Dahl 1998; Bechara et al. 1993; Rosenfeld 2000). Reviews of predation impact studies have concluded that predators can have a strong negative impact on their prey, and that inconclusive results of some individual studies are due to the different feeding ecology, and behaviour of both the predators and their prey (Wooster and Sih 1995; Wooster 1994; Dahl and Greenberg 1996).

The Harlequin Duck National Recovery Plan identified the destruction, alteration, and contamination of both wintering and breeding habitat as major factors affecting harlequin ducks (Montevecchi et al. 1995). The Exxon Valdez oil spill in 1989 caused over 1,300 deaths to the harlequin duck population wintering in Prince William Sound, Alaska and the effect of this contamination event is still being felt by this population

(Esler et al. 2002). Alterations on breeding streams likely to have impacts include: urbanization, deforestation, tillage, irrigation, dam construction, channel alteration, logging, mining, flood control, and the extermination of mammals such as beaver (Minshall et al. 1985). The construction of dams for hydroelectric generation and the resultant flow regulation change both the flow and temperature of the water, strongly modifying the physical habitat which affects the biology and ecology of the freshwater organisms (De Crespin De Billy et al. 2002; Horne and Goldman 1994). In British Columbia, the construction of the Terzaghi Dam in 1960 drastically altered the flow and nature of the Bridge River. The establishment of the dam and creation of the Carpenter Reservoir dewatered and obliterated a 4 km river reach directly below the dam. In 2001 this reach was revitalized following a controlled release currently under review by BC Hydro (Walton and Heinrich 2004).

The purpose of this study was to examine factors affecting the aquatic insect community, and how this affects harlequin duck distribution. My specific objectives were to determine (1) how flow variability affects aquatic insect communities on harlequin duck breeding streams and (2) how harlequin ducks distribute themselves with respect to aquatic insects. I predicted that (1) higher levels of flow variability would result in lower availabilities of aquatic insects and (2) harlequin ducks would congregate in areas with higher levels of aquatic insect availability.

2.3 Methods

2.3.1 Aquatic insect sample method

To measure prey availability I needed to measure the density of aquatic insects vulnerable to predation (Goudie and Jones 2005; De Crespin De Billy et al. 2002). The aquatic insect community available to harlequin ducks on the breeding stream was not adequately quantified using conventional sampling methods. Both Surber and Hess methods were limited in their applicability in these lotic environments due to the coarseness of the substrate (Hunt 1997). Traditionally, kick sampling has been employed to measure the abundance of aquatic insects available to harlequin ducks, but not only was this method destructive to the stream benthos, sorting and processing the samples was very time consuming, and both the substrate surface and interstitial spaces are sampled unpredictably (Vennesland 1996).

Vennesland (1996) and McCutchen (2001) developed the 'five-rock' sample method to better describe the aquatic insects available to harlequin ducks in the Maligne River system. This method revealed patterns of aquatic insects similar to kick sampling (McCutchen 2001; Vennesland 1996) but was superior in its ability to sample aquatic insects available to harlequin ducks on the substrate surface, and allowed a more representative estimate of density by considering the surface area sampled. To collect a five-rock sample, five approximately hand-sized cobbles were sequentially and randomly selected from the river substrate at each sample site. Successive samples were collected moving upstream to minimize disturbance to insects. An aquatic D-net was positioned downstream of each rock as it was as picked up, and the aquatic insects on all surfaces of the rock were brushed off the rock and into the net. Each rock's volume was estimated

(+/- 25 mL) by water displacement in a graduated cylinder. Insects from each sample were placed in a labelled vial and stored in a 90% ethanol solution. Each sample was later processed: the insects were counted, and separated into family groups with similarly-sized individuals. Each group was dried for 24 h at 30°C and weighed to the nearest microgram. Based on the volume of each rock in the five-rock sample, the surface area was calculated using the formula:

$$\text{surface area (cm}^2\text{)} = 13.875 * \log \text{volume (cm}^3\text{)}^{3.603}$$

from McCutchen (2001). The availability of prey was a density value (g/m^2), expressed as the total mass of (dry) insects divided by the total surface area

2.3.2 Aquatic insect sample regime

Five-rock samples were collected as part of habitat sampling conducted on seven 5 km reaches during the 2003 and 2004 breeding seasons, and was intended to provide descriptions of the stream habitat. Sample stations were established at 500 m intervals with a randomly selected starting site, as well as wherever harlequin ducks were encountered. Five-rock samples were taken at alternating habitat sample stations, and at all harlequin duck stations established. At each sampling location three five-rock samples were collected (one at the station marker, one 10 m downstream, and one 10 m upstream).

In addition, intensive sampling took place in July 2003, on three reaches. During these sample sessions consecutive five-rock samples were taken at 10 m intervals along 150 m reaches of the Yalakom River, Seton River, and Cayoosh Creek. During the 2004 breeding season intensive samples were collected on eight reaches located on four rivers surrounding Lillooet, BC (Bridge River, Yalakom River, Cayoosh Creek, and Seton River), and four others in the Pemberton to Whistler area (Birkenhead River, Ryan River, Rutherford Creek, and Cheakamus River). On each river 200 m was delineated with 20 stations at 10 m intervals. During each sample session five-rock samples were collected at either odd or even numbered stations where possible. Samples at specific stations were not taken when the spring freshet disallowed access to the stream substrate due to water depth and velocity.

Together these procedures yielded a total of 271 five-rock samples on seven rivers in 2003, and 467 five-rock samples on eight rivers in 2004. These five-rock samples were used to calculate an average availability measurement on each river. An average of 39 (11 SD) samples in 2003, and 58 (19 SD) samples in 2004 per river were used to calculate the availability of aquatic insects on each river. These estimates were assumed to be representative of each river.

2.3.3 Harlequin duck survey

Harlequin duck surveys were conducted along seven 5 km reaches in 2003 and seven 5 km reaches in 2004. Harlequin surveys were conducted during the pre-breeding period (April 30 - May 23 in 2003, May 4 – 26 in 2004). Surveys were conducted following the standard harlequin duck survey protocol outlined in the Provincial Resource Inventory Committee Standards (BC Ministry of Environment 1998). Each survey team consisted of at least two observers, who hiked upstream adjacent to the stream channel and continuously scanned for birds with the aid of binoculars. Where thick riparian vegetation prohibited continuous viewing of the stream, observers attempted to access the stream every 50 to 100 m and scanned up and down stream. Each duck observation was recorded and coded according to the stream, year, and number of observations on each river reach. Harlequin duck presence, location, and abundance also were observed and recorded by J. Bond during her radio-telemetry work with breeding female harlequin ducks and these observations were used to supplement and confirm densities from the habitat surveys. Harlequin duck densities were calculated as the number of ducks divided by the length of the surveyed reach. In 2004 the harlequin duck density recorded on Rutherford Creek during the habitat survey was an underestimate due to a large storm at the time of the survey. Only males were observed during this survey which lead me to believe females were forced to take cover, and were on nests at the time of the survey. I therefore adjusted this density to include the mates of each male surveyed.

2.3.4 River levels & flow variability

Daily mean river level data were obtained from the Water Survey of Canada for the Yalakom River, Cayoosh Creek, Seton River, and Cheakamus River for both 2003 and 2004. Daily mean river level data was obtained from BC Hydro from stream gauges located in the Lower Bridge River and from Summit Power from stream gauges located in the Ryan River. Daily mean river level data for Rutherford Creek were obtained from Cloudworks Energy for 2000 and 2001 and were not available for 2003 and 2004 because the stream gauge was damaged in 2002 during construction of the Independent Power Project. River level variability was calculated as the variance of daily river levels from April 1st to July 1st , which encompassed the study period.

2.3.5 Statistics

All analyses were run in JMP academic version 4.0.4. The aquatic insect availability data were plotted and examined for outliers. The Bridge River was deemed an outlier and omitted from all analyses. This point had an exceptionally high availability for 2004, exceeding by two-fold the next highest observation, and falling more than five standard deviations from the mean. I presume that the extraordinarily high insect density is due to re-establishment of the river reach below the Terzaghi Dam from Carpenter Reservoir following the initiation of a permanent flow release in August, 2000. More birds (including harlequin ducks) were seen in 2004 than in earlier years on this reach, and bird use has been increasing in each year following initial flow release (Walton and Heinrich 2004).

The relationship between flow variability and aquatic insect availability was examined using an ANCOVA testing the effects of flow variability, year, and their interaction on aquatic insect availability. Availability among rivers was tested using a one-way ANOVA in each year of the study to determine if there was a difference among river reaches. Availability between years on each river was tested using a t-test. The relationship between harlequin duck density and availability was analysed using an ANCOVA testing the importance of year, availability and their interaction term. Model selection in the ANCOVA was performed using backward selection, removing factors with $p > 0.10$.

2.4 Results

Flow variability differed greatly between rivers (Figure 2.1). The Bridge River below the Terzaghi Dam was least variable, while Cayoosh Creek showed the greatest variability. The differences result from the nature of the river's origin and surrounding geomorphology. The Bridge River was fed exclusively by water released from the dam, which provided a steady flow regardless of weather. In contrast, Cayoosh Creek drained a large lake with no dam, and was fed by many tributaries along its course through a steep-sided valley, in which rainfall quickly swelled the creek. Over all the rivers, variability was greater in 2003 than in 2004, and rivers retained their ranking relative to one another. As one would expect, the absolute magnitude of the difference between years was greatest in the most variable rivers.

As predicted by the harsh-benign hypothesis, there was a negative relationship between aquatic insect availability and flow variability (Figure 2.2). The relation held not only when comparing rivers, but also when comparing years, as in all rivers the decrease in flow variability in 2004 was accompanied by an increase in aquatic insect availability. Both factors (flow variability, $p = 0.0229$, $F = 9.23$; year, $p = 0.0541$, $F = 5.71$) as well as the interaction term (year*flow variability, $p = 0.0668$, $F = 5.00$) were important factors and the model had an overall r^2 of 0.87.

Aquatic insect availability also varied strongly and significantly between rivers ($p<0.001$ in both years; Figure 2.3), varying approximately 4-fold in 2003 and 5-fold in 2004. Availability was overall greater in 2004 in all reaches measured, with significant increases on the Bridge River, Cayoosh Creek, Cheakamus River, Seton and Yalakom Rivers (all $p<0.0001$) (Figure 2.4). Availability in 2003 and 2004 were positively related, so that the relative food availability across rivers was similar over the two years of study (2003 availability = 0.05 + 0.21 * 2004 availability, $r^2 = 0.44$).

Also there was an overall positive relationship between aquatic insect availability and harlequin duck density (Figure 2.5). The model of harlequin duck density indicated that availability ($p = 0.0155$, $F = 8.48$), and year ($p = 0.0542$, $F = 4.75$) were both explained significant explanatory variation in harlequin duck density ($r^2=0.46$). The linear relationships between harlequin duck density and aquatic insects had a positive slope with a significantly elevated relationship in 2003, meaning that there were more harlequin ducks per insect in 2003 (2003: $y = 9.02 (x) + 0.72$, 2004: $y = 9.02 (x) + 0.06$).

2.5 Discussion

My study supports the hypothesis that flow variability is important to the aquatic insect community (Giller and Malmqvist 1998; Allan 1995; Hildrew and Giller 1994). Aquatic insect availability was higher in both rivers and years with lower levels of flow variability, which is consistent with the harsh-benign hypothesis (Giller and Malmqvist 1998). Disturbance from spring freshets, floods, and natural flow fluctuations play important roles in maintaining the physical nature of the substrate by controlling particle size, and stability (Allan 1995; Hynes 1970). Reduction of flow variability may lead to the stability and deposition of smaller particles in the substrate, ultimately altering its overall physical characteristics, and aquatic insect community (Horne and Goldman 1994).

Harlequin ducks distributed themselves positively in relation to food availability. In Jasper, Alberta, Canada harlequin duck densities also corresponded to aquatic insect densities over four years and across three sections of the Maligne River (Hunt 1997; McCutchen 2001). Food availability is a principle factor limiting avian reproductive success by influencing many different reproductive characteristics (Daan et al. 1988;

Martin 1987; Boutin 1990). Laying date, clutch size and reproductive success was advanced as a result of more favourable food years, territories or habitats for over thirty different bird species (Martin 1987). Lack (1954; 1966) declared that food abundance prior to egg-laying was essential for successful breeding and Perrins (1970) hypothesized that the timing of reproduction is in fact constrained by the energetic demands of egg synthesis in the season when food is least available, preventing females from breeding at the optimal time for hatchling survival.

The effects of food limitation on reproduction and population dynamics may be particularly important for waterfowl because of the high energetic demands on breeding females. The daily energetic requirements for egg production alone are over twice the Basal Metabolic Rate for waterfowl in comparison to 13-41% in passerines, due to the need to create energy rich eggs and precocial young (Robbins 1993; Monaghan and Nager 1997). Breeding waterfowl studies have found that food limitation may cause delayed breeding, reduced clutch and egg size, chick development, and fledging success resulting in overall decreased reproductive success (Rohwer 1992; Toft et al. 1984). Gardarsson and Einarsson (1994) observed a significant correlation between food abundance and production in the tufted duck (*Aythya fuligula*), common scoter (*Melanitta nigra*), eurasian wigeon (*Anas penelope*), greater scaup (*Aythya marila*), and harlequin ducks on Lake Myvatn, Iceland and found that the reproductive performance of these ducks was related to changes in spring populations.

My research confirms earlier work suggesting that the aquatic insect food resources on breeding grounds are important for breeding harlequin duck females. For example, Hunt (1997) found that only those female harlequin ducks that gained considerable body mass in the pre-breeding period attempted to breed (Hunt 1997). Isotopic evidence has shown that harlequin ducks mainly utilise food available on the breeding grounds for egg formation (Bond 2005). My data indicate higher food availability in 2004 to breeding female harlequins and this increase is paralleled with higher levels of breeding propensity and success in 2004 over the previous year. Breeding propensity, which is the proportion of reproductively capable females that initiate egg production, was higher in 2004 (94.7%, 95% CI = 10.8%) than in 2003 (85.7%, 95% CI = 20.2%) (Bond 2005). Similarly, earlier nest initiation dates were earlier in 2004 (138, +/-5, 95% CI, day of year) than 2003 (148, +/-6, 95% CI, day of year). Both these measures fit with the premise that higher food availability in 2004 allowed for improved breeding success.

My research supports the conservation of high quality breeding habitat for breeding harlequin ducks taking into consideration the aquatic insect community. Harlequin duck use of 'club' sites, which are known areas of high aquatic insect productivity, and their preference for areas with higher food availability support the importance of areas with high food availability (Hunt 1997; Bengston and Ulfstrand 1971). In Chapter 4 I discuss my recommendations in terms of management and conservation implications.

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Figure 2.1 Flow variability for rivers in the study area.
Variability is the calculated variance of daily river level from April 1st to July 1st. Black bars represent 2003, white bars represent 2004. Rutherford Creek variability measures are for 2000 & 2001. Seton and Bridge River points for 2004 are not missing but near zero.

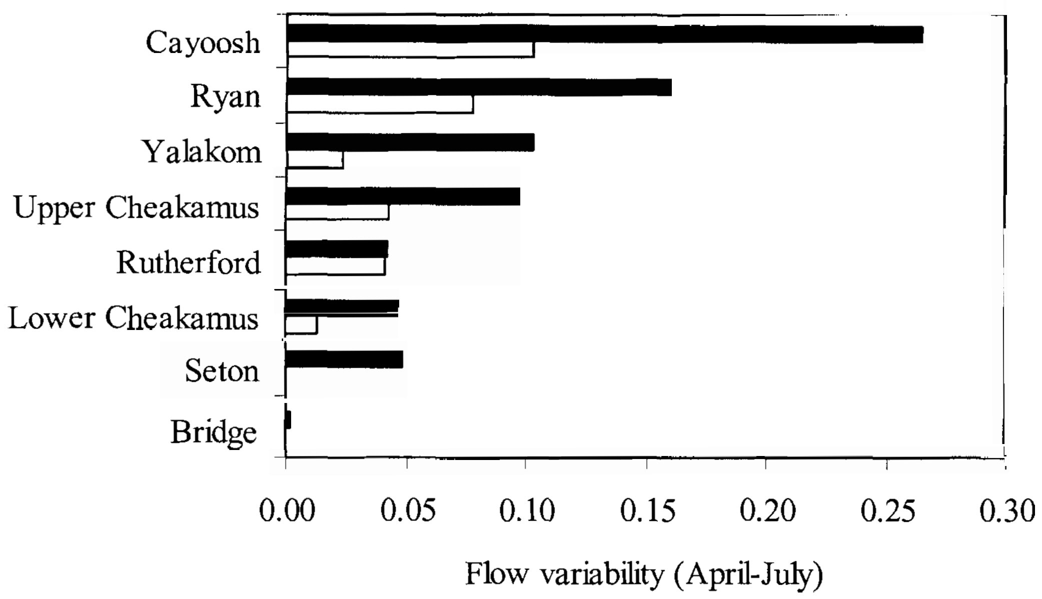


Figure 2.2 Aquatic insect availability and flow variability of study rivers. Cayoosh Creek (Δ), Cheakamus River (*), Seton River (○), Ryan River (+) and Yalakom River (□). Solid black symbols represent 2003, black and grey symbols represent 2004. Line equations, 2003: y = -0.26 (x) + 0.18, 2004: y = -0.98 (x) + 0.23 from model ($r^2 = 0.87$).

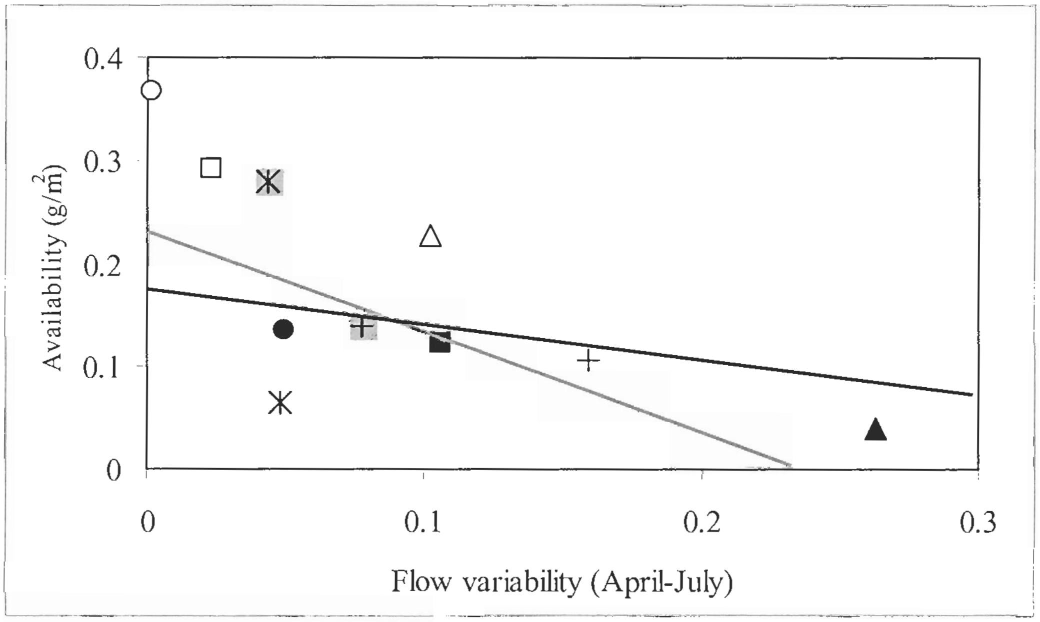


Figure 2.3 Mean aquatic insect availability measured in 2003 and 2004 (+/- 95% CI). The point closest to y axis represents Rutherford Creek, which was measured only in 2004. Dotted line represents 1:1 ratio.

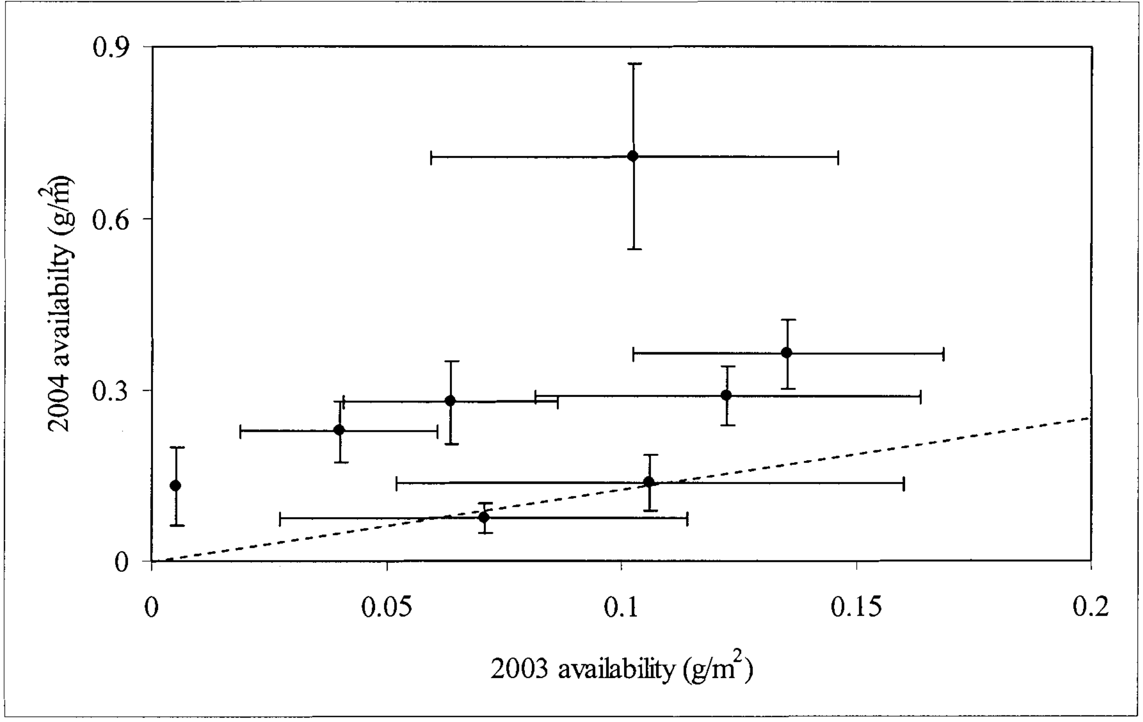


Figure 2.4 Aquatic insect densities of rivers measured in study during the 2003 and 2004.
Each point represents a river's mean aquatic insect availability (Error bars are 95% CI). Black bars are 2003, grey bars are 2004.

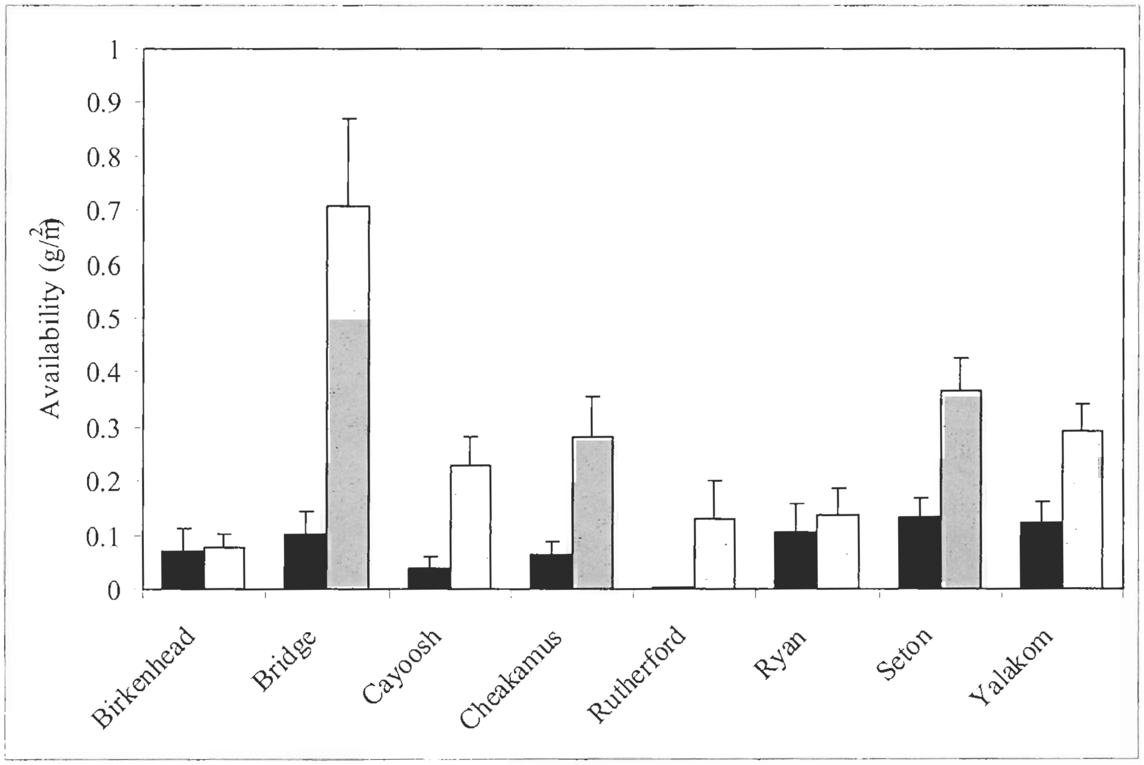
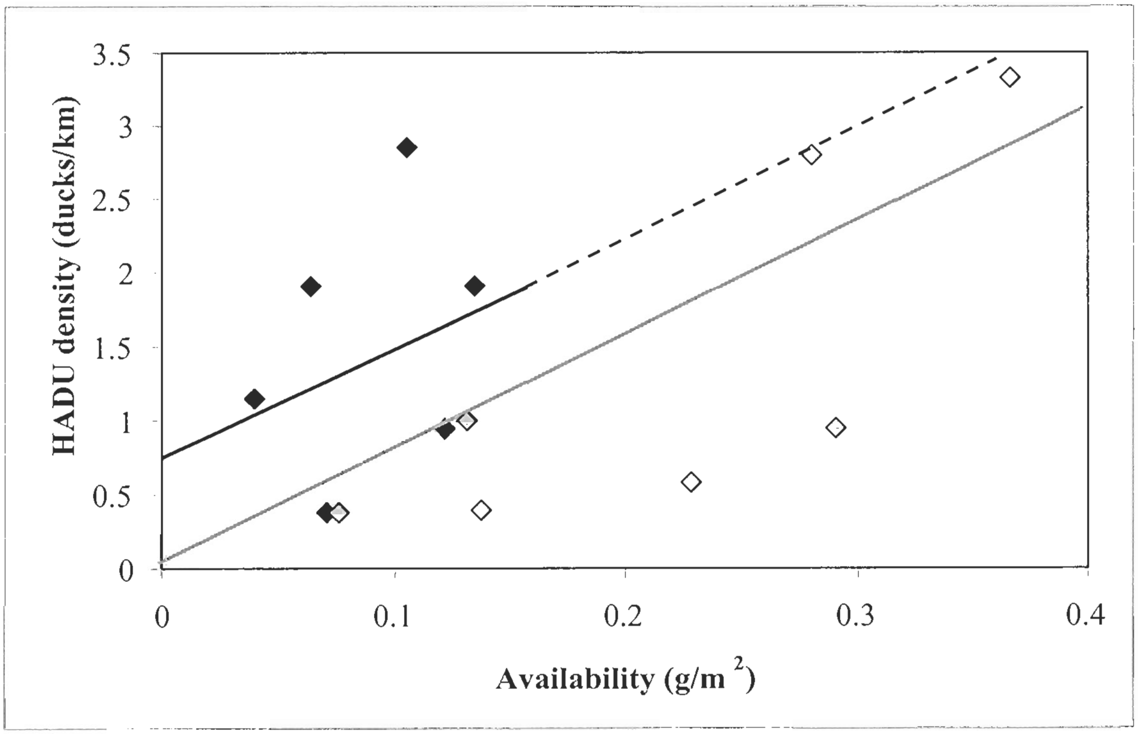


Figure 2.5 Aquatic insect and harlequin duck availabilities from study. 2003 = black, and 2004 = grey ($r^2 = 0.46$). Line equations, 2003: y = 9.02 (x) + 0.72, 2004: y = 9.02 (x) + 0.06. Dotted line for 2003 extrapolated beyond data.



CHAPTER 3:
THE INFLUENCE OF FISH ON HARLEQUIN DUCK PREY AVAILABILITY ON BREEDING STREAMS.

3.1 Abstract

I investigated interactions among harlequin ducks, fish and their shared aquatic insect prey in eight river systems in the Southern Coast Mountain Range in British Columbia, Canada. I collected data throughout these systems on the distribution, and density of harlequin ducks, fish and aquatic insects, and used path analysis to determine the relative strength and direction of interactions among these groups. I found that fish did not influence harlequin ducks through a direct reduction in the amount of available aquatic insects. The negative correlation measured between harlequin ducks and fish is postulated to be the result of a Behaviourally Mediated Indirect Interaction (BMII) between the two predators in which aquatic insects exhibit anti-predator behaviours in the presence of fish, reducing their availability to harlequin ducks. I also suggest that the widespread introduction of fish into historically fishless reaches may have resulted in a decline of harlequin duck breeding habitat quality, contributing to low productivity and recruitment measured in winter populations.

3.2 Introduction

Ecologists have the daunting task of trying to understand the complex structure and interactions between species that comprise natural communities and ecosystems. Studying and examining these interactions is important in order to make informed management decisions regarding species being affected by anthropogenic modifications to their natural habitat. Interactions between species in ecosystems are typically studied as individual components based on density-dependent phenomena (Allan 1995; Werner and Peacor 2003). I argue that in order to understand community interactions research must additionally take into account trait plasticity and its effect on interactions.

The opportunity for predation effects as a result of density dependent phenomena does exist in streams and limnologists are increasingly aware of the ability of fish to alter other components of the communities in which they reside (Minshall et al. 1985; Horne and Goldman 1994). Studies have shown that fish species are capable of reducing the density of aquatic insects (Holomuzki and Stevenson 1992; Bechara et al. 1993; Rosenfeld 2000). Rainbow trout (*Oncorhynchus mykiss*) in a southern Ontario stream reduced the density of the stonefly *Paragnetina media* by 35% as a result of direct predation, and emigration (Feltmate and Williams 1989). Bullhead (*Cottus gobio*) reduced seven different invertebrate taxa, and direct predation by bullhead was more important than avoidance behaviour in determining densities in six of the seven taxa (Dahl 1998).

Biotic effects may however be overwhelmed by stochastic abiotic disturbances and events, and the degree of predation effects experienced by a community is a function of their prey and environmental attributes (Holomuzki and Stevenson 1992; Soluk and Collins 1988a; Dahl and Greenberg 1998). More complex substrates reduce fish predation effects by providing areas for refuge (Holomuzki and Stevenson 1992; Bechara et al. 1993; Rosenfeld 2000). Aquatic insects that graze on the tops of rocks for periphyton are more prone to fish predation effects than detritivores, which reside mainly in interstitial spaces (Rosenfeld 2000). Analysis of habitat and aquatic insect characteristics also suggests that prey are most vulnerable to fish predation in reaches with unregulated flow regimes (De Crespin De Billy et al. 2002). Predation effects in experiments are reduced when immigration rates are capable of replenishing depleted populations (Cooper et al. 1990; Rosenfeld 1997; Holomuzki and Stevenson 1992). Fish predation experiments frequently use fish species that feed from both the substrate surface and from insects drifting in the water column. A meta-analysis by Dahl & Greenberg (1996) found that benthic-feeding fish had a much larger effect on prey than drift feeding, which could be due to the fact that drift-feeding fish may obtain up to 80% of their diet from terrestrial items that fall into streams (Dahl 1998).

Predators, such as fish, may affect the benthic stream insect community directly by consumption, as well as indirectly by the alteration of spatial and temporal patterns of prey activity, distribution, and life histories (Allan 1995). When making decisions about how to behave, animals must trade off danger and energy acquisition or reproduction (Kats and Dill 1998). Prey typically increase their use of refuges and decrease their movement outside of refuges when predation risk is high because activity levels strongly influence prey vulnerability (Werner and Anholt 1993; Lima and Dill 1989; Sih 1987).

Benthic aquatic insects respond to the presence of fish in two ways. They may leave the immediate vicinity of the fish by drift or benthic movements, or they may remain and alter their patterns of movement, such as exposure on stone surfaces, thus reducing their susceptibility (Soluk and Collins 1988a). Predation risk posed by fish has been shown to reduce the daytime activity levels, and increase refuge use in many different families of aquatic insects (Culp and Scrimgeour 1993; McIntosh and Peckarsky

1996; Bechara et al. 1993). Ware (1973) tested a model of prey preference for rainbow trout (*Oncorhynchus mykiss*) and found that prey motion was the most important factor in determining which individuals were predated.

In natural communities animals are usually susceptible to predation by more than one type of predator (McIntosh and Peckarsky 1999). Prey respond to the threat of mortality by altering their life history traits, morphology, development, and behaviour in order to reduce their vulnerability to predation (Feltmate et al. 1992; Lima 1998; Lima and Dill 1989). Predators that share a common prey base interact when the prey response to one predator affects the foraging efficiency of the other (Werner and Peacor 2003).

Fish share this aquatic insect prey with other predators. Predatory aquatic insects may reduce the densities of their prey and may have significantly stronger effects than vertebrate predators (Wooster and Sih 1995). Birds may cause major effects on prey assemblages in some circumstances (Allan 1995). American dippers (*Cinclus mexicanus*) have been shown to reduce the density of exposed grazing mayflies (family Heptageniidae), and the filter-feeding caddisfly *Dicosmoecus gilvipes*, though the density reduction may have resulted at least partially from predator avoidance by the insects (Harvey and Marti 1993). Harlequin ducks also share the aquatic insect prey on streams, using them to obtain the energy needed for breeding on streams (Bond 2005).

Competition has been documented between fish and waterfowl. High dietary overlap between goldeneyes (*Bucephala clangula*) and fish (*Perca* spp.) in conjunction with reciprocal densities could not rule out competition between goldeneyes and fish in lakes (Eadie and Keast 1982). Goldeneyes also increased their use of lakes after fish removal, suggesting that fish are capable of reducing the availability of food items to these birds (Eriksson 1979). Competitive interactions between red-necked grebes (*Podiceps grisegena*) and fish result in niche separation, in which grebes use relatively fish-free reed bed areas in lakes, where aquatic insect densities were 5-10 times greater (Wagner and Hansson 1998). Moreover, fish are capable of causing cascading effects in stream food webs. For example, the development of a stream community in the presence of steelhead trout (*Oncorhynchus mykiss*) and roach (*Hesperoleucas symmetricus*) suppressed aquatic insect predators, releasing algivorous aquatic insects, resulting in an overall reduction in the algal standing crop (Power 1990). The possibility exists for an indirect interaction between fish and harlequin ducks because they both utilise the aquatic insects that reside on the stream substrate.

Harlequin duck breeding streams include an assemblage of many different aquatic insect families. These aquatic insects may be grouped according to their method of food acquisition, creating four major functional feeding groups. Detritivores feed on decaying and decomposing organic material (e.g. leaves and logs), filter-feeders collect fine particulate organic matter from the water column, grazers consume periphyton or algal growth found on the tops of the substrate, and predators feed on any or all of these other groups (Allan 1995; Horne and Goldman 1994). The River Continuum Concept uses physical variable of streams including: width, depth, temperature, velocity, and flow volume in order to predict the assemblage and relative abundances of these functional feeding groups (Vannote et al. 1980). Harlequin ducks breed on low to mid-order streams that are fast flowing with a cobble/boulder substrate with sun usually permeating to the stream substrate despite surrounding riparian vegetation (Robertson and Goudie 1999). The River Continuum Concept would predict that the aquatic insect community in harlequin duck breeding streams would have relatively low levels of detritivores due to the flushing of detritus from the substrate by the strong and variable water velocity; a strong population of grazing insects utilising periphyton, a variable population of filter-feeding insects, depending on the amount of suspended organic material; and a relatively consistent population of predatory insects feeding on the other groups.

The purpose of this study was to examine the relationship between harlequin ducks and fish to determine if they were indirectly interacting as a result of their shared prey base. This specific objectives were to examine (1) how harlequin ducks distribute themselves with respect to fish; and (2) whether harlequin ducks and fish interact indirectly through a reduction in the availability of aquatic insects. I predicted that (1) the densities of harlequin ducks and fish will be negatively related , with the highest densities of harlequin ducks in fishless reaches; and (2) that an indirect interaction between harlequin ducks and fish will exist, mediated by both density and behavioural effects. I also expected to observe specific locations (e.g. lake outlets) with especially high production that sustain high densities of both harlequin ducks and fish. To investigate this I quantified the density of fish, and harlequin ducks, and availability of aquatic insects, in each of the four functional feeding groups, in a number of river reaches.

3.3 Methods

3.3.1 Aquatic insect sample method

Methods used for aquatic insect sampling were described in Chapter 2.

3.3.2 Aquatic insect sample regime

Methods for aquatic insect sample regime collection were described in Chapter 2.

3.3.3 Harlequin duck survey

Methods for harlequin duck survey were described in Chapter 2.

3.3.4 Fish data & rating

Data on the fish species present in each of the river reaches were obtained from reports by various government ministries, companies, and organizations, along with personal communication with local biologists, and personal observations. These data were used as inputs to seven different rating systems to calculate a rating for each stream reach. These rating systems use three different numeric assignments including: the use of the reach by anadromous species for spawning purposes; the relative number of returning coho salmon (*Oncorhynchus kisutch*) adults; the relative density of resident rainbow trout (*Oncorhynchus mykiss*) fry and parr; the presence of bull trout (*Salvelinus confluentus*) or dolly varden (*Salvelinus malma*); the presence of cutthroat trout (*Oncorhynchus clarki clarki*); and the presence of benthic-feeding species including: mountain whitefish (*Prosopium williamsoni*), suckers (family *Catostomidae*), sculpins (family *Cottidae*), and longnose dace (family *Cyprinidae*). The fish data for each river reach and the fish rating systems are detailed and summarized in Appendix A.

3.3.5 Statistics

Path analysis is a specialized form of multiple regression that allows consideration of more complicated schemes with more than one dependent variable and the effects of dependent variables on one another (Mitchell 2001). By assessing the importance of various interactions between variables, path analysis can predict which interactions are important in a community (Wootton 1994). Before conducting a path analysis a specific theoretical diagram must be created according to available information and research on the system, and this diagram will be used in the analysis to calculated correlation co-efficients based on observed data (Mitchell 2001). One statistical issue with path analysis is collinearity, which arises when two or more of the casual variables are correlated (Wootton 1994). Sample size is also a frequent problem faced when conducting path analysis, and the recommended sample size of at least 5-20 samples per path calls for this study to have 10-40 samples based on the two paths examined (Wootton 1994; Englund and Evander 1999). Therefore a sample size of n=16 restricts my ability to make inferences regarding the results from this analysis.

Before performing the path analysis I created a specific path diagram which allowed fish to effect harlequin duck density through two separate paths. Path #1 was from fish to harlequin ducks, and was hypothesized to possibly represent a BMII. Path #2 was from fish to available aquatic insects to harlequin ducks and tested for the presence of a DMII. I examined causal variables (fish and aquatic insect availability) to ensure that co- linearity was not an issue. Path analysis was conducted using all seven fish rating systems, aquatic insect availability and harlequin duck densities for each river reach. Path analysis calculated a total correlation between fish and harlequin ducks, which was the sum of standardized regression co-efficients for path #1 and path #2. Path #2 was the product of the standardized partial regression coefficients calculated for fish to aquatic insects and aquatic insects to harlequin ducks. The sensitivity of the path analysis to the exact fish rating system was analysed by comparing the results from the path analysis from each fish rating system.

The correlation between fish rating (system #1) and harlequin duck density was calculated in JMP version 4.0.4. The interaction between fish and ducks was examined with a linear regression. This was run including and excluding the Lower Seton River data points, because this reach is a 'club site' where ducks gather in relatively large numbers with undefended territories (Hunt 1997; Gardarsson and Einarsson 1994). These ducks could also easily move between the Lower Seton River and the Seton Power Canal located less than a kilometre away which boasts a similar highly productive aquatic insect community below Seton Lake. This area was also used as a 'club' site during the breeding season by harlequin ducks.

3.4 Results

Aquatic insect communities differed between river reaches in overall availability (Figure 3.1) and in the relative composition of functional feeding groups (Figure 3.2). The mean aquatic insect availability was 0.19 g/m^2 (range 0.04 - 0.69 g/m^2, n = 16) in these study reaches. Predaceous aquatic insects comprised 15.1% (range 2.1 - 48.6%, n = 16) and grazing aquatic insects comprised 58.6% (range 35.8 – 81.6%, n = 16) of the mean aquatic insect availability. Their combination means an average of 73.7% (range 42.0 – 95.1%, n = 16) of the aquatic insect community comprised of these mobile aquatic insects. Filter-feeding aquatic insects comprised 26.3% (range 4.9 – 58.0%, n = 16) of the aquatic insect community and constitute the entire sessile portion of the aquatic insect community (Figure 3.2).

The mean density of harlequin ducks from study reaches was 1.23 ducks/km (SE = 0.26, range = 0.00 – 3.33, n = 16). The mean fish rating (using rating system #1) was 7.1 (SE = 0.8, range = 0.0 – 10.0, n = 16).

Before conducting the path analysis I plotted the harlequin duck density against the total fish rating to check for outliers. The Lower Seton River was located at a lake outlet and lies within 1 km of the Seton Lake Power Canal. These areas were both known to be highly productive, and contain dense simuliid populations. This area was a harlequin duck 'club site', similar to those described at the Maligne Lake Outlet in Jasper National Park, Canada, and the Lake Myvatn Outlet in Iceland (Hunt 1997; Gardarsson and Einarsson 1994). Harlequin ducks observed at all other locations were apparently birds on breeding territories. The two points from the Lower Seton River (Figure 3.3) therefore seemed to lie outside of the data set for a biologically sound reason. The inclusion of the Lower Seton River points lessens the strength of the negative relationship between harlequin duck density and the fish rating, as was seen by the differences in slope (with Lower Seton ($r^2 = 0.18$): $y = -0.13 (x) + 2.14$; without Lower Seton ($r^2 = 0.62$): $y = -0.23 (x) + 2.50$) (Figure 3.3). I retained the Lower Seton River points in the path analysis because its inclusion could represent a natural area and density dependent phenomenon where highly productive aquatic insect communities facilitate the co-occurrence of both groups in high densities, and in order to maximize the sample size.

Path analysis revealed a negative overall correlation between harlequin duck density and the fish rating index for all rating schemes. The analysis further revealed that this correlation results from a large, negative interaction between fish and harlequin ducks (path #1), and a smaller, positive interaction on the fish to aquatic insect to harlequin duck (path #2). Based on fish rating system #1, the overall correlation between fish and harlequin ducks is -0.451, which is the sum of the strong, negative relationship between fish and ducks (standardized partial correlation coefficient = -0.484), and the product of the two small, positive relationships between fish and aquatic insects (standardized partial correlation coefficient = 0.243), and aquatic insects and harlequin ducks (standardized partial correlation coefficient = 0.135) (Figure 3.4).

These basic results did not depend on the exact fish rating system used. Under all seven fish rating systems, the strong negative correlation between harlequin duck density and fish (path #1), and the weak positive correlation on the fish to insect to duck (path #2), were maintained (Table 3.1). The negative correlation between fish and harlequin ducks was strongest and attained statistical significance under all three of the fish rating systems that included only categories with drift feeding fish species, and excluded benthic feeding fish (Table 3.1).

3.5 Discussion

While understanding the complex series of interactions in ecosystems is indispensable, research has mainly addressed direct density mediated interactions, neglecting indirect effects (Krivtsov 2004; Werner and Peacor 2003). Basic Density Mediated Interactions (DMI) are typically measurements of how a predator/consumer impacts its prey/resource through direct consumption (Preisser et al. 2005; Krivtsov 2004). Species pair relationships are typically studied through experimental alteration of species densities unless it is technically impossible or ethically unjustified to alter a selected species, whereupon path analysis may be undertaken to examine interactions (Wootton 1994; Palomares et al. 1998). The experimental alteration of fish, harlequin ducks, or aquatic insects is neither technically feasible, nor ethically justified at the scale of an entire river reach. However, examination of the distribution and density of these species in their natural state allows us to investigate the presence and strength of direct and indirect interactions between fish and harlequin ducks. Small sample size restricts my ability to make inferences from this study however it is generally noted that large sample sizes are rarely achieved in ecological studies (Palomares et al. 1998).

Density Mediated Indirect Interactions (DMII) are a series of direct interactions, where the impact is caused by a change in density induced by a predator/consumer (Werner and Peacor 2003). The initiating species reduces the density of a shared resource (the transmitting species) causing an effect on another species (the receiving species) (Dill et al. 2003). In this system I found no evidence that fish (initiators) were affecting harlequin ducks (receivers) indirectly via the density of prey (transmitters) available. The existence of a weak positive interaction between fish and aquatic insects indicates that fish were utilising areas with higher prey availabilities. The effects of fish predation on aquatic insect density are diverse, some showing strong effects, with others showing little or no effect on benthic aquatic insects (Dahl and Greenberg 1996). Drift-feeding fish typically reduce the level of density effects due to their reliance on the terrestrial component of the stream drift (Dahl and Greenberg 1996; Dahl 1998). A meta-analysis by Wooster (1994) has shown that while fish predation effects have a significant effect on prey density, other predators (e.g. predaceous insects) may have a significantly stronger effect.

There is increasing awareness regarding the widespread contribution of Trait Mediated Interactions (TMI) and the effects of predator intimidation on predator prey interactions (Werner and Peacor 2003; Lima and Dill 1990; Preisser et al. 2005; Bolnick and Preisser 2005). A TMI is the non-consumptive impact of predation risk on prey, where prey alter physiological, developmental, morphological, and/or behavioural traits in order to reduce predation risk (Bolnick and Preisser 2005; Werner and Peacor 2003; Preisser et al. 2005). A meta-analysis showed that the impacts of predation risk (63% of the total predator effects) on prey demographics can be at least as strong as direct consumption (51% of the total predator effects) (Preisser et al. 2005). Prey may be forced to occupy different habitats, change activity levels, or alter their foraging schedule and behaviours to lower predation risk (McIntosh and Townsend 1994). Sub-lethal costs of predator avoidance were greater than direct losses to consumption in the mayfly *Baetis bicaudatus*, due to lower growth rates (Peckarsky and McIntosh 1998).

Predators can strongly reduce consumer-resource interactions causing trait mediated effects that have stronger effects than density mediated effects on prey and their resources in a wide variety of taxa (Peacor and Werner 2004; Luttberg et al. 2003). Trait Mediated Indirect Interactions (TMII) result from an initiator species causing a phenotypic change in a transmitter species which alters the per capita effect on the receiving species (Werner and Peacor 2003; Relyea and Yurewicz 2002). When examining indirect interactions the trait mediated effects amplified from predator to prey to resource whereas density mediated effects attenuated, and in aquatic ecosystems TMII's accounted for 93% of the total predator effect (Preisser et al. 2005). Prey may readily incur the fitness costs of predator avoidance when facing continually present and highly mobile predators (e.g. fish) (Schmitz et al. 2004).

The aquatic insect community on harlequin duck breeding streams can easily accommodate trait mediated interactions. A substantial portion of the aquatic insect community consists of grazing and predatory aquatic insects, which are highly mobile. Grazing aquatic insects experience the largest effects of fish predation in comparison to other groups because of their requirement to access periphyton on the substrate surface (Rosenfeld 2000; Kohler and McPeek 1989). These stream reaches also have very coarse substrates providing ample refugia (i.e. rock interstices), which have been shown to reduce fish predation rates and success (Holomuzki and Messier 1993; Holomuzki and Stevenson 1992; Dahl and Greenberg 1998; Bechara et al. 1993; Rosenfeld 2000). The stonefly *Paragnetina media* selected areas with higher current speeds, where the interstices weren't filled with fine particles (Feltmate et al. 1986). Predation risk from fish has been shown to reduce the daytime activity levels and increase refuge use in many different families of aquatic insects (Culp and Scrimgeour 1993; McIntosh and Peckarsky 1996; Bechara et al. 1993). The presence of the mottled sculpin (*Cottus bairdi*) reduced the amount of time the stonefly *Agnetina capitata* spent on the sides and tops of rocks, and decreased the amount of time spent moving on the substrate (Soluk and Collins 1988a).

A Behaviourally Mediated Indirect Interaction (BMII) is a special form of TMII, where the presence of the initiator species causes a behavioural shift in the transmitter, resulting in a per capita effect on the receiving species (Dill et al. 2003; Werner and Peacor 2003). Predators have important influences on behavioural decisions made by prey including when and where they feed, mate, forage, and disperse (Lima and Dill 1990; Forrester 1994). The threat of predation is enough to force prey to modify their behaviour, affecting trade-off decisions between activities such as foraging, and predator avoidance (Bolnick and Preisser 2005; Werner and Peacor 2003; Schmitz et al. 2004). A BMII may exist between two predators when the presence of one predator (initiator), causes a response in the prey (transmitter), which renders another predator (receiver) less effective (Werner and Peacor 2003; Bolker et al. 2003; Preisser et al. 2005). The presence of the predatory dragonfly larvae *Anax longipes* caused a reduction in activity in green frog larvae *Rana clamitans*, reducing the predation success of the larval salamander *Ambystoma tigrinum* on the frog larvae (Relyea and Yurewicz 2002).

The consistent presence of the negative correlation between fish and harlequin ducks (even with the use of several different fish rating schemes) confirms the suppressing effects of fish presence on harlequin duck densities. The inclusion of benthic feeding species reduced this correlation in strength and statistical significance, however this does not eliminate their importance in these systems. My inability to accurately define and differentiate densities of benthic feeding fish species inhibited the power of our analysis to detect the effects of these species on harlequin ducks.

The negative relationship between harlequin ducks and fish measured in this study demonstrates that harlequin ducks were avoiding areas with higher fish densities and better-developed fish communities. Perhaps fish have a fondness for dim sum, and ducks are not using reaches with fish in them because of a direct physical interference. The negative correlation was not the result of differing habitat requirements as fish have been successfully introduced into previously fishless harlequin duck breeding reaches. In the Maligne River system trout and char were successfully stocked into Maligne Lake in the 1920's. Consequently the Middle Maligne River flowing from Maligne Lake now boasts a substantial population of these fish in a reach that was historically fishless and used by breeding harlequin ducks (McCutchen 2001). Harlequin ducks and fish do not feed on one another effectively eliminating a major mechanism for the negative correlation and reciprocal distributions.

This study supports the potential existence of a BMII between harlequin ducks and fish. I hypothesize that fish are effectively reducing the foraging efficiency of harlequin ducks on shared reaches due to the effect of fish presence on aquatic insect behaviour. Harlequin duck breeding streams in this study contain abundant mobile aquatic insect communities, including many families that have been shown to reduce their daytime use of substrate surfaces, and activity levels in the presence of fish. Habitat data simultaneously collected from a complimentary project reports that the stream substrate on study rivers is largely comprised of boulders (average = 42.7%, SE = 6.3%, range = 2.5 – 77.3%, *n* = 13) and cobble (average = 47.3%, SE = 5.2%, range = 22.3 – 95.0%, *n* = 13) (Esler 2006) providing ample refugia. Availability in this study was measured as the density of insects located on rocks small enough for harlequin ducks to flip over and therefore all insects on these rocks are 'available' to the ducks nonetheless the movement of aquatic insects beneath boulders and larger cobbles would reduce the availability of a large portion of the aquatic insect community, consequently reducing harlequin duck foraging efficiency.

A BMII between harlequin ducks and fish also explains observations in the Maligne Lake system in Jasper, BC, Canada (McCutchen 2001). The Maligne River system contains three reaches, isolated from each other by the geography and geomorphology of the surrounding watershed. The Upper Maligne River is completely fishless due to a set of falls at its outlet into Maligne Lake, the Middle Maligne is frequented by rainbow trout (*Oncorhynchus mykiss*) which inhabit that reach, and Maligne Lake, while the Lower Maligne maintains a small, non-breeding population of fish from infrequent overspills of Medicine Lake into the Lower Maligne (McCutchen

2001). Harlequin ducks correspondingly do not use the Middle Maligne River reach, where fish are now present due to introduction in the 1920's, although there is evidence of historical nesting in this area. Breeding females in this system delayed nest initiation and egg laying to access higher-altitude fishless reaches and produced broods that had greater duckling masses than their low elevation counterparts at a given age, suggesting that food availability on these reaches was an important positive influence on duckling growth (Hunt 1997). Food availability was also important for rearing ducklings and this implicates that a reduction in prey availability may also negatively affect other stages of the harlequin duck reproductive cycle contributing to low productivity.

The historical fish predation regime of harlequin duck breeding streams is important because the aquatic insect community is highly adapted to fish predation (Allan 1982; McIntosh and Townsend 1994). Adaptive behaviours may become fixed in aquatic insect populations when predation risk is invariable and predictable, or when gathering information regarding predation risk is too energetically expensive (Forrester 1994; McIntosh and Townsend 1994; Tikkanen et al. 1996). The mayflies *Nesameletus ornatus*, and *Baetis bicaudatus* both maintained inflexible anti-predator behaviours suggesting that these behaviours may have become fixed in the population (McIntosh and Townsend 1994; Cowan and Peckarsky 1994). An experiment conducted during this study showed that mayflies in the family Ephemerellidae from a historically, densely populated fish reach maintained nocturnal activity levels, only coming to the surface of stones to feed in complete darkness (See Appendix B: Predator Odour Experiment). The stonefly *Diura bicaudata* always co-occurs with fish in nature and correspondingly was strongly nocturnal in both the presence and absence of fish, whereas the caddisfly *Rhyacophila* *nubila* inhabits streams with and without fish predators and maintained its behavioural plasticity (Huhta et al. 1999). Aquatic insects maintain behavioural flexibility to adjust their behaviour to current levels of predation risk. Mayflies *Baetis bicaudatus* originating from a fishless reach exhibited behavioural plasticity by altering their diel periodicity following the addition of brook trout (*Salvelinus fontinalus*) odour (McIntosh and Peckarsky 1996).

At a UN conference in Norway in 1996, experts from 80 countries concluded that the introduction of alien invasive species were a major threat to biodiversity, and conservation (Cambray 2003). Alien, sport fish introduction has been rampant across North America and the world the highly lucrative rainbow trout (*Oncorhynchus mykiss*) is now estimated to be distributed in at least 82 countries world wide (Horne and Goldman 1994; Cambray 2003). The addition of new species may have large effects when they exploit resources already being used by other species, and the introduction of even relatively few new predators into areas where they were previously rare or absent can cause a response in entire prey populations (Werner and Peacor 2003; Kohler and McPeek 1989; Preisser et al. 2005; Townsend 1996). The introduction of fish caused both morphological and behavioural changes in amphibian larvae, due to fish occurrence in their natural habitat (Teplitsky et al. 2003), and the cryptomonad *Plagioselmis prolonga* experienced morphological changes in response to fish stocking (Kim et al. 2003). The widespread introduction of brown trout (*Salmo trutta*) across New Zealand since the 1860's has resulted in displacement of native galaxiid fish species, and has caused fixed anti-predator behaviours in the mayfly *Nesameletus ornatus* in trout bearing streams (McIntosh and Townsend 1994).

Fish introduction and enhancement has occurred in my study area. Nita and Alpha Lakes were initially stocked with rainbow trout in the 1920's and 1955 respectively, and both were subsequently stocked in the 1970's. These fish move downstream into Millar Creek where they cannot return into Alpha Lake due to the presence of falls. These fish may consequently move downstream to the Upper Cheakamus River, a reach used by breeding harlequin ducks, and are incapable of returning to Millar Creek due to the presence of another set of falls (Krzesinska 1995). A local lake system emptying into the Ryan River through Vans Creek was assessed and stocked with rainbow trout. Stocking was successful and trout were observed recently, however the high gradient, and confined channel of Vans Creek has prevented the movement of these fish into the Ryan River (Stockwell 2002). Permanent stocking efforts are required on other lakes (e.g. Jane and Crater Lake) and introduction into other 'barren' lakes (e.g. Gin and Tonic Lake) and their tributaries has been suggested (Krzesinska 1995). On the Yalakom River low levels of fish use motivated fisheries enhancement activities on the river, including blasting to improve fish passage conditions on a steep, bouldery section 15 km upstream from its confluence with the Bridge River. From 1981 to 1993 regular fry releases of chinook and coho were conducted and two releases of steelhead were conducted in the 1980's (Griffith 1995; Conlin 1994). Habitat assessments and theoretical modelling on the Yalakom River in 1994 identified enhancement potential for rainbow trout (steelhead included), bull trout, and chinook salmon and calculated that an additional 20,000 late summer rainbow trout/steelhead yearlings could be supported on the lower Yalakom. Fry release of steelhead and chinook fry was recommended as the most practical and appropriate method of enhancement, however it was also recommended that effects on resident bull trout and rainbow trout populations be carefully considered when releasing fry into this system (Griffith 1995).

Food availability on harlequin duck breeding grounds is absolutely necessary for breeding success. Isotopic evidence has shown that harlequin ducks utilise aquatic insect prey from breeding streams for egg formation (Bond 2005). Females that fail to accumulate sufficient body mass on the breeding streams may delay breeding (Hunt 1997), and data from this study have also shown that breeding propensity was highest in the year with higher levels of food availability (See Chapter 2). I therefore believe that the widespread introduction and enhancement of fish species into historically fishless reaches could cause a reduction of food available to harlequin ducks resulting in reduced breeding habitat quality. The effects of introduction may also have contributed to the drastic harlequin duck range contraction that has occurred in the northwestern United States, where breeding ducks have forgone lengthy inland migrations due to the widespread reduction in prey availability on these streams. The pervasive nature of this impact and its negative effect on productivity and recruitment could contribute to population decline for harlequin ducks in western North America.

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Table 3.1 Results from path analysis using all seven fish rating systems. Bold type indicates statistical significance. Rating schemes are described in Appendix A (Table A.1). HADU = harlequin duck.

Fish Rating System	Standardized partial regression coefficients			Fish => Duck Correlation
	Fish => HADU	Fish => Insect	Insect => HADU	
#1	-0.484	0.243	0.135	-0.451
#2	-0.563	0.132	0.092	**-0.551**
#3	-0.434	0.208	0.108	-0.412
#4	-0.531	0.064	0.052	**-0.528**
#5	-0.248	0.283	0.088	-0.223
#6	-0.440	0.204	0.108	-0.418
#7	-0.526	0.083	0.062	**-0.521**

Figure 3.1 Mean aquatic insect availability on the studied river reaches for 2003 (top) and 2004 (bottom).
Predaceous aquatic insects (☐), grazing aquatic insects (■), filter-feeding aquatic insects (▨). Predaceous and grazing aquatic insect groups are mobile.

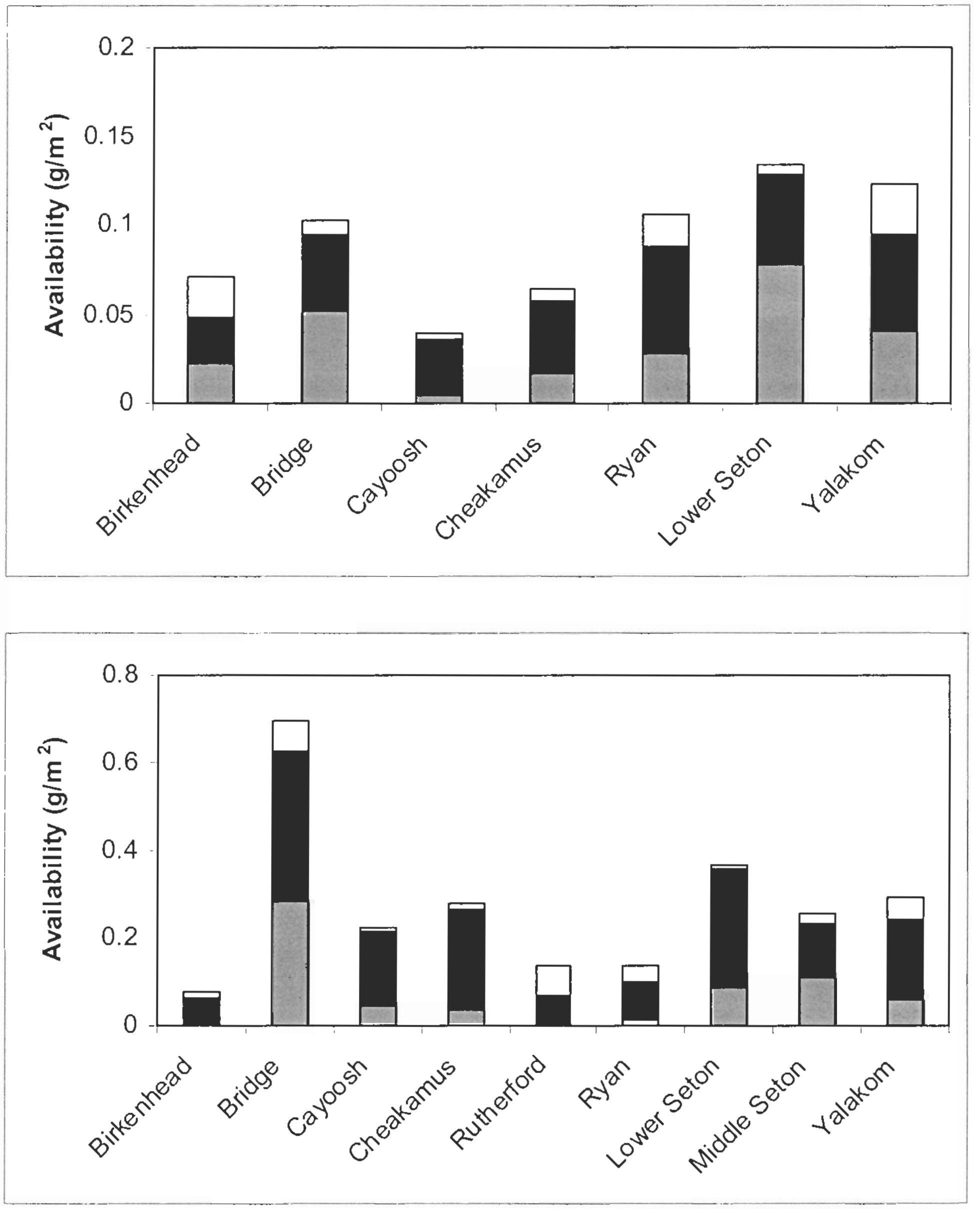


Figure 3.2 Functional feeding group composition of studied river reaches in 2003 (top) and 2004 (bottom).
Predaceous aquatic insects (☐), grazing aquatic insects (■), filter-feeding aquatic insects (▨). Predaceous and grazing aquatic insects are mobile.

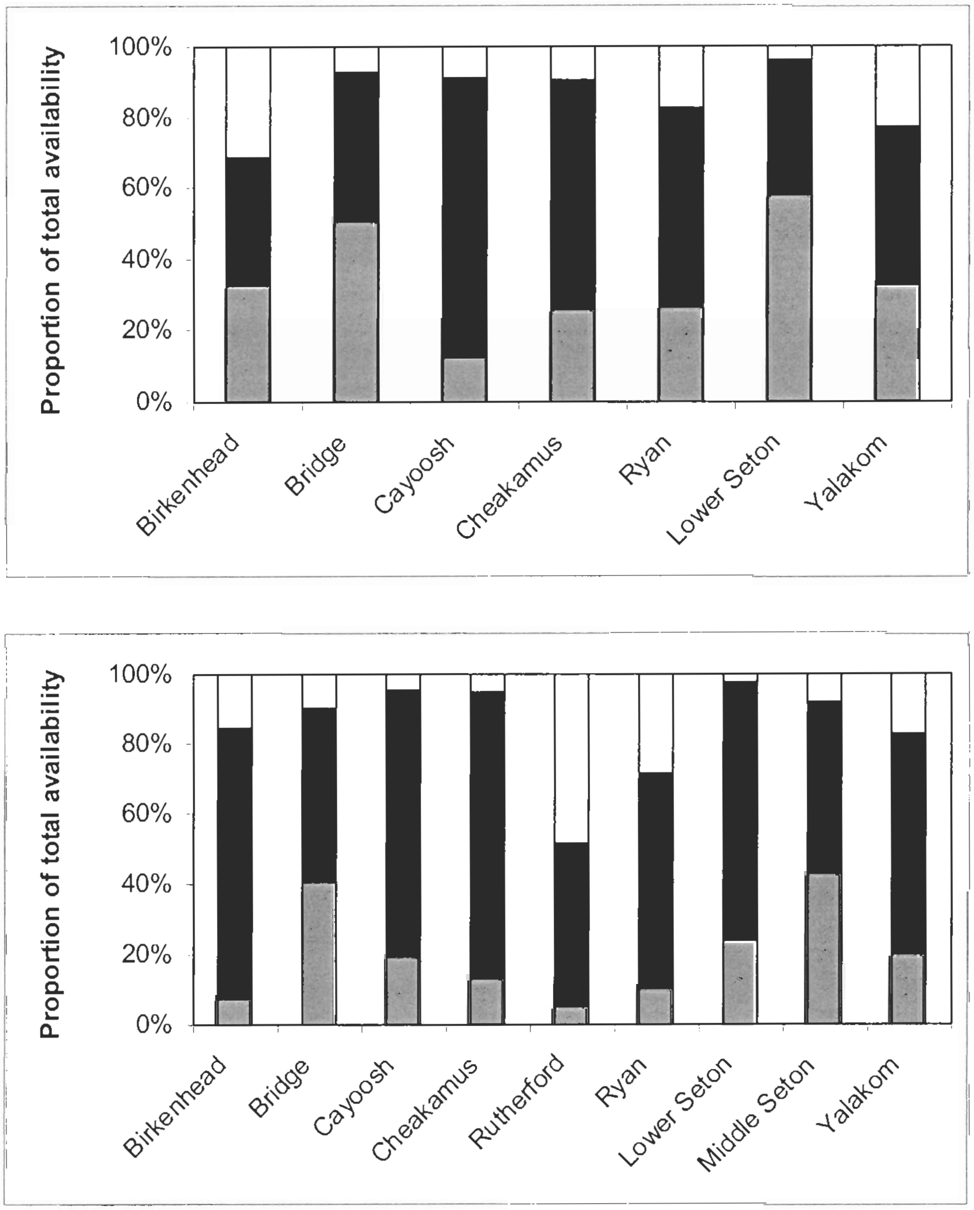


Figure 3.3 Harlequin duck density versus total fish rating (using fish rating scheme #1). Lower Seton River points are identified in grey. Line equations, grey: (includes Lower Seton River, $r^2 = 0.18$) $y = -0.13(x) + 2.14$; black: (without Lower Seton River, $r^2 = 0.62$) $y = -0.23(x) + 2.50$.

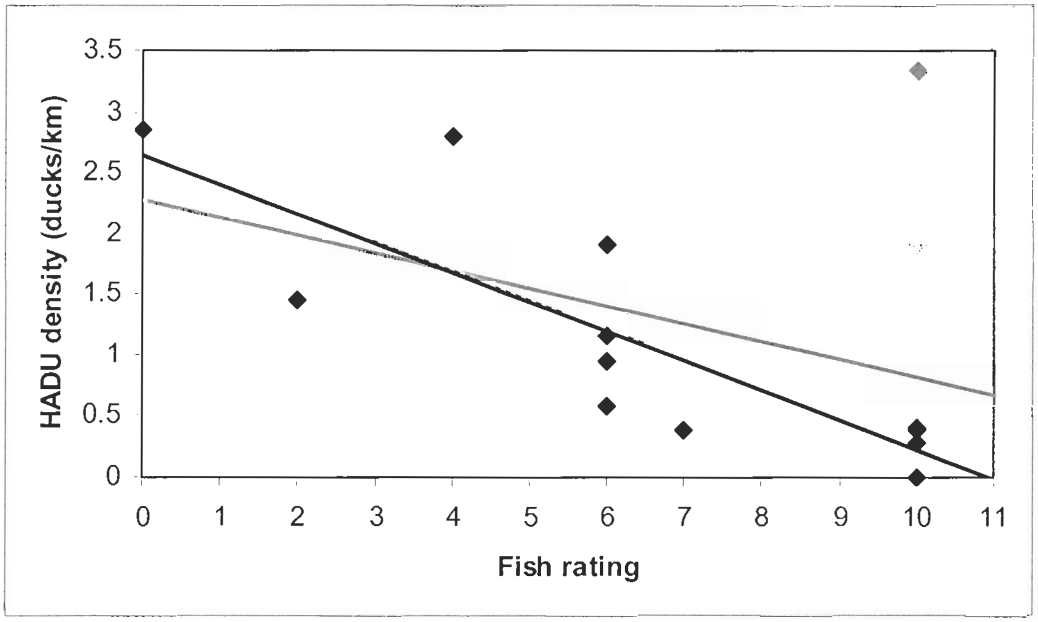
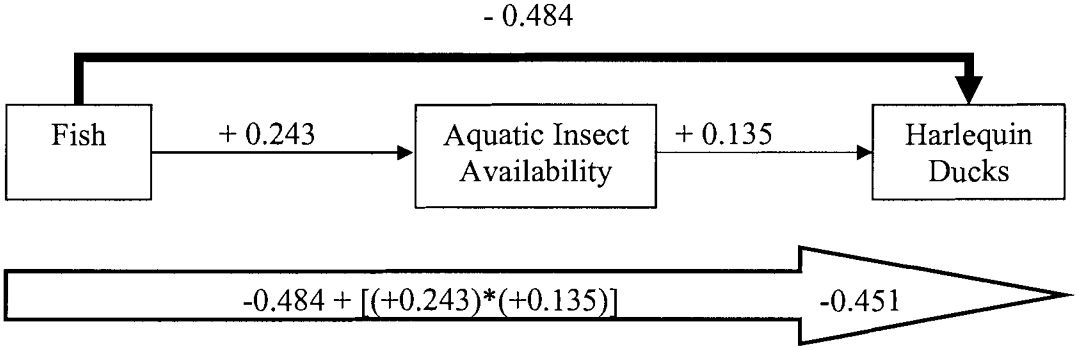


Figure 3.4 Path diagram of interactions between fish and harlequin ducks. Diagram depicts the correlation as a sum of the two separate paths calculated as a product of their standardized partial regression coefficients. Results are from path analysis using fish rating scheme #1. Arrow widths are proportional to their contribution to the total interaction.



CHAPTER 4:
GENERAL CONCLUSIONS, RECOMMENDATIONS, AND FUTURE DIRECTIONS

4.1 Conclusions

Recent studies have raised concern regarding the low productivity and recruitment of harlequin ducks (*Histrionicus histrionicus*) in British Columbia, Canada (Rodway et al. 2003; Smith et al. 2001). This study was aimed at expanding our knowledge of the relationship between harlequin ducks and food resources on breeding streams to assess whether this may be hindering productivity. Harlequin duck productivity and recruitment have previously been linked to food availability on breeding grounds (Bengston and Ulfstrand 1971; Gardarsson and Einarsson 1994), and their distribution across breeding streams appears positively correlated with food availability (McCutchen 2001; Vennesland 1996; Hunt 1997). Reproduction in waterfowl is energetically demanding and food abundance prior to egg laying is crucial for successful breeding (Lack 1954; Lack 1956; Perrins 1970; Rohwer 1992; Toft et al. 1984), and recent research has shown that the food resources for egg production in harlequin ducks are obtained on breeding areas (Bond 2005). I investigated food availability on harlequin duck breeding streams, examining (1) the importance of flow variability on aquatic insect availability, (2) the distribution of harlequin ducks with respect to prey availability, and (3) the relationship between harlequin ducks and fish species, looking for evidence of an indirect interaction via their shared food resources.

I found that flow variability was an important factor affecting aquatic insect availability. The reduction of flow variability corresponded to an increase in aquatic insect availability across rivers, and in each of the river reaches studied the decrease in flow variability in 2004 corresponded to an increase in aquatic insect availability. Differences between river reaches could have been due to the buffering effects of lakes and reservoirs in addition to the highly productive nature of lake outlets.

I found that harlequin duck densities on breeding streams were positively related to food availability in both years of the study. Also, associated with the reduced flow variability and higher prey availability in 2004 reproductive performance by harlequin duck females was higher in 2004 (Bond 2005).

Harlequin ducks interact with fish indirectly through their shared prey. Both my fish rating index and harlequin duck density were positively correlated with my measures of prey availability with a strong negative interaction detected between fish and ducks. The indirect interaction was apparently not the result of fish reducing the density of aquatic insects. I hypothesize that the negative correlation between harlequin ducks and fish is a result of a behavioural change in the aquatic insects. Fish provoke aquatic insects to reduce their activity levels and increase use of refuges during the day to reduce predation risk posed by these visual predators (Culp and Scrimgeour 1993; McIntosh and Peckarsky 1996; Bechara et al. 1993). Harlequin duck breeding streams have a substrate largely composed of cobbles and boulders providing ample refuges in interstices. The aquatic insect communities in these streams also has a large mobile component containing many families that have been shown to exhibit these anti-predator behaviours. Fish presence in reaches may cause a BMII, which would explain the reciprocal distribution of these species where harlequin ducks avoid reaches with fish. The widespread introduction of fish throughout harlequin duck breeding streams may be contributing to low productivity and recruitment measured in wintering populations (Smith et al. 2001; Rodway et al. 2003).

4.2 Recommendations

My research documents the importance of food availability on harlequin duck breeding streams. I recommend that the aquatic insect community be taken into consideration when conserving, altering, or enhancing harlequin duck breeding habitat. In order to enhance and preserve harlequin duck food resources the flow regimes of stream reaches should be considered, monitored and maintained in a manner that both maximizes the aquatic insect availability, and proliferates the rocky, cobble substrate they require for feeding. This could mean testing and determining an optimal discharge rate, and flow regime with overall lower levels of flow variability, including periodic spates that would flush the reach preventing sedimentation.

The identification of the Seton Lake Outlet, and the associated Seton Lake Power Canal as important areas (i.e. club sites) to harlequin ducks should be considered. Females were predictably present on these reaches, which are highly productive areas with abundant aquatic insects for breeding females. The Seton Power Canal may provide a highly available food source to females in this area, because it contains extensive sessile Simuliid larvae on the simple, flat concrete walls. During the 2004 breeding season, the Seton Power Canal was drained for inspection and maintenance purposes during the harlequin duck's pre-breeding period, effectively removing its resources from the local system. I recommend that this form of maintenance and inspection on the Seton

Power Canal be restricted to time periods when harlequin ducks would not be present, typically before April, and after September.

My research provides evidence in support of an indirect interaction between harlequin ducks and fish species. Fish did not interact indirectly with ducks by reducing the density of aquatic insects, but through a postulated reduction in availability through induced behavioural changes. Some of the highest densities of harlequin ducks are found in fishless reaches throughout my study. The introduction of novel fish predators into historically fishless reaches would reduce food availability, which has been shown to be extremely important for successful breeding by female harlequin ducks. I recommend that decision-makers freeze the introduction of fish into harlequin river reaches that are presently fishless pending further investigation regarding this relationship. Harlequin duck breeding streams which have fish populations maintained by regular fry release events may be enhanced by arresting these actions. This information should be advocated to groups and organizations responsible for the initiation, management, and completion of fish introductions.

I found that the novel 5-rock sample method was capable of giving consistent, and reliable estimates of aquatic insect densities and community composition that are relevant for visual benthic feeding predators. I recommend that researchers attempting to quantify this community use this method for its convenience, reliability, and accuracy at measuring the density of aquatic insects available. However, I also recommend that researchers consider accounting for the location of aquatic insects on rocks sampled (i.e. top or bottom). The density of aquatic insects from this method does measure insects 'available' to harlequin ducks however location would insight into the importance of anti-predator behaviours in the aquatic insect community.

4.3 Future Directions

This thesis was motivated by studies revealing low productivity in harlequin duck populations along the British Columbia coastline. My results provide support for the hypothesis that widespread introductions of fish to previously fishless waters throughout the breeding range of harlequin ducks may be contributing to this low productivity. Three specific steps will be necessary to assess the hypothesis more fully. First, a better estimate is needed of whether the current level of productivity is low enough to cause harlequin duck population decline. This can be accomplished with some demographic modelling work using existing data. Second, some survey and mapping work should be undertaken to estimate the extent of fish introduction into otherwise suitable breeding streams throughout the harlequin breeding range. Third, a strong experimental test will be essential to really establish the hypothesis. This is not likely to be easy, but even in the absence of an experiment, there are predictions that might be tested. For example, the upper Birkenhead reach in my study system has low use by fish. I was unable to measure harlequin usage of the upper Birkenhead, but I predict high densities of harlequin ducks there.

For future work on the ground, an adaptive management approach could be very instructive. I recommend that, pending refinement and testing of this hypothesis, fish introductions into streams and rivers currently used for breeding by harlequin ducks be contemplated only if accompanied by some work that will enable us to learn something about the in-stream changes that follow such introductions. This would involve documenting harlequin duck use on a fishless reach, before and after fish introduction, alongside aquatic insect availability measurements. Further evidence could be provided by documenting the location of aquatic insects on the rocks during the day and at night. Fish removals could also be conducted on reaches with low, or historic harlequin duck use and the consequent level of use by harlequin ducks could be documented (providing there is a long enough study period to allow for harlequin duck site fidelity).

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APPENDIX A:
FISH DATA SUMMARY & RATING SYSTEMS

Rating systems

To compare the different river reaches it was necessary to create a fish rating system that adequately and fairly represented the fish communities present in each of the reaches. This task was difficult because fish data were reported with different units (e.g. fish/m^2 vs. g/m^2), gathered with various sampling effort and using assorted methods. Some reaches (e.g. Bridge River, Lower Seton River) had much more complete and current fish data than others, and studies were typically biased towards reporting the presence and densities of salmonids. In light of these constraints I was able to quantify each reach in terms of: use by anadromous spawning salmon (coho, steelhead, chum, pink, sockeye and chinook); relative use by spawning coho (*Oncorhynchus kisutch*) adults from escapement data; relative density of resident rainbow trout (*Oncorhynchus mykiss*); and presence/absence of bull trout (*Salvelinus confluentus*) or dolly varden (*Salvelinus malma*), cutthroat trout (*Oncorhynchus clarki clarki*), suckers (family *Catostomidae*), longnose dace (family *Cyprinidae*), mountain whitefish (*Prosopium williamsoni*), and sculpins (family *Cottidae*). From these data nine categories were created: 1) presence of spawning salmonids, 2) relative density of coho, 3) relative density of rainbow trout, 4) presence of dolly varden/bull trout, 5) presence of cutthroat, 6) presence of suckers, 7) presence of dace, 8) presence of mountain whitefish, 9) presence of sculpins. The presence of spawning coho, steelhead, chum, pink, sockeye and chinook salmon was given a category because the fry of these species would be present in the reach consuming aquatic insects before they migrate to the ocean, and therefore reaches containing spawning salmonids would have more complex and diverse fish communities than reaches without spawning salmon. The relative density of coho salmon was given a category because the fry of this species are known to remain in their spawning reaches for up to one full year (and could be up to two years) before migrating and these fry would be present and feeding upon aquatic insects throughout the entire harlequin duck breeding season. There were also sufficient data to make a relative comparison of the number of coho that were returning to the reaches for spawning purposes. The resident rainbow trout densities were given a category because these fish would be present in the reach predating aquatic insects and sufficient data allowed for the relative comparison of their densities. The presence/ absence of dolly varden/bull trout, cutthroat trout, suckers, dace, mountain whitefish, and sculpin were all given a category because their presence would add to the overall complexity and diversity of the fish community and they were not given more refined classification because of the sporadic and inconsistent reporting of these species. Three different numeric assignments were used for these categories including drift feeding species, benthic feeding species or both, creating seven separate rating systems (Table A.1). These rating systems were used to calculate a fish rating for each river reach (Table A.2). All seven rating systems were used for the path analysis to examine the effects of the fish rating system on the results, and to calculate the relationship between harlequin duck densities and fish.

Reach descriptions

Birkenhead River

The Birkenhead River is distinctly divided into two separate reaches, above and below the Birkenhead Canyon where an impassable set of falls prevents the upstream migration of anadromous fish species (Cook 1983). Below the falls Birkenhead River supports spawning grounds for: chinook, chum, coho, pink, sockeye salmon, and steelhead trout (FISS 2006). Coho salmon spawn in this reach from October to January, and the fry rear in freshwater for one to two years (Cook 1983). Escapement numbers show an average of 3472 returning coho adults from 1981 to 1991 (Figure A.1) (FISS 2006). Resident drift feeding species include: rainbow trout, bull trout/dolly varden, and cutthroat trout. Benthic feeding species include: sculpin, mountain whitefish, and lamprey (Figure A.3) (Cook 1983; FISS 2006).

Bridge River

The fish population of the Lower Bridge River extending below the Terzaghi Dam has been well documented. The entire reach is accessible to anadromous and resident fish species. It is used by: chinook, coho, pink, sockeye salmon, and steelhead trout. Coho spawn in the area from Camoo Creek at Horseshoe bed to above the confluence with the Yalakom River from September to December (Lister and Beniston 1995). Escapement numbers show an average of 900 returning adults to this reach based on numbers from 1990-1999 (Figure A.1) (FISS 2006). Resident drift feeding fish species include rainbow trout (fry and parr) at an average density of 22.8 fish/m^2 based on electroshock fishing during 1993 (Figure A.2) (Lister and Beniston 1995), an average of 465 g/100 m^2 (J. Sneep unpublished data), and bull trout. Benthic feeding fish species include: mountain whitefish, sculpin, and suckers (Figure A.3) (Lister and Beniston 1995; Uunila and Guy 2002; FISS 2006). A local fisheries biologist supported this reach being assigned a fish rating of 'high' (A.E. Tisdale personal communication).

Cayoosh Creek

Cayoosh Creek has a small hydroelectric generating dam (Walden North) at the base of an impassable set of falls (FISS 2006). Below this dam spawning channels facilitate the spawning activities of: steelhead trout, chinook, and coho salmon. On average two pair of coho adults return to spawn in this area, and many fry move to the neighbouring Seton River to rear because of its warmer temperatures (A.E. Tisdale personal communication). Escapement data report an average of 31 returning adults between 1989 and 1998 (Figure A.1) (FISS 2006). Benthic feeding species include: mountain whitefish, and suckers (Figure A.3) (FISS 2006; A.E. Tisdale personal communication). A local fisheries biologist suggested this reach receive a fish rating of 'low' (A.E. Tisdale personal communication).

Cheakamus River

The Cheakamus River has two distinct reaches. The Upper Cheakamus River flows from Cheakamus Lake to Daisy Lake, while the lower flows from the Daisy Lake dam to its confluence with the Squamish River. The Lower Cheakamus river is mostly accessible to anadromous fish species. It is used by: chinook, chum, coho, sockeye, and pink salmon, as well as dolly varden, and steelhead trout (Lewis and Guy 1996). The standing stock of juvenile chinook, coho, steelhead, sculpins and lampreys were estimated by electroshock removal in 1988 and the standing crop averaged 3.01 g/m^2 (range of 0.95 to 5.8) (Lewis and Guy 1996). Coho spawn on this reach from December to January, and their fry remain in freshwater for one to two years before returning to the ocean. The presence of an impassable set of falls at Butterfly Creek (about the 17 km mark) prevents the upstream migration of anadromous species, as does the Daisy Lake dam (University of Victoria 1989). The reach above these falls supports resident rainbow trout and is believed to be at capacity for this species (Lewis and Guy 1996). Benthic feeding species in the Lower Cheakamus reach may include: sculpin, and mountain whitefish (Figure A.3) (FISS 2006). The Upper Cheakamus River supports resident rainbow trout and possibly dolly varden/ bull trout populations (Knight 1991). Rainbow trout studies on the area below Millar Creek gave an average of 0.48 fish/m^2 (Figure A.2) (Knight 1991) and this would be an overestimate of the rainbow trout density above the Millar Creek confluence because there is little supportive habitat (University of Victoria 1989). No known benthic feeding species have been recorded in this reach (Knight 1991).

Rutherford Creek

The Rutherford Creek reach is highly turbulent with numerous areas of high velocities. No known anadromous spawning occurs in the reach due to the presence of falls on the Green River, and velocity barriers at the mouth of the Rutherford Creek. Resident drift feeding species include: rainbow trout, and dolly varden/bull trout. Trout were observed swimming upstream at the cement weir at the site where water is diverted for the independent power project. No benthic feeding species have been recorded.

Ryan River

For the purposes of this study the Ryan River has been divided into two reaches. The Lower Ryan River starts at the impassable falls at the 8 km mark to the confluence with the Lillooet River, and the Upper Ryan River reach was above the impassable falls (Stockwell 2002). The Lower Ryan River supports spawning activities for: chinook, coho, pink, and sockeye salmon along with a possible anadromous cutthroat population (Conlin 1994). Coho spawn in this area from October to January and an average of 135 adults have returned each year from 1978-1992 (Figure A.1) (FISS 2006). Resident drift-feeding species include: rainbow trout, dolly varden/ bull trout, and cutthroat trout

(Stockwell 2002; FISS 2006). Benthic-feeding species on this reach include the sculpin (Figure A.3). The Upper Ryan River is completely fishless due to the presence of the impassable falls.

Seton River

The Lower Seton River is completely accessible to anadromous fish species and is supplemented with spawning channels. This reach is heavily used for spawning by: chinook, coho, pink, and sockeye salmon, and steelhead trout (FISS 2006; Triton Environmental Consultants Ltd. 1996; Lister and Beniston 1995). Coho spawn in this reach mainly within 1 km downstream of the lake outlet from October to January, and their fry emerge from March to May (Triton Environmental Consultants Ltd. 1996). The fry remain in the system for at least one year and smolts leave with the spring freshet (A.E. Tisdale personal communication). An average of 118 adult coho returned each year to use this reach from 1991-1999 (Figure A.1) (FISS 2006). Resident drift-feeding species include cutthroat trout, rainbow trout, and dolly varden/ bull trout (FISS 2006). Rainbow trout densities are estimated at 1.6 fish/m^2 based on electroshock removal technique including both fry and parr (Figure A.2) (Lister and Beniston 1995). Benthic-feeding species in this reach include: mountain whitefish, sculpin, sucker, and longnose dace (Figure A.3) (FISS 2006; A.E. Tisdale personal communication; Lister and Beniston 1995; Triton Environmental Consultants Ltd. 1996). A local fisheries biologist suggested this reach receive a fish rating of 'moderate' (A.E. Tisdale personal communication).

Yalakom River

The Yalakom River consists of two different reaches. A barrier about 10 km downstream of Beaverdam Flats prohibits upstream migration of anadromous species. Below this barrier the Yalakom supports spawning of: chinook, coho, pink, sockeye salmon, and steelhead (FISS 2006; Komori 1997; Griffith 1995). Coho are reported to spawn in this reach from September to January however escapement data reports an average of 0 returning adults from 1985-1994 (Figure A.1) (FISS 2006). Resident drift-feeding species include rainbow trout, and bull trout (Conlin 1994; Griffith 1995). Rainbow trout densities are estimated at 0.1 fish/m^2 based on the electroshock removal technique in 1994 for both fry and parr (Figure A.2) (Conlin 1994). Benthic-feeding species noted are: sculpin, mountain whitefish, and longnose Dace (Figure A.3) (FISS 2006; Komori 1997).

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Table A. 1 Summary of fish rating systems, and point allocations for seven different rating schemes.

	Anadromous spawning salmon	Coho escapement	Rainbow trout	Dolly varden/ bull trout	Cutthroat trout	Sucker	Dace	Mountain whitefish	Sculpin	TOTAL POINTS
Rating #1 All	Y=1 N=0	High=3 Med=2 Low=1 None=0	High=3 Med=2 Low=1 None=0	Y=1 N=0	Y=1 N=0	Y=1 N=0	Y=1 N=0	Y=1 N=0	Y=1 N=0	13
Rating #2 Drift	Y=1 N=0	High=3 Med=2 Low=1 None=0	High=3 Med=2 Low=1 None=0	Y=1 N=0	Y=1 N=0	-------	-------	-------	-------	9
Rating #3 All	Y=1 N=0	Y=1 N=0	Y=1 N=0	Y=1 N=0	Y=1 N=0	Y=1 N=0	Y=1 N=0	Y=1 N=0	Y=1 N=0	9
Rating #4 Drift	Y=1 N=0	Y=1 N=0	Y=1 N=0	Y=1 N=0	Y=1 N=0	-------	-------	-------	-------	5
Rating #5 Benthic	-------	-------	-------	-------	-------	Y=1 N=0	Y=1 N=0	Y=1 N=0	Y=1 N=0	4
Rating #6 All	Y=3 N=0	High=3 Med=2 Low=1 None=0	High=3 Med=2 Low=1 None=0	Y=3 N=0	Y=3 N=0	Y=3 N=0	Y=3 N=0	Y=3 N=0	Y=3 N=0	27
Rating #7 Drift	Y=3 N=0	High=3 Med=2 Low=1 None=0	High=3 Med=2 Low=1 None=0	Y=3 N=0	Y=3 N=0	-------	-------	-------	-------	15

Table A. 2 Summary of results for all river reaches from each fish rating system used for sensitivity analysis.

River Reach	Rating #1	Rating #2	Rating #3	Rating #4	Rating #5	Rating #6	Rating #7
Birkenhead	10	8	7	5	2	20	14
Bridge	10	7	7	4	3	20	11
Cayoosh	6	4	6	4	2	14	8
Lower Cheakamus	6	4	5	3	2	14	8
Upper Cheakamus	2	2	2	2	0	4	4
Rutherford	2	2	2	2	0	4	4
Upper Ryan	0	0	0	0	0	0	0
Lower Ryan	7	6	6	5	1	15	12
Seton	10	6	9	5	4	24	12
Yalakom	6	3	6	4	2	16	7

Table A. 3 Fish rating according to rating system #1 for each of the studied river reaches.

River Reach	Anadromous spawning of salmonids		Coho escapement		Rainbow trout density		Dolly varden or bull trout presence		Cutthroat trout presence		Sucker presence		Dace presence		Whitefish presence		Sculpin presence		Fish rating (points)
Birkenhead	Y	1	H	3	M	2	Y	1	Y	1	N	0	N	0	Y	1	Y	1	10
Bridge	Y	1	M	2	H	3	Y	1	N	0	Y	1	N	0	Y	1	Y	1	10
Cayoosh	Y	1	L	1	L	1	Y	1	N	0	Y	1	N	0	Y	1	N	0	6
Lower Cheakamus	N	0	N	0	M	2	Y	1	Y	1	N	0	N	0	Y	1	Y	1	6
Upper Cheakamus	N	0	N	0	L	1	Y	1	N	0	N	0	N	0	N	0	N	0	2
Rutherford	N	0	N	0	L	1	Y	1	N	0	N	0	N	0	N	0	N	0	2
Upper Ryan	N	0	N	0	N	0	N	0	N	0	N	0	N	0	N	0	N	0	0
Lower Ryan	Y	1	L	1	M	2	Y	1	Y	1	N	0	N	0	N	0	Y	1	7
Seton	Y	1	L	1	M	2	Y	1	Y	1	Y	1	Y	1	Y	1	Y	1	10
Yalakom	Y	1	N	0	L	1	Y	1	N	0	N	0	Y	1	Y	1	Y	1	6
POINTS=>	Yes = 1 No= 0		High = 3 Med = 2 Low = 1 None = 0		High= 3 Med = 2 Low = 1 None = 0		Yes = 1 No = 0		Yes = 1 No = 0		Yes = 1 No= 0		Yes = 1 No= 0		Yes = 1 No= 0		Yes = 1 No= 0		

Note: Differences between low, moderate and high are at least one order of magnitude.

Figure A. 1 Coho escapement data. The data collected here are based on information found in the Fisheries Information Summary System (FISS 2006). Values are the average escapement numbers for: 1981-1991 (Birkenhead), 1990-1999 (Bridge), 1989-1998 (Cayoosh), 1978-1992 (Ryan), 1991-1999 (Seton), and 1985-1994 (Yalakom).

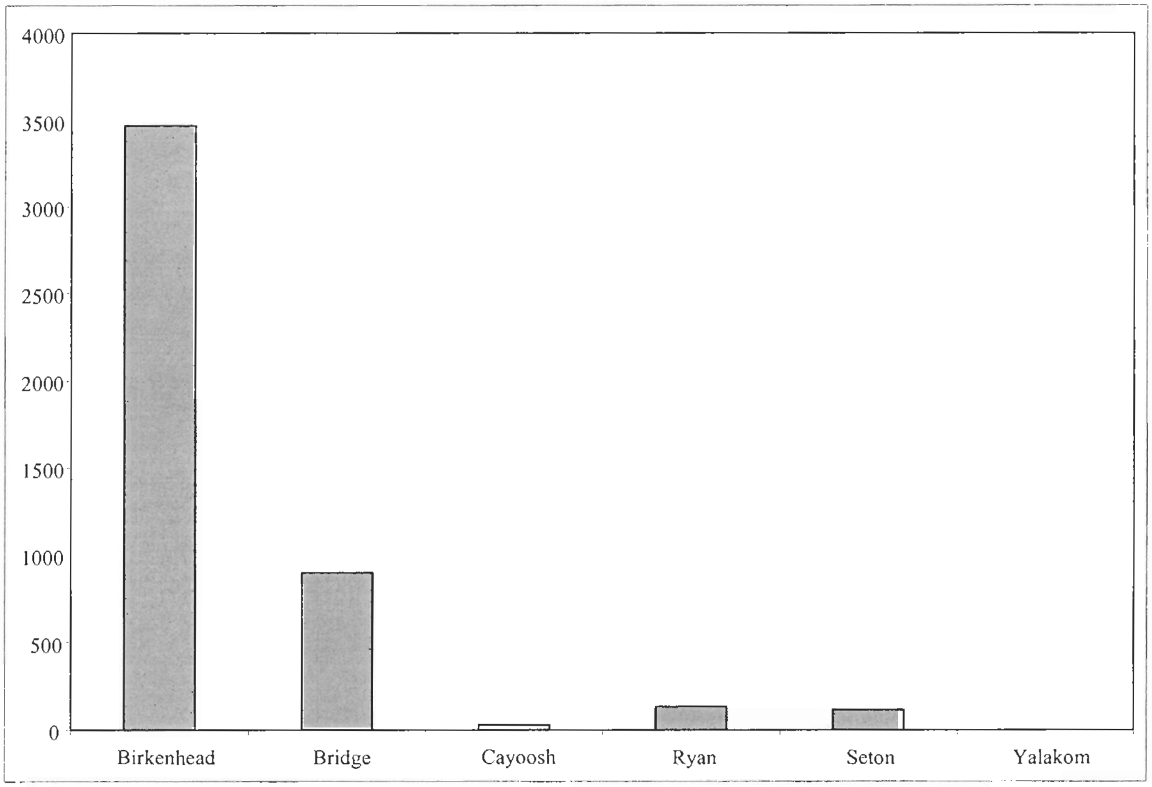


Figure A. 2 Rainbow trout density estimates. All estimates include both fry and parr. Bridge is the average of 31 sample sites located above and below the Yalakom River confluence taken on two occasions during 1993. Seton is the average of 19 sample sites below Seton Lake taken on two occasions in 1993. Yalakom is the average of 6 sample sites located above and below the barrier taken on five separate occasions during 1993.

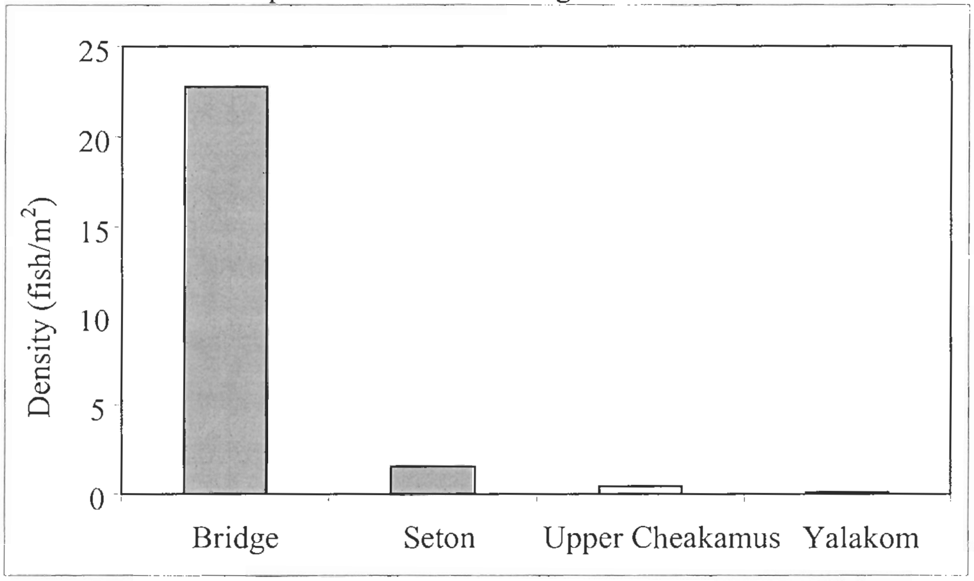
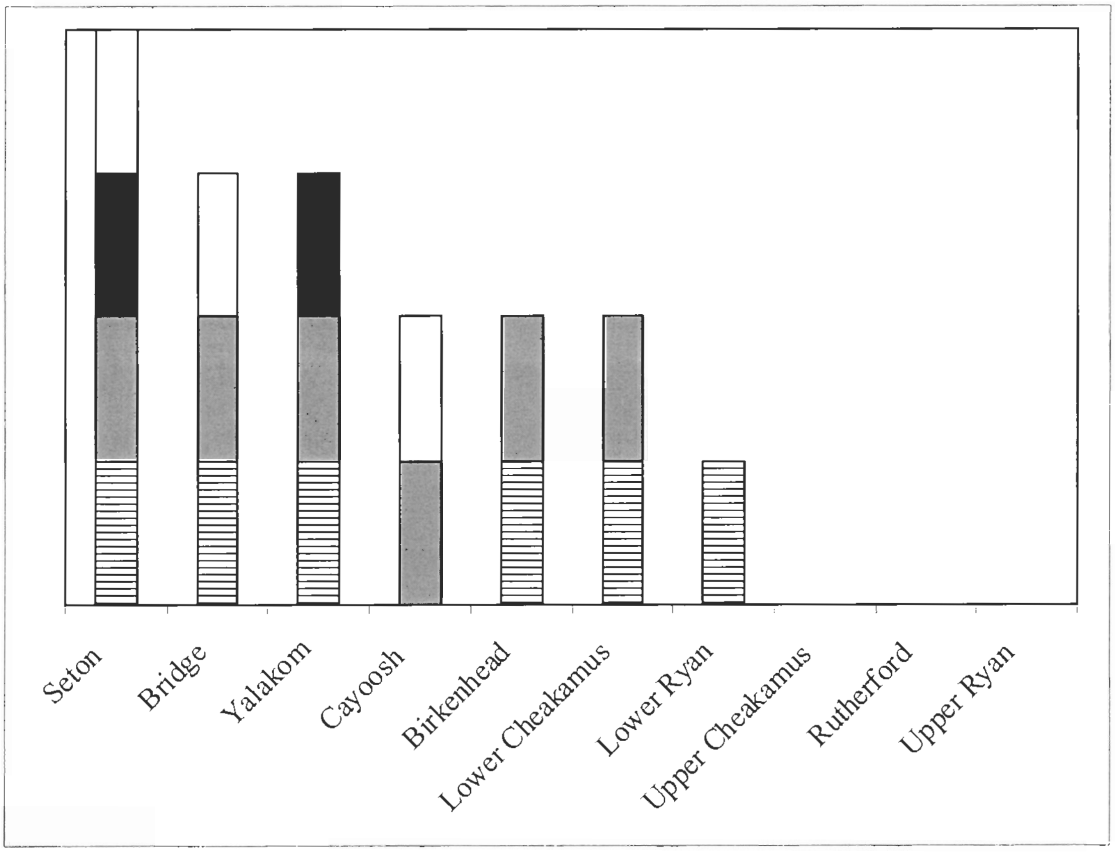


Figure A. 3 The presence/absence of benthic-feeding species. Sculpin (▤), mountain whitefish (▨), dace (■), sucker (□).



APPENDIX B:
PREDATOR ODOUR EXPERIMENT

Introduction

Prey may respond to the threat of mortality posed by predators by altering their life history traits, physiology, morphology, development, and behaviour, in order to reduce the predation risk incurred while foraging (Allan 1995; Feltmate et al. 1992; Lima 1998; Lima and Dill 1990). Prey increase their use of refuges and decrease movement outside of refuges when predation risk is high because activity levels have a strong effect on prey vulnerability to predators (Werner and Anholt 1993; Lima and Dill 1990; Sih 1987). Predation risk posed by fish has been shown to reduce daytime activity levels and increase refuge use in many different families of aquatic insects (Culp and Scrimgeour 1993; Cowan and Peckarsky 1994). Families that graze on periphyton best illustrate trade-off decision making between foraging and predation risk, because of their need to access stone tops to feed on attached algal cover (Rosenfeld 2000). For example, activities of *Baetis bicaudatus* in Western Colorado were highly concentrated during nocturnal periods in a trout-bearing stream relative to those from a fishless stream (Cowan and Peckarsky 1994). Sipholnurid mayflies *Nesameletus ornatus* in New Zealand streams containing brown trout (*Salmo trutta*) exhibit strong nocturnal periodicity in their activity levels (McIntosh and Townsend 1994).

In this appendix, I describe the results of a field experiment designed to investigate whether aquatic insects in the Order Ephemeroptera, family Ephemerellidae reduce their daytime activity and visibility under rainbow trout and harlequin duck predation risk. I predicted that ephemerellids would exhibit aperiodic activity and visibility levels in the absence of predation risk (i.e. predator odours), and would exhibit nocturnal activity with low daytime visibility under perceived predation risk from rainbow trout (*Oncorhynchus mykiss*) and harlequin ducks (*Histrionicus histrionicus*).

Methods

The field experiment was conducted from August 2-16, 2004, at the confluence of Hell Creek, and the Bridge River, approximately 50 km north of Lillooet, BC, Canada. Water was diverted from the fishless Hell Creek into a large (250 litre) holding tank, which in turn was gravity fed into nine experiment trays, each with an average flow rate of 1.90L/min +/- 0.40 (95% CI). The average depth of the water mid-length along the tray was 6.5cm +/- 0.6 (95% CI). Each tray measured 3 m in length and 15 cm in width at tray bottom, 20 cm in width at tray top and 15 cm in height. Each tray was lined with orange plastic to ensure water retention in the tray, and to provide colour contrast between the mayflies and the tray.

Forty-five (five per tray) hand-sized, flat rocks were selected from Hell Creek. Each was examined to ensure that the topside had ample algal cover and the bottom-side was algae free. These rocks were placed in the trays at 5 cm intervals. I collected 135 ephemerellid mayflies from Hell Creek for each run of the experiment. Fifteen mayflies were randomly assigned to each tray at the beginning of each experimental run, giving an average density of three ephemerellids per rock, approximately matching the density measured in Hell Creek.

Four experimental treatments were represented in each of eight replicates of the experiment, carried out on separate days. In preparation for a run, the trays were thoroughly cleaned at noon, and the rocks and nymphs were randomly assigned to each tray. Trays were randomly assigned a treatment of either: Control (n=17), duck odour (n=18), fish odour (n=19), or duck & fish odour (n=18). The fish odour treatment was created by housing a rainbow trout (*Oncorhynchus mykiss*) in a 25 L aquarium. The trout was fed ephemerellids during its stay in the aquarium. Water from the aquarium was gravity-fed into the fish odour treatment trays at noon and flowed continuously for the 12h of the experiment. The duck odour treatment was created by mixing 20 mL of harlequin duck faeces (collected previously) with 2 L of de-ionized water; 5 mL of this solution was introduced into each tray 15 min prior to each observation.

The number of aquatic insects visible on the tops of rocks was recorded for each tray at 2h intervals (daylight - 2pm, 4pm; dusk -6pm, 8pm; night - 10pm, 12am). In full darkness a red light, which is undetectable to the aquatic insects, was used to aid observations (Elliott 1977). The number of aquatic insects in each tray were counted at the end of the experimental run and the resultant measure was termed 'activity', expressed as the percentage of insects visible on the top of rocks in each tray.

Activity (%) was analysed using a multiple linear regression with backwards selection using light (day, dusk, night), treatment (control, duck, fish, fish & duck), or light by treatment interaction, weather (cloudy, sunny), and days since the beginning of the experiment as factors.

Results

I found that ephemerellid activity was strongly affected by light levels regardless of the predator-odour treatment (Figure B.1). Ephemerellids from this system increased their activity at night relative to full sunlight and dusk conditions (Figure B.2, Table B.1, B.2). The importance of light was confirmed by the reduced model containing light ($F=149.25$, $p<0.0001$) and days from the beginning of the experiment ($F=6.42$, $p=0.0117$) which accounted for 41.6% of the variation in the data (Table B.3). Activity decreased slightly with days since the beginning of the experiment by an average of 0.18% per day or 2.5% over the course of the experiment (Table B.3).

Discussion

The activity levels of aquatic insects in this experiment were strongly effected by light levels. Ephemerellids for this experiment exhibited strong, nocturnal activity levels despite their treatment, including the complete absence of predator odours. These results suggest that this trait may not exhibit plasticity in this population, and has become fixed. These individuals originated from Hell Creek, a fishless tributary of the Bridge River. However these individuals would be the offspring of dispersing adults from the Bridge River, which has been historically highly populated with fish species. A trait may become fixed in a population that has co-evolved with fish predation risk and when the costs of gathering information about predation risk exceeds the costs for lost foraging, breeding, or dispersal opportunities (Forrester 1994; McIntosh and Townsend 1994; Tikkanen et al. 1996). The mayfly *Ephemerella subvaria* only moved to the tops of stones at night even in the absence of a free swimming sculpin *Cottus bairdi*, and presence of a predatory stonefly *Agnetina capitata*, reflecting a possible fixed behaviour pattern in this population (Soluk and Collins 1988b).

During the course of the experiment American dippers (*Cinclus mexicanus*) were observed foraging in Hell Creek. Following further exploration an active dipper nest was discovered at the base of the falls near the culvert intake. The presence of dippers in this stream could have had an effect on the behaviour of aquatic insects in this reach. Dipper predation reduced the number of exposed heptageniid mayflies, but failed to produce similar effects in other families of aquatic insects (Harvey and Marti 1993). The effect of American dipper predation risk has not been examined on the family used in my study, and I cannot know whether their presence would induce anti-predator behaviours in this population. The water intake for this experiment was at the opposite end of the culvert below the falls and I therefore cannot guarantee that waters used were completely free of predator odours.

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Table B. 1 Parameter estimate results of multiple linear regression with all factors (r^2 = 0.4243).

Variable	Levels	DF	Estimate	Pr > [t]
Intercept		1	0.1709	<0.0001
Light	Dusk	1	-0.1392	<0.0001
	Full Sunlight	1	-0.1265	<0.0001
	Night	0	0	.
Treatment	Duck & Fish	1	-0.0265	0.1325
	Duck	1	-0.0002	0.9890
	Fish	1	-0.0055	0.7497
	Control	0	0	.
Light * Treatment	Dusk * Duck & Fish	1	0.0234	0.3481
	Dusk * Duck	1	0.0094	0.7052
	Dusk * Fish	1	-0.0004	0.9881
	Dusk * Control	0	0	.
	Full * Duck & Fish	1	0.0202	0.4169
	Full * Duck	1	-0.0142	0.5689
	Full * Fish	1	-0.0068	0.7834
	Full * Control	0	0	.
	Night * Duck & Fish	0	0	.
	Night * Duck	0	0	.
	Night * Fish	0	0	.
	Night * Control	0	0	.
Weather	Cloudy	1	-0.0094	0.3242
	Sunny	0	0	.
Days from start of experiment		1	-0.0022	0.0087

Table B. 2 Type III test results from multiple linear regression with all factors ($r^2 = 0.4243$).

Source	DF	F Statistic	Pr > F
Light	2	147.51	< 0.0001
Treatment	3	0.60	0.6163
Light * Treatment	6	0.50	0.8064
Weather	1	0.97	0.3242
Days	1	6.94	0.0087

Table B. 3 Parameter estimate results from a multiple linear regression with only Light and Days from beginning of experiment factors, ($r^2 = 0.4160$).

Variable	Light	DF	Estimate	Std Error	Pr > [t]
Intercept		1	0.1575	0.0081	<.0001
Light	Dusk	1	-0.1311	0.0086	<.0001
	Full	1	-0.1268	0.0086	<.0001
	Night	0	0	.	.
Days		1	-0.0018	0.0007	0.0117

Figure B. 1 Visibility measures from predator odour experiment. Day (☐), Dusk (☐), Night (■). Error bars are 95% CI.