Variation in Harlequin Duck Distribution and Productivity: The Roles of Habitat, Competition, and Nutrient Acquisition

Prepared with Financial Support of:
BC Hydro Bridge-Coastal Fish and Wildlife Restoration Program (BCRP)

Fiscal Year 2005-06
(Year 3 of a 3-year project)
BCRP Project Number: 05.W.Br.03

April 2007

Prepared by:
Dr. Dan Esler, University Research Associate
Dr. Ron Ydenberg, Professor and Director
Jeanine Bond, MSc Student
Sunny LeBourdais, MSc Student

Centre for Wildlife Ecology
Department of Biological Sciences
Simon Fraser University
Burnaby, BC V5A 1S6

EXECUTIVE SUMMARY

This project, led by the Centre for Wildlife Ecology at Simon Fraser University, was designed to address the factors that influence harlequin duck distribution and productivity in the southern Coast Mountains. This research project supports the Bridge Coastal Fish and Wildlife Restoration Program mandate of habitat restoration by filling the information gaps that currently inhibit informed management. This work provides the scientific background necessary to understand how variation in habitat (including that related to hydroelectric operations and other human activity) affects harlequin ducks, and prescribe mitigation or restoration activities that would improve harlequin duck productivity. This project evaluated how variation in habitat would affect harlequin ducks in three ways. The first was to develop models describing the relationship between harlequin duck distribution and habitat attributes (for example, stream slope, width, substrate, vegetation, and prey availability) at a regional scale. The second was to evaluate the importance of breeding streams as a source of nutrients for reproduction. And, third, we considered factors that influence benthic invertebrate availability, particularly stream flow variability and the occurrence of fish.

We found that many of the habitat attributes that we measured were not strong predictors of harlequin duck presence or variation in density. Stream slope was moderately supported, with streams with steeper gradients having lower densities of harlequin ducks. Therefore, modifications to streams for power production (e.g., independent power projects [IPP]) should be directed at reaches with higher slopes, from the perspective of harlequin duck conservation. Also, we found tendencies of harlequin ducks to occur at higher densities in reaches with higher densities of aquatic invertebrates. Because invertebrate densities are higher in streams with stable flow regimes, this has direct implications for management of streams for harlequin ducks.

Using stable isotope analysis, we determined that female harlequin ducks build their eggs almost entirely from nutrients acquired on breeding streams, rather than from nutrient reserves built on coastal wintering sites. This indicates that maintenance of abundant prey resources on breeding streams is an appropriate management goal for conserving harlequin ducks.

Finally, we detected a negative relationship between fish and harlequin ducks. We suggest that this relationship stems from changes to behaviour of aquatic insects in the presence of fish, namely that invertebrates hide in the substrate to avoid fish predation and subsequently are less available for harlequin ducks. We suggest that the widespread introduction of fish may be a factor in the broad-scale depression of harlequin duck productivity that has been described for harlequin ducks that winter in coastal BC. From a conservation perspective, this finding further illustrates that introductions of fish into previously fish-free streams, or enhancements of fish populations, will have consequences for other members of stream communities,

including harlequin ducks. These consequences should be considered as part of fish management activities.

Overall, we found that human-induced changes to breeding streams do not necessarily have negative consequences for harlequin ducks. For example, flow stability in the Bridge River due to the controlled release regime from Terzaghi Dam has led to high densities of aquatic invertebrates and, presumably, high habitat quality for harlequin ducks. Also, construction of IPPs on steeper sections of streams may not affect harlequin ducks; for example, we found high densities of harlequin ducks above the IPP on Rutherford Creek, including in the impoundment directly behind the dam. In addition, the power canal from the Seton River supports high densities of invertebrates and serves as a gathering site for harlequin ducks. However, changes to streams in higher quality harlequin duck habitat (i.e., areas with relatively low slopes and high invertebrate densities) can have negative consequences on abundance and productivity. For example, highly variable releases from dams would result in reductions in prey availability, and higher likelihood of flooding of harlequin duck nests. Also, introduction or enhancement of fish numbers could reduce habitat quality for harlequin ducks through changes to invertebrate densities and behaviour. Clearly, the original footprint of large dams constructed for power production affected large amounts of harlequin duck habitat. This study offers insights into the attributes of remaining habitats that can be maintained or enhanced, with the goal of increasing harlequin duck numbers and productivity.

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1. INTRODUCTION

Harlequin ducks (*Histrionicus histrionicus*) are of conservation concern across the continent, and they are thought to be particularly sensitive to habitat degradation (Robertson and Goudie 1999, Smith et al. 1999). Like other sea ducks, harlequin ducks spend the nonbreeding portion of their annual cycle in nearshore coastal environments. Harlequin duck breeding habitat, however, is unusual, as they nest and raise broods along fast-flowing streams in mountainous terrain. Changes to the attributes of these breeding streams could affect harlequin duck productivity and, subsequently, population dynamics. We initiated this project to determine the attributes of breeding streams that correspond to harlequin duck density and productivity and, further, to explore the mechanisms by which variation in habitat affects the ducks. In turn, this information is intended to provide advice for conserving harlequin ducks, through recommendations for habitat restoration or mitigation and for placement of projects that could affect ducks.

There is evidence suggesting that constraints on harlequin duck populations are exerted on breeding streams. A long-term program examining harlequin duck demography in the Strait of Georgia (led by the Canadian Wildlife Service and the Centre for Wildlife Ecology, SFU) concluded that recruitment was not compensating for annual adult mortality, and that productivity was likely too low to sustain populations (Robertson and Goudie 1999, Smith et al. 2001, Rodway et al. 2003). However, there have been only a small number of studies that have attempted to link harlequin duck distributions or productivity to habitat features on breeding streams (Bruner 1997, Rodway 1998, Wright et al. 2000, Hill and Wright 2000, Freeman and Goudie 2001, Heath et al. 2006). This project was intended to build upon these studies by considering habitat – duck relations on a regional scale and, also, by considering specific mechanisms by which habitat variation could affect productivity.

Hydroelectric development in the Bridge-Coastal region resulted in loss of harlequin duck habitat, through flooding of streams, and changes to harlequin duck habitat as a result of riparian vegetation and benthic invertebrate changes downstream from hydroelectric operations. Effective restoration of harlequin duck habitat requires a clear understanding of the habitat attributes that are positively related to harlequin duck abundance and productivity. We view this study as the first, important step in habitat restoration, which is filling the information gaps that currently inhibit informed management. This work was designed to (1) describe, on a regional scale, the relationship between habitat attributes and harlequin duck distribution, abundance, and productivity, and (2) explore the mechanisms that explain observed variation. We think that this approach is critical for understanding both whether changes in habitat related to hydroelectric development affect harlequin ducks and how habitat change affects ducks.

Habitat – species relationships are important to establish to direct conservation activity. Knowing the habitat attributes that are positively correlated with abundance and/or productivity provides an indication of key features of the environment, suggests mechanisms by which habitat influences the species of interest, and indicates features that could be manipulated to increase densities or productivity. Further, models can be used in a predictive sense to estimate the value of areas that have not been surveyed, which in turn can be used to direct anthropogenic development to less valuable habitat. To understand the relationship between habitat and harlequin duck distribution and productivity, we conducted surveys on sections of streams in 2003 and 2004, where we also documented a suite of habitat attributes. We used these data to describe variation in harlequin duck densities as a function of habitat features. Similar approaches have been applied to the question of harlequin duck breeding distribution (e.g., Bruner 1997, Rodway 1998, Wright et al. 2000), including on breeding streams in British Columbia (Hill and Wright 2000, Freeman and Goudie 2001). However, most of these were conducted on a single watershed; we undertook a region-wide approach that allowed drawing inference across a range of watersheds and habitat types.

In addition to the broad-scale description of patterns in harlequin duck distribution and productivity, we investigated two specific mechanisms that we consider critically important for understanding how breeding habitat (and changes to that habitat) influence harlequin duck productivity. These mechanisms address the premise that availability of invertebrate prey may have an important influence on harlequin duck habitat selection and productivity. This premise is supported in the literature. For example, Gardarsson and Einarsson (1994) described close correlation between varying food supply and waterfowl populations. For harlequin ducks specifically, Bengston and Ulfstrand (1971) indicated effects of food availability on breeding propensity, and Rodway (1998) suggested that harlequin ducks were food-limited on breeding streams. The specific questions that we addressed are: (1) does foraging on breeding streams constitute an important part of the energy and nutrients required for clutch formation? and (2) do flow variability and fish abundance influence the availability of harlequin duck invertebrate prey? Answers to these questions provide insight into links between food, tropic interactions, and subsequent harlequin duck productivity.

<u>Is food on breeding streams an important source of nutrients and energy for clutch formation by harlequin ducks?</u> Egg synthesis in birds involves production of yolk, albumen, and eggshell, which are derived from lipid, protein, and mineral macronutrients (Carey 1996). Energetic and nutritional costs of egg formation by waterfowl are high relative to most other birds (King 1973). Waterfowl clutches are comprised of numerous, large, energy-dense eggs and daily costs of egg synthesis are high, as much as 200% of the female's basal metabolic rate (Alisauskas and Ankney 1992). Waterfowl employ an array of strategies to meet high clutch formation costs, including storing and using endogenous nutrient reserves away from breeding areas, relying on food sources at breeding areas, or a combination of these approaches. There are a number of factors that influence the best strategy for acquiring egg nutrients, including the ability of hens to carry reserves during migration, food abundance and quality on nonbreeding and breeding areas, and other behavioural and physiological constraints. These issues have never been addressed for harlequin ducks. In this part of the project, we documented the relative contribution of breeding stream foods for meeting the nutritional and energetic demands of clutch formation. In

turn, this lends important insight into how, and at what life stages, breeding stream quality is important for harlequin duck productivity.

Do fish and flow variability affect suitability of stream habitats for breeding harlequin ducks? The aquatic insect community in a stream is influenced by both abiotic and biotic factors. Abiotic factors 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 (Hildrew and Giller 1994, Allan 1995; Giller and Malmqvist 1998;). Predation, competition, disease, and parasitism are all biotic factors that may also affect the aquatic insect community (Hynes 1970, Allan 1995).

Under a variety of ecological conditions, fish predation has been documented to have strong impacts on macroinvertebrate communities (Thorp 1986), which may be the result of changes in density or behaviour. The introduction of fish has been identified as a major threat to biodiversity, and conservation of native species (Horne and Goldman 1994, Cambray 2003). The addition 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 reductions in aquatic insect availability as a consequence of density and/or behaviourally mediated indirect interactions. The devaluation of harlequin duck breeding habitat could contribute to diminishing productivity and recruitment seen in wintering populations. For this part of the study, we used detailed observations of fish, invertebrate and harlequin duck distributions to evaluate spatial relationships and analyze the potential interactions that could have important influences of harlequin duck breeding habitat quality.

Taken together, this 3-pronged approach offers important new insights into the factors that influence harlequin duck habitat use, abundance, and productivity on breeding streams. As highlighted below, we believe that these findings will provide clear recommendations for conservation activities to improve stream quality for harlequin ducks and novel insights into the underlying mechanisms that lead from variation in habitat to variation in duck abundance or productivity. We trust that this work will be useful for restoring or managing streams affected by hydroelectric development, improving habitat quality on other streams for mitigation or other purposes, identifying habitats that are appropriate for either development or protection, and offering insight into broad-scale mechanisms that might explain population declines or low recruitment in Pacific coast harlequin duck populations.

2. STUDY AREA

Because this project was designed to address, on a regional scale, the factors that influence harlequin duck distribution and productivity, the work occurred within several of the watersheds that fall under the BCRP, including the Bridge, Seton, and Cheakamus Rivers (Figs 2.0.1 and 2.0.2). We also included several watersheds within the Bridge-Coastal Region that are not specifically listed under the BCRP, to allow contrast with streams that have not had hydroelectric development. These included Cayoosh Creek (which drains into the Seton River), the Yalakom River (which joins with the Bridge River), Rutherford Creek, Ryan River, and Birkenhead River. These represent a variety of habitat types and duck densities and allow broad inference.

Figure 2.0.1 Locations of study stream segments that were surveyed for harlequin ducks and habitat attributes in the Lillooet region of our study area.

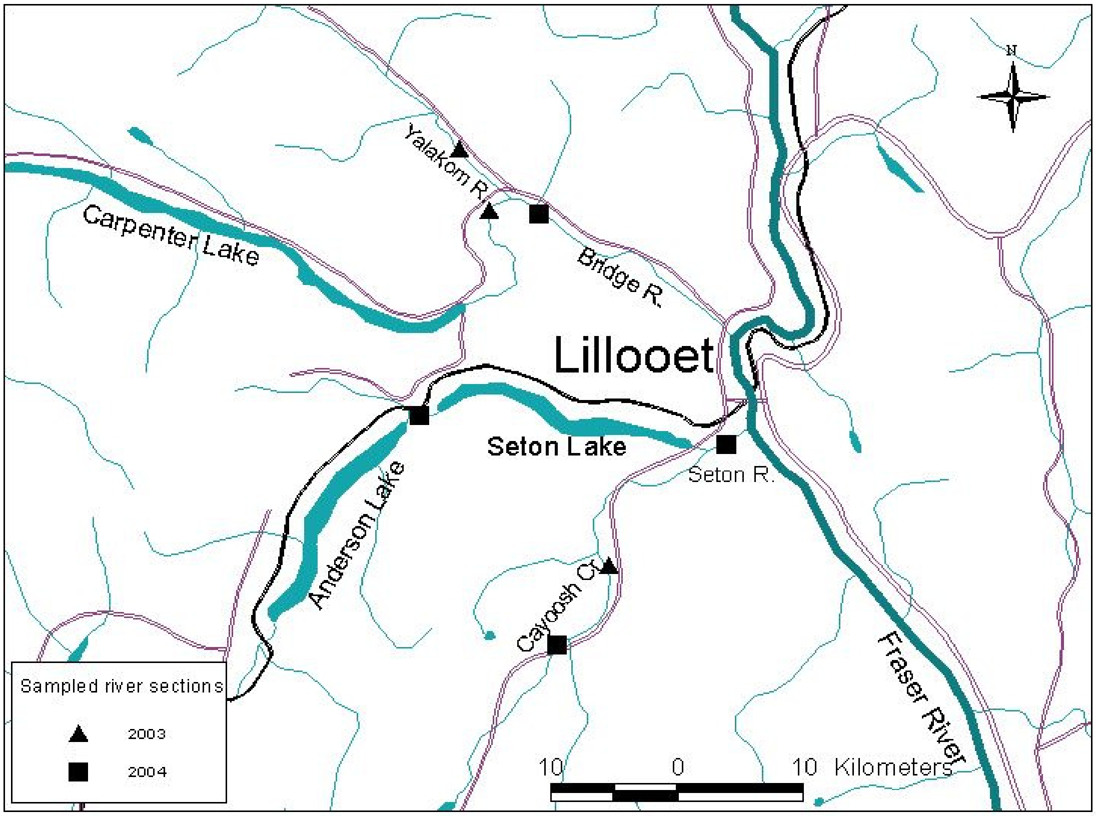
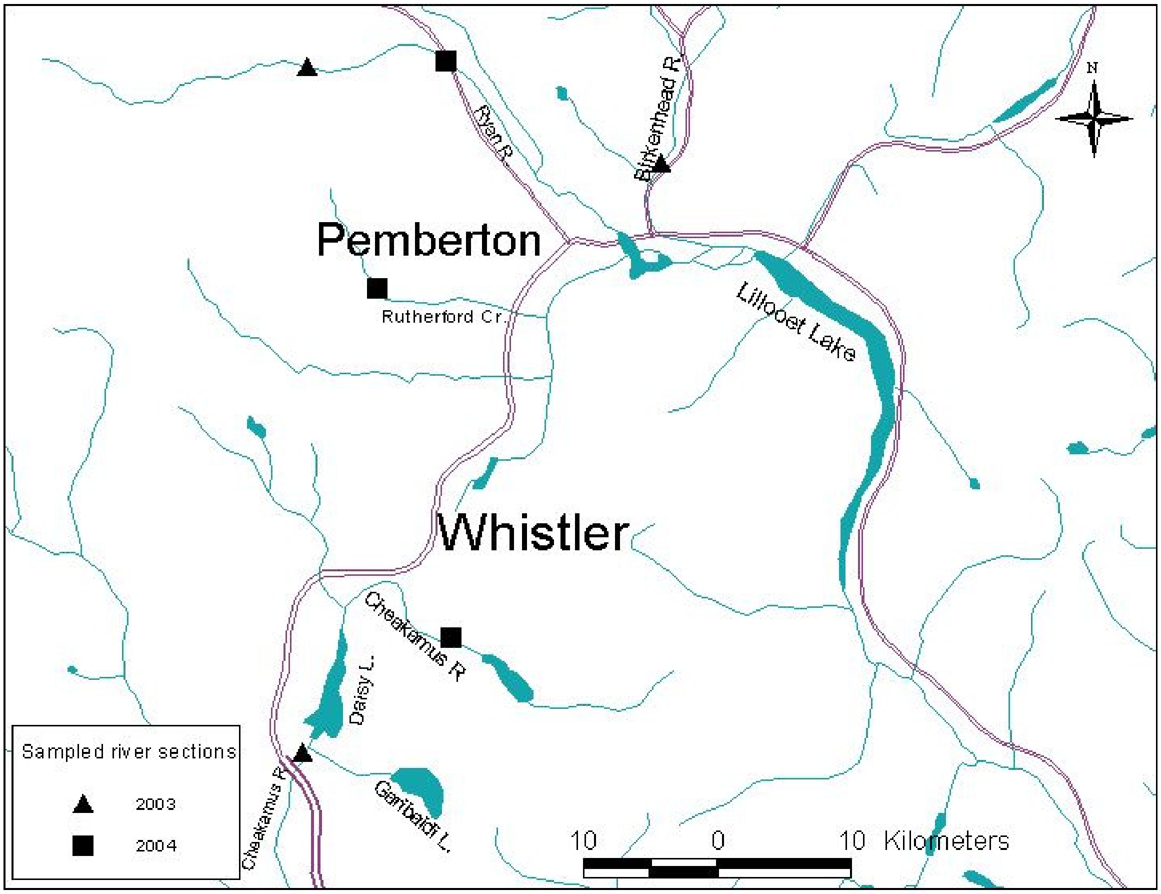


Figure 2.0.2 Locations of study stream segments that were surveyed for harlequin ducks and habitat attributes in the Pemberton region of our study area.



3. METHODS

3.1. Habitat Associations

The first part of the project, linking harlequin duck distribution data with habitat information, required duck surveys and detailed measurement of habitat attributes, as described below.

3.1.1. Pair Surveys

In both 2003 and 2004, seven streams sections, roughly 5 km in length, were selected based on access and contribution towards representation across a range of harlequin duck densities and habitat attributes (Tables 3.1.1 and 3.1.2). Each of these were surveyed once during the pair arrival and laying period (30 April to 23 May) prior to freshet. Surveys were conducted following standard harlequin duck survey protocol outlined in the Provincial Resource Inventory Committee Standards. In brief, each survey team consisted of at least 2 observers, who hiked upstream adjacent to the stream channel and continuously scanned for birds with the aid of binoculars. At each observation we recorded: the number of individuals, sex of each, band code if banded, and behaviour. Behaviour was described first as “in water” or “hauled out”. Dominant behaviour was then described as: “feeding” or “other”, which included any other behaviour such as resting, preening, courting, or alert/evasive.

3.1.2. Brood Surveys

Brood surveys were conducted on the same reaches as pair surveys, and followed the same protocol. Brood surveys were conducted from 17 July to 6 August 2003 and 16 July to 22 July 2004. At each harlequin duck observation, the number of hens, the number of ducklings, and the age class of ducklings (Class Ia, Ib, Ic, IIa, IIb, and III) were recorded. Adult males were never detected during these surveys, as they had already returned to coastal molting and wintering areas. Age class designations followed those of Gollop and Marshall (1954), in which: Ia = totally down covered, Ib = down-covered but color fading, Ic = body elongating, IIa = first feathers on sides and tail, IIb = > half of body covered with feathers, IIc = small amount of down on back, and III = fully feathered but incapable of flight. Behaviour was described in the same manner as for pair surveys.

Table 3.1.1 Location of selected stream stretches for habitat harlequin duck surveys, 2003.

Stream	***Reach length (km)***	***Start description***	***Start GPS***	***Start alt (m)***	***End description***	***End GPS***	***End alt (m)***	***Map***
Seton River	4.22		50 40 54.4 121 55 36.4	700	Seton Dam	50 40 10.2 121 58 38.6	225	92i/12
Bridge River	5.00	Yalakom R confluence	50 51 48.4' 122 10 21.2	440	d/s of Yankee CK	50 49 58.0' 122 11 53.6	475	92j/16
Yalakom River	5.28	Buck Ck	50 52 57.0 122 12 07.0	535	FSR Bridge	50 54 46.0 122 14 20.6	685	92j/16
Cayoosh Creek	5.24	trib. d/s of Downton Ck	50 36 13.6 122 06 11.2	655	u/s of Downton Ck	50 33 49.4 122 05 35.8	715	92j/9
Birkenhead River	5.25	Owl Ck	50 20 58.6 122 43 41.8	275	u/s of bailey bridge	50 23 03.2 122 42 25.0	335	92j/7
Ryan River	5.07	tributary confluence	50 27 06.8 123 05 19.0	685	No reference	50 27 37.0 123 08 40.0	715	92j/6
Cheakamus River – lower	5.27	highway pullout	49 56 14.4 123 10 01.6	300	highway bridge	49 58 33.8 123 08 39.0	360	92g/14

Table 3.1.2 Location of selected stream stretches for habitat harlequin duck surveys, 2004.

Stream	*Reach length (km)*	*Start description*	*Start GPS*	*Start alt (m)*	*End description*	*End GPS*	*End alt (m)*	*Map*
Seton River I (SEI)	4.22	Fraser R confluence	50 40 54.4 121 55 36.4	215	Seton Dam	50 40 10.2 121 58 38.6	225	92I/12
Seton River II (SEII)	3.0	Seton Lake	50 42 29.8 122 16 09.8	235	Anderson Lake	50 42 10.0 122 18 08.8	265	92J/9
Bridge River	5.0	Camoo Bridge	50 49 39.8 122 06 45.2	350	bottom of horseshoe bend	50 51 27.4 122 09 27.2	395	92J/16
Cayoosh Creek	5.0	Gott Creek	50 32 15.6 122 07 47.0	815	small trib from east	50 30 35.2 122 10 07.6	915	92J/9
Cheakamus River	5.0	No reference	50 02 28.6 123 00 44.2	745	Cheakamus Lake	50 01 40.4 122 57 19.4	855	92J/2 & 92J/3
Rutherford Creek	6.1	Km 12 bridge abutment	50 16 55.6 123 00 43.4	790	north Rutherford Creek	50 18 33.2 123 03 55.2	855	92J/6
Ryan River	5.1	1.5 km south of Ryan River Rd	50 26 17.8 122 55 54.4	235	No reference	50 27 47.4 122 59 01.6	320	92J/7

3.1.3. Habitat Measurement

We measured a broad suite of habitat features that we speculated, or had been demonstrated in previous studies, to be important determinants of harlequin duck abundance or productivity. During pair surveys, we measured “time-sensitive” habitat attributes, that is, habitat features that change over time and hence measurement could not be deferred until later in the season. These were measured at systematically located points along each stretch of creek, starting with a randomly selected first point and then at every 500 m thereafter. These points were measured as linear distances from the start point or the last habitat station, using a GPS; we did not attempt to measure the 500 m as a stream distance, given logistical and technological constraints. Also, habitat attributes were measured at the location of each duck sighting. Each site for habitat measurement consisted of a 20 m section of stream (10 m upstream and 10 m downstream of the habitat sampling point or the exact duck location). The time-sensitive habitat attributes that were measured during the pair surveys included: stream width, flow rate, water depth, water temperature, pH, substrate, slope, number of in-stream boulders, and invertebrate abundance. Also, the presence of gravel bars, islands, and nearby tributaries was noted in the comments section. Each of the sites for habitat measurements was GPSed and flagged to facilitate measurement of remaining (vegetation) habitat features later in the summer.

The habitat sampling methods that we used are described below; note that time sensitive attributes are indicated by an asterisk.

Invertebrate Abundance* – We sampled aquatic invertebrates from surface rocks at every other systematic habitat site, beginning at the second site, using a 5-rock technique (McCutchen and Ydenberg 2005). We started at the downstream end of the habitat site and worked upstream, to avoid disturbing insects before they have been sampled. Each sample consisted of gathering 5 fist-sized cobbles. An aquatic D-net was positioned downstream of each rock as it was picked up and the invertebrates on the surface of the cobble were removed into the net using a brush. Volume of each rock was measured by water displacement (+/- 25 mL) in a graduated cylinder. Invertebrates were extricated from the net and put into plastic sample containers with water. A total of 3 sampling sites per habitat site (at 10 m downstream of the station, at the station point, and at 10 m upstream) were completed, for a total of 15 rocks. Invertebrate samples were transferred into labeled vials and preserved in a solution of 70% ethanol at the end of the day.

Flow type* - We estimated the areal proportion of the 20 m habitat sampling section that fell into the flow type categories below to the nearest 5%. Flow types that were present but less than 5% were indicated by “trace” on the data sheet. Categories for flow type included: pool, which was still or nearly still water in a broadened area of the stream; glide, when the water was flowing, even quickly, but there was no surface turbulence; riffle, areas where whitewater occured, through either flow over rocks or high volume passage through constrained areas; and cascade, which occured in areas with > 4% gradient where water was rushing and tumbling through the channel.

Substrate size and composition* – We visually estimated areal percentage of each substrate type (bedrock, boulder, cobble, gravel, and sand) in 20 m stream sections centered at each random and duck site. Proportion of each substrate type was estimated to the nearest 5%.

Number of exposed boulders* - Number of exposed boulders, i.e., rocks that were not being topped with water at any time, were counted in the 20 m stream section centered on each random and duck site. Boulders were a minimum of 1 m apart to constitute a unique exposed boulder to avoid including clusters of closely situated rocks as separate boulders.

Stream width* – We visually estimated the wetted stream width to the nearest meter. We took 3 measures: 1 at the exact station point and 1 each at 10 m up- and downstream.

Stream depth* – We visually estimated the "maximum" and "mean" depth at each random and duck site to the nearest 1/10 of a meter. This was done as a transect across the stream at the station point and at the 10m points above and below the station.

Flow rate* - We measured stream velocity by timing the movement of a stick through a 10m section of stream, done 3 times to generate an average.

Temperature* - Temperature was measured once in each survey reach using a digital instream thermometer.

pH – pH was measured once in each survey reach using a digital instream pH meter.

Slope – This was measured with a clinometer from one end of the 20 m stream section to the other.

Vegetation Sampling - Vegetation was described for the 20 m habitat sampling segment. Measurements were taken for the stream bank opposite of the observers. We measured the maximum horizontal distance that overhanging vegetation extended over the stream bed. We defined overhanging vegetation as vegetation within 1.5 m above the stream surface that extended over the stream bed. We also estimated the mean overhang, as the mean horizontal distance that overhanging vegetation extended over the stream bed. We also recorded the linear extent of overhang, which was the length, to the nearest 0.5 m, of the shoreline (within the 20 m sampling section) that had overhanging vegetation. We measured woody debris in a manner similar to overhanging vegetation, with woody debris defined as logs and sticks that were partially in the water and break the water surface. We recorded the maximum horizontal distance that woody debris extended into the stream bed. We also estimated the mean horizontal distance that woody debris extended into the stream bed. Also, we recorded the length, to the nearest 0.5 m, of the shoreline that had woody debris. Finally, we measured vegetation cover, which incorporated both height and density attributes. At 3 different heights above the lower extent of vegetation, we described the linear distance, to the nearest 0.5 m, that was open, with open defined as allowing visibility beyond a plane extending vertically from the edge of the river channel. This was estimated for the band from 0 to 1 m above the point where vegetation first occurs (or the stream bed if no vegetation at all is present, such as on talus slopes), for the 1-5 m band, and for the 5-10 m band. Large boulders and steep banks that fell into the vertical plane were included in the cover estimate.

3.1.4. Statistical Analyses

We evaluated relationships between harlequin ducks and habitat attributes in 2 ways: (1) using logistic regression to evaluate the probability of duck presence as a function of habitat features, and (2) using general linear models to examine correlations between densities of harlequin on a stream and average habitat attributes for those same streams. In both of these analyses, we excluded data from Rutherford Creek in 2004; the harlequin duck survey for that reach was interrupted by poor weather, and an attempt to repeat the survey and habitat samples was affected by high water. We know that the duck density measured during the survey was biased low, given our observations during the capture portion of the study, so we removed the stream from the analyses.

Presence/absence analysis – In this analysis, we contrasted habitat attributes at sites used by ducks with the systematic sites without ducks where habitat data were collected. We used a binary response variable indicating harlequin duck presence or absence in a logistic regression framework, with habitat attributes as explanatory variables.

For analysis, the measured habitat attributes were summarized for each station (both with and without ducks). We created a single value for each variable at each station, using the following approach:

Invertebrate availability was summarized for each station in units of g dry mass per m^2. The volume of each sampled rock was converted to an estimate of surface area (in cm^2) using the formula: Surface Area = 13.875 * log Volume $^{3.603}$. Surface area of all rocks for each station were added to estimate total area sampled. Invertebrates were dried to a constant mass in the laboratory, to generate dry mass data for each station, and then dry mass per surface area was calculated.

Substrate was considered as the average % cobble of each sampling station. Of all observations, measures of cobble and boulder combined accounted for 91% of substrate type designations, with other subtrates being poorly represented. Cobble was chosen as the representative level because it was most common and any measure of cobble also provided an approximation of boulder (i.e., 100 – cobble ≈ boulder).

Number of exposed boulders was measured once per station and was directly included as a continuous variable in analyses.

Stream width was represented by the average width calculated from the 3 measurements per station.

Slope was measured once per station and was directly included as a continuous variable in analyses. Flow type and flow rate were not included in analyses, as these were highly correlated with, and thus redundant to, slope.

Overhanging vegetation was calculated as linear extent X average horizontal overhang, resulting in an areal estimate of overhanging vegetation.

Woody debris was calculated as linear extent X average horizontal extent, similar to that for overhanging vegetation.

Vegetation cover was calculated as:
((0-1m veg cover/20)*0.3333) + ((1-5m veg cover/20)*0.3333) + ((5-10m veg cover/20)*0.3333). This equation provides the total % openness for the 20 linear meters and 10 horizontal meters of shoreline surveyed. By multiplying each horizontal section by 0.3333, the formula gives greatest weight to the 0-1 m horizontal vegetation, medium weight to the 1-5 m horizontal vegetation, and the least weight to the 5-10 m horizontal vegetation.

We used an information-theoretic approach to contrast logistic regression models (Burnham and Anderson 2002). The candidate set of models included various groupings of explanatory variables. To limit the numbers of models, we included or excluded variables in groups of related variables. The first group, *INVERTS*, included only the invertebrate availability variable. The next group, *ABIOTIC*, included the variables describing physical features of the streams, including: substrate, number of exposed boulders, stream width, and slope. The final group, *VEG*, consisted of the variables describing vegetation structure, including: overhanging vegetation, woody debris, and vegetation cover. By considering the data in this way, we explicitly addressed the relative effects of food, physical habitat, and stream vegetation on harlequin duck distribution.

Our candidate model set included all additive combinations of explanatory variable groupings, i.e., model structures included:
DUCK PRESENCE (1/0) = *INVERTS*
DUCK PRESENCE (1/0) = *ABIOTIC*
DUCK PRESENCE (1/0) = *VEG*
DUCK PRESENCE (1/0) = *INVERTS* + *ABIOTIC*
DUCK PRESENCE (1/0) = *INVERTS* + *VEG*
DUCK PRESENCE (1/0) = *ABIOTIC* + *VEG*
DUCK PRESENCE (1/0) = *INVERTS* + *ABIOTIC* + *VEG*
We also included a null model, in which variation in duck presence was not explained by any of the variables we measured.

We constrasted models using AICc (Burnham and Anderson 2002), which balances model fit against model complexity. The model with the lowest AICc value is the most parsimonious (provides good fit without overfitting with uninformative parameters), and we interpreted the model ranking such that parameters in the more parsimonious models are well-supported for explaining variation in duck presence. We calculated ΔAICc, which is the difference in AICc values between the most parsimonious model and each subsequent model (Burnham and Anderson 2002), which aids in contrasting models. We also calculated AIC weights (AICw) for each model, which indicates the relative support for each model; AICw sum to 1 across models, and models with high AICw have strong support from the data (Burnham and Anderson 2002). Finally, we calculated parameter likelihoods for each variable, as another measure of support for individual parameters (in this case, groups).

Variation in density analysis – We followed a very similar approach when evaluating variation in harlequin duck density across streams. However, in this case, the response variable was duck density calculated across each stream as the number of ducks observed divided by the length of the surveyed stream segment. The explanatory variables were the same as described above; however, in this case, the data used for the analysis were the averages for each of these attributes for each stream, across all of the systematic sampling sites (i.e., data collected at duck observation sites were not included in averages).

We conducted simple linear regressions for each variable, and also conducted an information-theoretic analysis using the sample variable groupings and candidate model set as described above. We calculated AICc, ΔAICc, AICw, and parameter likelihoods, as described above.

3.2. Nutrient Allocation

3.2.1. Sample Collection

To address the question of nutrient allocation to clutch formation by harlequin ducks, we captured, sampled, radio-marked and released females. We captured harlequin ducks on breeding streams from arrival through the egg-laying period, using an established and effective method of mist-netting. We used an 18 m mist net with a mesh size of 127 mm. We set the net across the stream using two 3 m conduit poles that were guyed out with cord and ensured that the net was set up above water. Captured birds were quickly removed from the net.

Body mass was determined by placing each duck, restrained in a Velcro strap, on a digital scale and recording to the nearest gram. All ducks were fitted with a US Fish and Wildlife Service stainless steel band on the right leg and a coded, colour tarsus band (orange with black or black with white) on the left leg. Morphometric measurements were taken on all ducks, including exposed culmen length and diagonal tarsal length to the nearest 0.01mm, as well as wing chord (flattened and straightened), wing stub, and the length of the ninth primary to the nearest mm. Sex was determined by plumage characteristics and age class was estimated by the depth of the Bursa of Fabricius where bursas ≤ 3mm are after third year (ATY), bursas 4-10mm are third year (TY), and bursas >10mm are second year (SY) (Mather and Esler 1999).

We employed stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) to investigate nutrient allocation to egg formation. Marine ecosystems are more enriched in the heavier stable isotope relative to terrestrial or freshwater ecosystems, and therefore, stable isotope signatures can be used to track origins of nutrients from marine or freshwater sources (Michener and Schell 1994, Hobson et al. 2000, Klaassen et al. 2001). Because harlequin ducks migrate between marine wintering grounds and terrestrial breeding grounds, their stored nutrients differ isotopically from locally available nutrient sources. To measure isotopic signatures of stored nutrients, we collected body tissues including blood (<2ml) and a small subcutaneous lipid biopsy from the abdomen. We also collected stream invertebrates to measure stable isotope signatures of diet items on breeding streams, and marine invertebrates and harlequin duck tissue samples from the Strait of Georgia to indicate isotopic profiles from nonbreeding areas. These items were stored in vials and frozen until analysis (see Appendix IV).

To measure the relative contributions of marine and freshwater nutrients to harlequin duck clutches, we collected eggs for subsequent isotopic analyses. Female harlequin ducks are cryptic, solitary nesters, and in order to find nests, each female captured on breeding streams was attached with a radio transmitter using a subcutaneous anchor and glue (Appendix IV). Radio-tagged females were monitored at least once a week to locate nests, and one egg was removed at random from each discovered clutch. Clutches ranged from five to seven eggs. Each egg was boiled for easy separation and then frozen. We also collected two complete clutches, one from a female that was killed by a predator and the other from a female that abandoned her nest after it flooded.

3.2.2. Laboratory Methods

Samples for carbon and nitrogen stable isotope ratio analyses were prepared at Simon Fraser University and then sent to the Department of Soil Sciences at the University of Saskatchewan for isotope ratio determination. Samples were separated into lipid and non-lipid components, if necessary, because of potential differences in allocation of these nutrients to eggs. Samples analysed for this study included abdominal lipid (n = 18), cellular fraction of blood (n = 60), freshwater invertebrates (lipid, n = 5, and non-lipid, n = 9), lipid-free egg yolk (n = 23), egg yolk lipid (n = 23), and egg albumen (n = 23). These samples were dried, ground, lipid-extracted, and then measured using continuous-flow isotope ratio mass spectrometry (see Appendix IV for more details). All isotope values per sample are expressed in delta (δ) notation, a ratio of the heavier to lighter isotope relative to standards in parts per thousand.

3.2.3. Statistical Analyses

To evaluate the relative contributions of source nutrients (marine or freshwater) to eggs, single-isotope linear mixing models for carbon and for nitrogen were employed (Phillips & Gregg 2001). Because lipid contains very little nitrogen, only carbon stable isotope values were used to model origins of this macronutrient (Hobson *et al.* 2005). These analyses compare the stable isotope signatures of egg contents to those of putative nutrient sources (diet items and harlequin duck tissues collected on both nonbreeding and breeding areas) to estimate the relative contributions of each to composition of eggs.

3.3. Biotic and Abiotic Influences on Food Availability

We approached this issue as an evaluation of variation in invertebrate abundance as a function of environmental attributes and presence of predators. This question was addressed in part by comparing the broad distribution patterns of fish, invertebrates, and ducks across the different study streams. Some of these data (duck and invertebrate abundance) are generated by the survey and habitat protocol described above. River flow data and fish information were gleaned from existing sources or from direct sampling, and additional invertebrate sampling was used for this part of the study. The methods for this aspect of the study are described in more detail in Appendix V, but are summarized below.

3.3.1. Aquatic Insect Samples

Aquatic insect samples were obtained using the 5-rock method in 2003 and 2004 (Appendix V; see also habitat sampling above). During habitat surveys aquatic insect samples were collected from habitat stations, and from locations where harlequin ducks were sited (see habitat sampling methods). Intensive aquatic insect samples also were taken from single sites throughout the season on all eight rivers in 2004. All samples were labelled, stored, processed, and all data were entered into a database for statistical analysis.

3.3.2. River Level Data

Daily mean river level data were obtained from the Water Survey of Canada (Campo, pers. comm.) for the Yalakom River, Cayoosh Creek, Seton River, and Cheakamus River for both 2003 and 2004. Daily mean river level data were obtained from BC Hydro from stream gauges located in the Lower Bridge River (Sneep, pers. comm.) and from Summit Power from stream gauges located in the Ryan River (Croft, pers. comm.). The river level variability was calculated as the variance of daily mean river levels from April 1st to July 1st, which encompassed the period when we were sampling.

3.3.3. Fish Data

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 in order to create a fish rating based on: the use of the reach by anadromous species for spawning purposes; the comparative 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*); and the presence of Cutthroat trout (*Oncorhynchus clarki clarki*); and the presence of benthic-feeding species including: Mountain Whitefish (*Prosopium williamsoni*), Suckers (family: *Catostomus*), Scuplins (family: *Cottus*), and Dace (family: *Rhinichthys*) (see Apendix V).

3.3.4. Statistical Analyses

We used path analysis to evaluate relationships among harlequin ducks, fish, and aquatic invertebrates. 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 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).

Before performing the path analysis we created a specific path diagram that allowed fish to affect harlequin duck density through two separate paths. Path #1 was from fish to harlequin ducks, and was hypothesized to possibly represent a behaviourally mediated indirect interaction (Appendix V). Path #2 was from fish to available aquatic insects to harlequin ducks and represented the presence of a density mediated indirect interaction. 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.

4. RESULTS

4.1. Habitat Associations

We successfully completed surveys for harlequin ducks on 5 km stretches on seven study streams in 2003 and six streams in 2004; we felt that the 2004 Rutherford Creek survey did not accurately represent the harlequin duck densities known to occur there. Data for pair surveys are summarized in Table 4.1.1; we were successful in detecting a wide range of harlequin ducks densities, which is important for our analysis. As with duck densities, habitat attributes varied considerably between and within study reaches, allowing consideration of relationships between harlequin duck distribution and habitat features.

We found that the null model was best supported for explaining the likelihood of duck presence and absence (Table 4.1.2), suggesting that the habitat attributes that we measured were not strong predicators on harlequin duck occurrence. However, the model with *INVERTS* only was next best supported, receiving more than half the support of the null model. The *VEG* and *INVERTS* + *VEG* models received modest support. Similarly, we found that the parameter likelihood was highest for INVERTS (0.38), offering modest support that invertebrate density were related to the presence or absence of harlequin ducks.

When evaluating variation in harlequin duck densities across streams, we found that the only variable that was related to duck densities using univariate linear regressions was slope. Harlequin duck densities (birds/km) tended to increase with decreasing slope (in degrees), based on the following equation:

Duck density = 3.19 (0.74 SE) – 1.26 (0.45)*slope

In our information-theoretic model selection analysis, we found that the null model received most support (Table 4.1.2) for explaining variation in density. However, of the explanatory variables that we considered, only *INVERTS* showed any evidence of support, with a parameter likelihood of 0.16.

Table 4.1.1 Densities of harlequin ducks during pair surveys on study streams in the Coast Mountains.

YEAR	*STREAM*	*# DUCKS*	*DUCKS/KM*
2003			
	Cayoosh Creek	6	1.15
	Yalakom River	5	0.95
	Bridge River	0	0.00
	Seton River I	8	1.90
	Birkenhead River	2	0.38
	Cheakamus River – lower	10	1.90
	Ryan River	15	2.85
2004			
	Seton River I	14	3.33
	Seton River II	0	0.00
	Bridge River	2	0.40
	Cayoosh Creek	0	0.00
	Cheakamus River	14	2.80
	Rutherford Creek	3	0.49**
	Ryan River	2	0.39

Note: For streams represented in both years, different sections of those streams were surveyed in different years (see Table 3.1.1 and 3.1.2), with the exception of Seton River I.
**The values for Rutherford Creek are known to be biased low due to weather difficulties during surveys and auxiliary information of bird abundance. Rutherford Creek was excluded from analyses of habitat use.

Table 4.1.2 Results from analyses evaluating habitat attributes related to harlequin duck presence (top) and variation in harlequin duck density (bottom) on breeding streams in the southern Coast Range, British Columbia, 2003 and 2004.

Response Variable	Explanatory Variables[1]	ΔAICc	AICw
Duck Presence (1/0)	*Null*	0.00	0.45
(n = 73)	*INVERTS*	1.09	0.27
	VEG	2.28	0.15
	INVERTS + VEG	2.91	0.11
	ABIOTIC	7.03	0.01
	INVERTS + ABIOTIC	8.21	0.01
	ABIOTIC + VEG	10.35	0.00
	INVERTS + ABIOTIC + VEG	10.58	0.00
Density (birds/km)	*Null*	0.00	0.84
(n = 13)	*INVERTS*	3.34	0.15
	ABIOTIC	11.02	0.00
	VEG	11.63	0.00
	INVERTS + VEG	18.16	0.00
	INVERTS + ABIOTIC	20.48	0.00
	ABIOTIC + VEG	60.37	0.00
	INVERTS + ABIOTIC + VEG	105.68	0.00

[1] *INVERTS* = dry mass of aquatic invertebrates per m2

ABIOTIC = grouping of physical stream factors including slope, substrate, stream width, and number of exposed boulders

VEG = grouping of vegetation variables, including overhanging vegetation, instream woody debris, and shoreline vegetation openness.

4.2. Nutrient Allocation

Over the two field seasons, we successfully captured and radio-marked 34 adult female harlequin ducks (Table 4.2.1). Twenty-two females were confirmed on nests (Table 4.2.2), and 13 of those nests successfully hatched out at least one duckling.

Table 4.2.1 Numbers of harlequin ducks captured and radioed during spring 2003 and 2004 in the southern Coast Mountains. All radios were deployed on females.

Note that 5 five females radioed in 2004 were recaptures of females radioed in 2003.

STREAM	*FEMALES*	*MALES*	*RADIOS ATTACHED*
Cayoosh Creek	11	14	11
Yalakom River	2	2	2
Bridge River	6	5	6
Ryan River	2	3	2
Rutherford Creek	8	12	8
Seton River	2	3	2
Birkenhead River	0	0	0
Cheakamus River	1	4	1
Brandywine Creek	1	3	1
Downton Creek	1	0	1
TOTAL	**34**	**46**	**34**

Table 4.2.2.Nesting information of radio-marked female harlequin ducks in the southern Coast Mountains.

Harlequin Duck Nest Summary 2003

Nest	# of eggs	Incubation initiation	Nest site	Nest fate	Number of Ducklings: Class 1A	Class 1C	Class 2B
Yalakom River 1	5	May-19	island	flooded by river	0		
Cayoosh Creek 1	5	May-24	cliff ledge	depredated	0		
Bridge River 1	7	May-25	boulder in river	flooded by rain	0		
Seton Lake	5	May-25	cliff ledge	successful	2	0	0
Rutherford Creek 1	5	May-26	island	successful	1	1	1
Ryan River Tributary	5	May-26	island	successful	unk		
Cayoosh Creek 2	5	May-27	island	successful	3	3	1
Ryan River	7	Jun-02	island	unknown	0		
Rutherford Creek 2	6	Jun-15	root wad	successful	2	1	unk

Harlequin Duck Nest Summary 2004

Nest	# of eggs	Incubation initiation	Nest site	Nest fate	Number of Ducklings: Class 1A	Class 1C	Class 2B
Seton River 1	6	May-01	island	successful	4	3	3
Bridge River 2	7	May-05	stream bank	depredated	0		
Yalakom River 2	7	May-08	island	female depredated	0		
Cayoosh Creek 3	5	May-12	island	successful	4	3	2
Seton River 2	6	May-17	island	successful	3	2	2
Rutherford Creek 3	6	May-19	bank of small tributary	depredated	0		
Cayoosh Creek 4	6	May-18	cliff ledge	successful	5	5	5
Cayoosh Creek 5	6	May-24	island	successful	5	0	
Rutherford Creek 4	6	May-23	stream bank	depredated	0		
Bridge River 3	7	May-25	cliff ledge	successful	2	2	2
Cayoosh Creek 6	5	May-25	island	successful	1	0	
Rutherford Creek 5	5	May-30	island	successful	3	3	unk
Brandywine Creek	6	Jun-04	cliff ledge	successful	3	3	3

Note: unknowns for number of ducklings usually because of radio-transmitter failure

Female harlequin ducks allocated almost entirely freshwater nutrients to egg formation. The carbon mixing model estimated that 100 ± 8% (± SE) of the nutrients for egg albumen and lipid-free yolk were derived from breeding stream sources, and that 100 ± 15% of the nutrients for yolk lipid also came from freshwater nutrients. The nitrogen mixing model produced similar results with freshwater sources making up 98 ± 4% of albumen and 89 ± 4% of lipid-free yolk.

The conclusion that harlequin duck eggs are produced almost entirely from freshwater nutrients is supported by examination of plots showing isotopic signatures from the marine and freshwater biomes (Figures 4.2.1 and 4.2.2). Carbon and nitrogen isotope values for non-lipid components of eggs were clearly clustered with the values for freshwater invertebrates, and were distinct from the cluster of values for blood collected on wintering sites. Similarly, carbon values for yolk lipid matched those of lipid in freshwater invertebrates and were dissimilar from carbon isotope values of abdominal lipid collected from harlequin ducks on wintering areas.

Figure 4.2.1 Lipid-free carbon and nitrogen stable isotope values for wintering blood, freshwater invertebrate prey, egg yolk, and egg albumen of harlequin ducks.

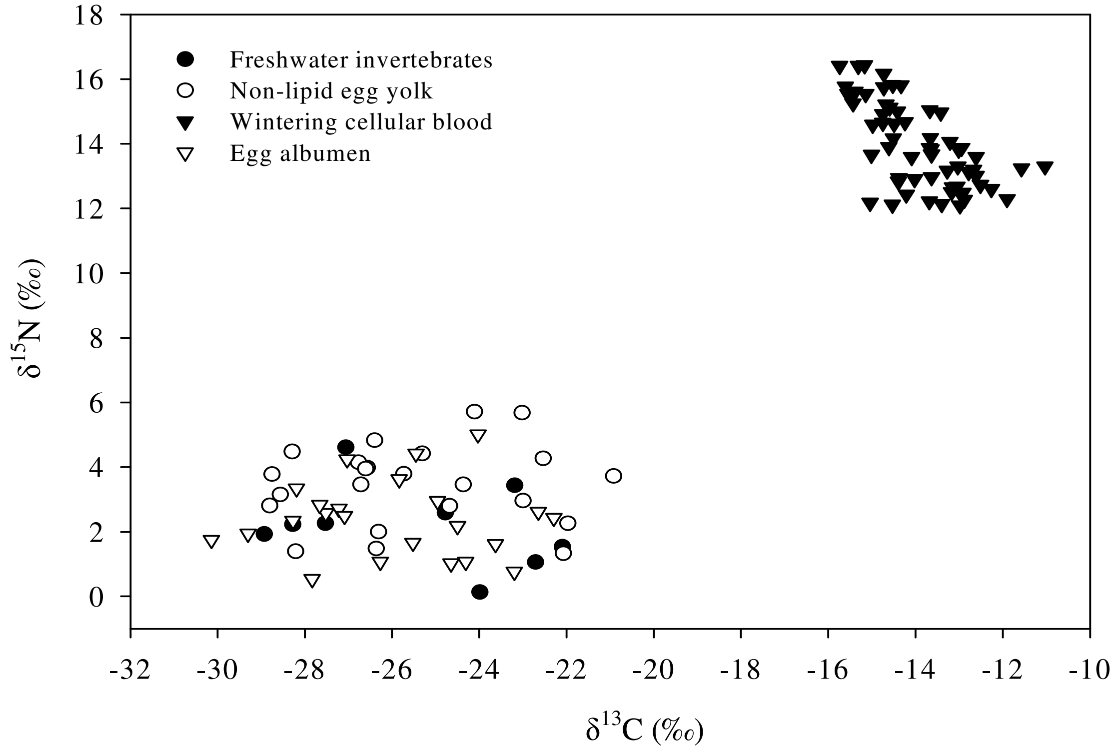
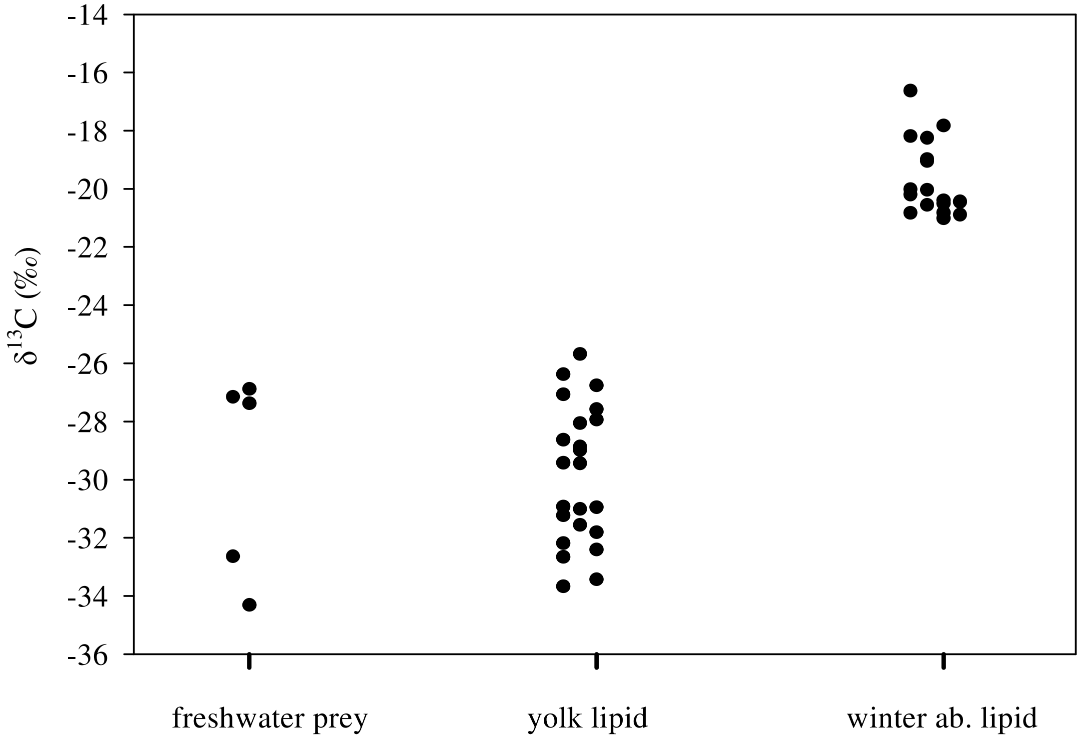


Figure 4.2.2 Carbon stable isotope values for lipid from freshwater stream invertebrates, and yolk lipid and winter abdominal lipid of harlequin ducks.



Also, we collected a complete clutch from a nest on the Bridge River in 2003 after it was flooded by rain and abandoned. We also collected the complete clutch of a female from the Yalakom River in 2004, after she was depredated. This gave us the opportunity to examine within-clutch variation in stable isotope signatures, to determine whether contribution of marine nutrients to eggs varied from the first through last eggs laid. Using coeffients of variation, we found that within clutch variation is low (~1%) compared to between clutch variation (>8%).

4.3. Biotic and Abiotic Influences on Food Availability

Our results showed that, based on the river level data, there was a negative relationship between aquatic insect availability and flow variability (Figure 4.3.1). 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=0.0052, F=15.94; year, p=0.0180, F=9.44) as well as the interaction term (year*flow variability, p=0.0216, F=8.66) entered the model, which had an overall r^2 of 0.89.

We also found that there was a positive relationship between aquatic insect availability and harlequin duck density (Figure 4.3.2). Our model of harlequin duck density found that aquatic insect densities (p=0.139, F=8.54), and year (p=0.0628, F=4.28) were both significantly explanatory for harlequin duck density (r^2=0.44, p=0.0345). The linear relationships between harlequin duck density and aquatic insects in the two years have identical slope, but the relationship is significantly elevated in 2003, meaning that there are more harlequin ducks per insect (2003: harlequin duck density = 9.5 (aquatic insect density) + 0.48); 2004: (harlequin duck density = 9.5 (aquatic insect density) – 0.16).

When comparing the fish and harlequin duck data, we found that a statistically significant negative interaction existed between harlequin ducks and fish (standardized regression coefficient = -0.551). This interaction is the result of a strong direct interaction between fish and ducks (standardized regression coefficient = -0.563), and a weaker positive indirect interaction via the prey (standardized regression coefficient = +0.121) (Figure 4.3.3).

Figure 4.3.1 Aquatic insect densities and flow variability's of the Bridge River (◊), Cayoosh Creek (Δ), Cheakamus River (*), Seton River (○), Ryan River (+) and Yalakom River (□).

Solid black symbols represent 2003, black and white symbols represent 2004.

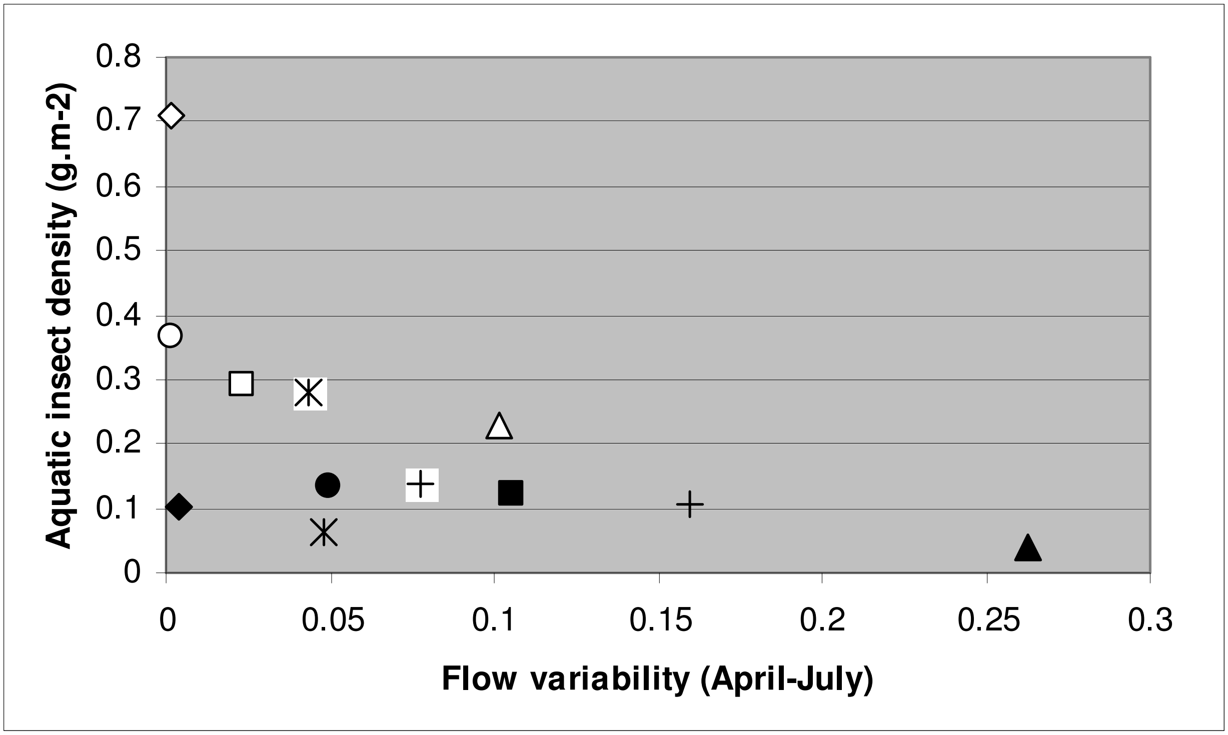


Figure 4.3.2 Aquatic insect and harlequin duck densities for 2003 (black), and 2004 (white).

Line equations from model, 2003: y=9.5(x)+0.48, 2004: y=9.5(x)-0.16 (r^2=0.44).

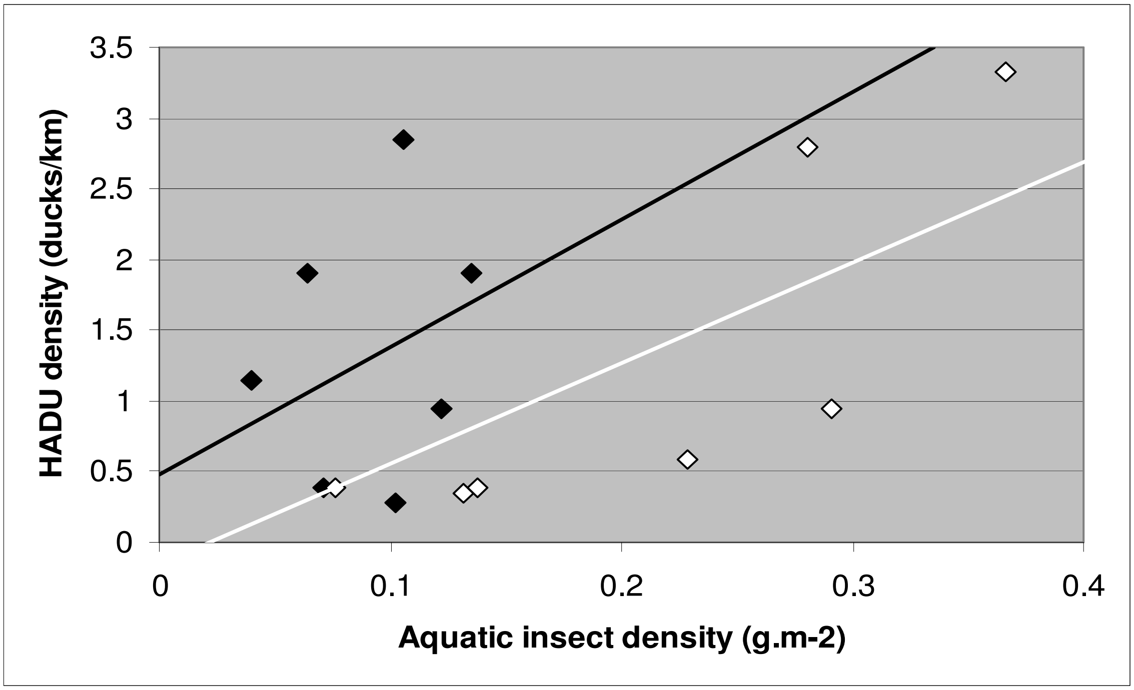
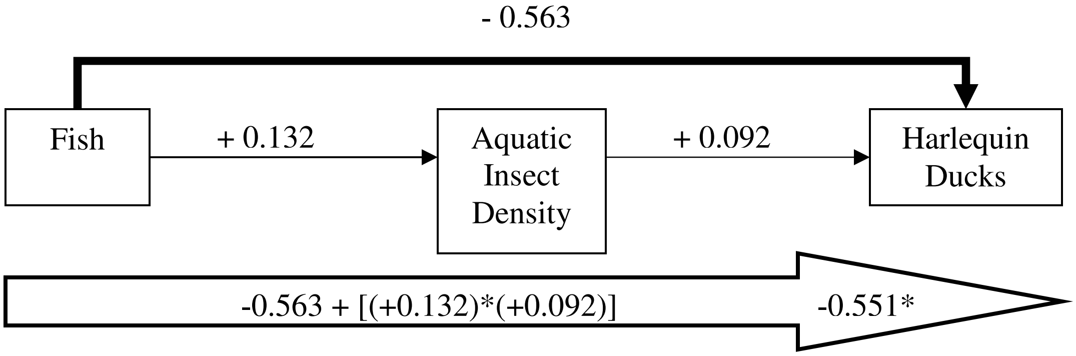


Figure 4.3.3 Path diagram of interactions between fish and harlequin ducks depicting the direct and indirect interactions and their standardized regression coefficients. The addition of the direct and indirect interactions are shown below the diagram.

* denotes statistically significant interactions. Arrow widths are proportional to their contribution to the total interaction.



5. DISCUSSION

5.1. Habitat Associations

Surprisingly, we did not find any particular habitat attribute that strongly and consistently correlated with harlequin duck presence or density. Our intent in this part of the project was to sample widely across streams within a region to determine factors that influence harlequin duck distribution at a scale that had not previously been addressed. Our results may indicate that there are not regionally-relevant features that dictate distributions at that scale, i.e., different factors may influence distributions on different streams. Alternatively, we may not have sampled some attributes that are important (e.g., predator densities; Heath et al. 2006). Finally, our sampling of some attributes was logistically constrained (e.g., aquatic invertebrates) and, in naturally variable systems, we may not have captured average values accurately. Despite these issues, some factors emerged as potentially important. First, slope was identified, in our univariate linear regression, to be negatively related to harlequin duck densities. This matches our observations outside of surveys; harlequin ducks tended to occur on stream segments with lower gradients. Also, we found several lines of evidence suggesting spatial relationships with invertebrates. In the habitat analyses, the *INVERTS* parameter was often better supported than other parameters, despite the Null model receiving strongest support. In other words, despite high levels of unexplained variation, invertebrate density explained more variation than other habitat features. Finally, more intensive aquatic invertebrate sampling (Appendix V) resulted in data with stronger, positive associations between ducks and their prey.

A review of the literature addressing harlequin duck breeding habitat use provides variable results as well. In Labrador, Rodway (1998) discovered that some physical features (such as substrate, stream width, and shoreline gradient) and vegetation attributes were related to harlequin duck densities. He also described higher numbers of some invertebrates in streams used by harlequin ducks compared to those that were unused. In contrast, Heath et al. (2006) found no differences among Labrador streams in terms of physical habitat attributes or prey availability, despite large differences in density and stability of harlequin duck populations; they concluded that raptor densities, which differed markedly across streams, were the primary determinant of harlequin duck habitat use. Hill and Wright (2000) found that harlequin ducks on the Bridge River (one of the rivers used in this study) occurred in streams reaches with higher gradients than random sites, a finding contrary to ours. Hill and Wright (2000) also suggested that harlequin ducks preferred reaches with areas for loafing, such as instream boulders. Prey availability has been linked to higher harlequin duck densities on the Skagit (Freeman and Goudie 2001) and Maligne Rivers (McCutchen and Ydenberg 2005). Freeman and Goudie (2001) found that harlequin ducks on the Skagit also preferred reaches with wider channels and occurred in streams with slopes between 1 and 7%, with most < 2%. They also detected no relationship with streamside vegetation. In contrast, Machmer (2001) concluded that streamside vegetation density was an important component of habitat used by harlequin ducks in the Salmo watershed, as well as areas with low stream gradients and numerous haul-out sites.

Despite the lack of consistent generalities, the important habitat features that we detected, slope and prey availability, have been regularly identified in other studies, and provide a basis for understanding and conservation. A large body of literature supports the notion of links between food availability and productivity of many birds, including waterfowl and, specifically, harlequin ducks. Perhaps many or all of the streams in our study region hosted aquatic insects that were adequate for breeding harlequin ducks and, thus, the links were not as strong as they might have been if food were limiting. Also, harlequin ducks are known to show high degrees of site fidelity throughout the annual cycle, including the breeding season. Therefore, even with changes in prey abundance, harlequin ducks may return to areas previously occupied, as long as minimum adequate levels of prey are available. The Bridge River offers a good opportunity to evaluate this phenomenon. With the stable flow regime instituted recently, invertebrate densities are high (Appendix V) and harlequin ducks are known to occur and nest (Appendix IV) on the rearch below the Terzaghi Dam. One might predict that colonization of this reach may take years or decades to reach densities dictated by the available prey, given the degree of fidelity.

5.2. Nutrient Allocation

We demonstrated that the nutrient allocation strategy for clutch formation by harlequin ducks in the southern Coast Mountains of British Columbia involves mostly freshwater sources. Therefore, female harlequin ducks are apparently dependent on stream productivity and access to invertebrate prey for egg production. One could speculate that, if females experience reduced food levels on streams during the clutch formation stage, this could impede their ability to produce eggs, which in turn could lead to consequences for population demographics. Although we have unequivocally demonstrated that stream-derived nutrients are used to build eggs, the potential for limiting effects of food has not been directly addressed. In other words, would a reduction in food availability lead to reduced productivity? Is there a threshold invertebrate density, beneath which reproductive effects are expressed? These are issues that have been debated (Gardarsson & Einarsson 2004, Goudie & Jones 2005), and future work on food limitation is clearly warranted. However, our findings are the first to show that freshwater invertebrates are used exclusively as a nutrient source for harlequin duck eggs, thereby demonstrating the potential for limiting effects to be expressed at that part of the reproductive cycle.

Because our results were based on a randomly chosen egg from each clutch, they represent the average strategy of nutrient allocation to egg production. There is some evidence to suggest, however, that there can be significant intraclutch variation in sources of egg nutrients. Both Barrow's Goldeneye (*Bucephala islandica*; Hobson et al. 2005) and Redhead (*Aythya americana*; Hobson et al. 2004) females allocated more endogenous stores to eggs laid early in the sequence than to later laid eggs. Our data do not support hypotheses of opportunistic marine endogenous transfer to eggs by harlequin ducks because variation within clutches was small and entirely within the freshwater range of isotope values. This suggests that values from a single egg per clutch for harlequin ducks are representative of each individual's strategy, and when pooled, allow appropriate inference about the average strategy of the population.

Some differences in isotope values were evident among clutches in our data. We suggest that this is not related to variation in strategies of nutrient acquisition and allocation among females, but rather, is due to differences in isotopic signatures across streams and freshwater diets. Other studies have found a lack of consistency in freshwater isotopic endpoints (Hobson et al. 2004, Hobson et al. 2005), and this is likely caused by different processes affecting each of the freshwater sources. In the study system, isotopic signatures between streams differed slightly and the exact prey composition of females' diets also likely differed, and these dissimilarities would lead to variation among eggs laid by different individuals. However, despite variation in signatures among clutches, the egg components fall almost entirely within the isotopic range of freshwater stream invertebrates.

Our studies also have described increases in female body mass during late winter, prior to migration, on marine wintering areas (Appendix IV, Bond and Esler 2006). We speculate that these nutrient reserves, although not invested in egg production, might be important for reproduction at later stages, such as incubation or brood-rearing, when a reduction in feeding time would allow greater incubation constancy and vigilance, respectively. As an interesting side note, we found that body mass dynamics were similar for females that consumed herring spawn and those that did not (Bond and Esler 2006), indicating that aggregation on herring spawn is likely not necessary for successful migration and reproduction.

Another important finding from this part of the project is that nearly all of the females occurring on streams were known to initiate reproduction (Appendix IV). Harlequin ducks have been speculated to be a species that shows high rates of nonbreeding, although measuring breeding propensity in free-living, cryptically-nesting species is challenging. We applied a method that used both yolk precursors and radio telemetry to evaluate breeding propensity, and by this approach determined that at least 92% of females captured on streams initiated reproduction (Appendix IV).

5.3. Biotic and Abiotic Influences on Food Availability

Our results show (i) that there was significant variation in availability of aquatic insects among the rivers we studied; (ii) that both fish rating indices and harlequin density were positively associated with our measure of insect availability; but (iii) our measures of fish presence and harlequin duck density were negatively associated. Our data are most consistent with the hypothesis that fish affected harlequins indirectly by reducing availability of prey through a trait-mediated indirect interaction.

A substantial portion of the aquatic insect community in our study consisted 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 (Kohler & McPeek 1989, Rosenfeld 2000). Therefore, it is plausible that trait-mediated indirect interactions (TMII) were acting within our system, and may explain the results we describe. In a TMII, the density of the transmitting species (in this case, the aquatic invertebrates) is not affected, but individuals alter physiological, developmental, morphological, and/or behavioural traits in ways that make them less available to the receiver, in this case ducks (Werner and Peacor 2003, Bolnick and Preisser 2005, Preisser et al. 2005). TMIIs are widespread when interactions involve predators, because of the powerful effects of predator intimidation (Lima & Dill 1990, Werner & Peacor 2003, Bolnick & Preisser 2005, Preisser et al. 2005). Prey may occupy different habitats, change activity levels, or alter their foraging schedule and behaviours to lower predation risk (Soluk & Collins 1988,McIntosh & Townsend 1994). With relevance to our study, 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 (Bechara et al. 1993, Culp & Scrimgeour 1993, McIntosh & Peckarsky 1996).

A TMII 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) that inhabit that reach and Maligne Lake, while the Lower Maligne maintains a small, non-breeding population of fish from infrequent overspills from Medicine Lake (McCutchen 2001). Harlequin ducks 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).

This research has implications for conservation of high quality breeding habitat for breeding harlequins taking into consideration the aquatic insect community and effects of the presence of fish. We speculate that the widespread introduction and enhancement of fish populations into historically fishless reaches could cause a reduction of food available to harlequins resulting in reduced breeding habitat quality.

6. CONCLUSIONS AND RECOMMENDATIONS

Our body of research resulted in several key findings. Based on the stable isotope results, aquatic insect food resources are clearly important for the egg formation stage of reproduction. Furthermore, the distribution of harlequin ducks is linked to aquatic insect density, although the strength of that relationship is not strong. Stream slope was related to harlequin duck densities, with ducks preferring streams with shallower slopes.

Finally, the presence of fish appears to have negative effects on harlequin duck densities, and we speculate that this is due to changes in aquatic insect behaviour induced in the presence of fish. In this section, we consider the conservation implications of this combined body of work.

Although the spatial links between harlequin duck densities and their aquatic invertebrate prey are weak, there are both conceptual and empirical suggestions that prey availability is an important aspect of harlequin duck breeding habitat. We have conclusively shown that costs of egg production are met almost exclusively through consumption of aquatic insects on breeding streams. In addition, brood-rearing females also presumably rely on local foods, and their growing young undoubtedly do. Therefore, maintenance of aquatic insect resources is an important aspect of harlequin duck conservation.

We have several specific recommendations with regard to maintenance of aquatic insect availability for harlequin ducks. First, it appears that insect densities in the recently rewatered Bridge River section between the Terzaghi Dam and the confluence of the Yalakom River are high, likely as a result of reduced flow variability (Appendix V). We conclude that this has resulted in high habitat quality for harlequin ducks, and have confirmed both occurrence and breeding by harlequin ducks on this reach. We recommend maintenance of stable flow, as well as continued tracking of harlequin duck (and other bird) activity in the reach. We suspect that harlequin duck densities will continue to increase. We caution that flow stability may result in deposition of fine sediments, which eventually could depress insect availability, in which case flushing the reach with high flows to reduce sedimentation (outside the harlequin duck breeding season) might be effective.

Similarly, the Lower Seton River hosts relatively high densities of harlequin ducks, as well as confirmed nests. Again, maintenance of a stable flow regime, particularly in the harlequin duck breeding season, is warranted. In addition, the associated power canal also hosts high numbers of harlequin ducks, particularly early in the spring prior to redistribution to breeding reaches. We recommend that drainage of the canal for maintenance occur outside of the harlequin duck breeding period when possible, leaving the high densities of aquatic insect prey found on the sides of the canal available for foraging ducks.

In addition, our findings indicate negative relationships between harlequin ducks and fish, and we speculate that it is a result of reductions in prey availability to harlequins when fish are present. This is an issue that has management implications not only for local enhancement of harlequin duck populations, but also at the contintental scale. Fish, particularly species preferred for their recreational value, have been introduced or enhanced for decades at large geographic scales. While it is well understood that changes to aquatic communties have cascading effects through trophic and behavioral interactions, a growing body of literature has made links to conservation concerns for other stream-dependent species. Harlequin ducks are thought to have lower productivity than is needed to maintain their populations, and the widespread introduction of fish is a mechanism that potentially explains such a broad-scale reduction in productivity. We recommend that fish introduction and enhancement, including that conducted by BCHydro/BCRP, should be evaluated not only in terms of effects on fish populations, but also effects on other components of the aquatic ecosystem.

Our habitat results did not reveal strong relationships between specific habitat features and harlequin duck densities. However, stream slope was identified, with harlequin ducks preferring lower gradient reaches. This has management implications for siting of independent power projects (IPPs); these should be directed to steeper gradients dominated by cascading reaches (as opposed to reaches dominated by riffle and glide) from the perspective of harlequin duck conservation. In the Rutherford Creek IPP, we detected considerable harlequin duck use upstream of the stockpen reservoir, including considerable use of the reservoir itself. We conclude that IPPs can be constructed without negative consequences to harlequin ducks if placed appropriately.

Unfortunately, habitat attributes that are more easily manipulated (e.g., streamside vegetation) were not related to variation in harlequin duck densities or presence/absence. Given the results of this study, and mixed results of previous studies, enhancing or restoring harlequin duck habitat is a challenging proposition. However, because harlequin ducks do show strong inter-annual site fidelity, efforts to protect areas that host high densities of harlequin ducks are warranted.

7. ACCOMPLISHMENTS

The scientific goals of this three-year research project have been met with success, and our results are clearly relevant for restoration and conservation of harlequin duck populations on BCRP streams and beyond. The scientific output from this work has been substantial, and includes the following two theses:

Bond, J. C. 2005. Nutrient acquisition and allocation strategies for reproduction by female harlequin ducks. Simon Fraser University.

LeBourdais, S. V. 2006. Harlequin duck (*Histrionicus histrionicus*) densities on rivers in southwestern British Columbia in relation to food availability and indirect interactions with fish. Simon Fraser University.

In addition, journal publications that are published, submitted, or in preparation from this study include:

Bond, J. C., and D. Esler. 2006. Nutrient acquisition by female harlequin ducks prior to migration and reproduction: evidence for body mass optimization. Canadian Journal of Zoology 84: 1223-1229.

Bond, J. C., D. Esler, and K. A. Hobson. 2007. Isotopic evidence for sources of nutrients allocated to clutch formation by harlequin ducks. Condor: in press.

Bond, J. C., D. Esler, and T. D. Williams. Submitted. Breeding propensity of harlequin ducks *Histrionicus histrionicus* estimated using yolk precursors and radio telemetry. Journal of Wildlife Management.

Bond, J. C., S. A. Iverson, N. B. MacCallum, C. M. Smith, H. J. Bruner, and D. Esler. Submitted. Variation in breeding season survival of adult female harlequin ducks. Condor.

Bond, J. C., and D. Esler. In preparation. Cross-seasonal body mass dynamics of male harlequin ducks: strategy for meeting the costs of reproduction.

Esler, D., R. Žydelis, T. L. Lewis, K. G. Wright, J. C. Bond, S. V. LeBourdais, and R. C. Ydenberg. In preparation. Habitat correlates of harlequin duck densities on breeding streams.

LeBourdais, S. V., and R. C. Ydenberg. In preparation. Prey availability, fish presence, and harlequin duck breeding density on rivers in southwest British Columbia.

In addition to our scientific accomplishments, we have engaged in a number of community interactions in relation to this project, as part of our Communications Plan. First, we maintained contact with the individuals and organizations that provided letters of support for the proposal, to let them know how the project was proceeding and to offer an opportunity for exchange of information. We also formally participated in several meetings and presentations of results in local communities (Appendix II). Finally, we have provided final data sets from the project to interested parties (e.g., Lillooet Tribal Council, Canadian Wildlife Service), with the hope that they can be used in conservation efforts in the future.

Another highlight of this project has been the participation of local members of the Lillooet Tribal Council, Cayoosh Creek Band, and Bridge River Band. We received a great deal of interest in the work, and hired several technicians locally and they proved to be enthusiastic and reliable field workers, which contributed greatly to the success of the project.

8. ACKNOWLEDGEMENTS

We are grateful for the financial support for the project provided by BC Hydro Bridge-Coastal Fish and Wildlife Restoration Program, the Centre for Wildlife Ecology at Simon Fraser University, and the Whispering Pines/Clinton Indian Band. We thank Ken Wright, Sam Copeland, Bobby Vinnie, Delphine Jacob, Carl Machell, Sam Iverson, Sean Boyd, Josh Weisner, Chester Alec, and Keith Hobson for field and laboratory help. Shaun Freeman provided an egg from the Skagit River watershed. We also thank Judy

Higham, Janice Doane, and Connie Smith for their efforts administering the project. We received logistical and administrative support from the Cayoosh Creek Band Office, particularly Bonnie Adolph, and the Lillooet Tribal Council Office, particularly Larry Casper.

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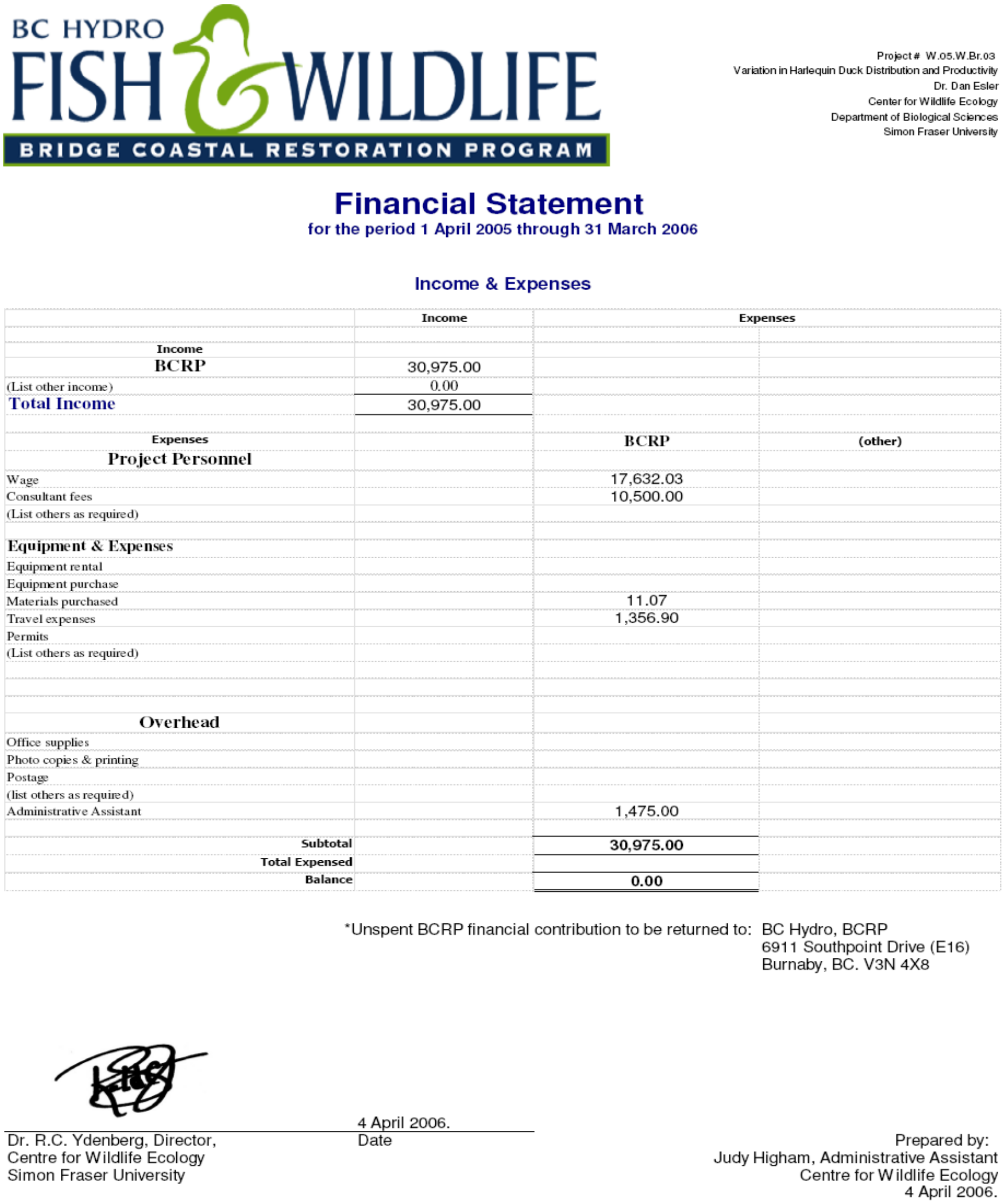
10. APPENDIX I – FINANCIAL REPORT



BC HYDRO FISH & WILDLIFE
BRIDGE COASTAL RESTORATION PROGRAM

Project # W.05.W.Br.03
Variation in Harlequin Duck Distribution and Productivity
Dr. Dan Esler
Center for Wildlife Ecology
Department of Biological Sciences
Simon Fraser University

Financial Statement

for the period 1 April 2005 through 31 March 2006

Income & Expenses

	Income	Expenses	
Income			
BCRP	30,975.00		
(List other income)	0.00		
Total Income	30,975.00		
Expenses		**BCRP**	**(other)**
Project Personnel			
Wage		17,632.03	
Consultant fees		10,500.00	
(List others as required)			
Equipment & Expenses			
Equipment rental			
Equipment purchase			
Materials purchased		11.07	
Travel expenses		1,356.90	
Permits			
(List others as required)			
Overhead			
Office supplies			
Photo copies & printing			
Postage			
(list others as required)			
Administrative Assistant		1,475.00	
Subtotal		**30,975.00**	
Total Expensed			
Balance		**0.00**	

*Unspent BCRP financial contribution to be returned to:
BC Hydro, BCRP
6911 Southpoint Drive (E16)
Burnaby, BC. V3N 4X8

Dr. R.C. Ydenberg, Director,
Centre for Wildlife Ecology
Simon Fraser University

4 April 2006.
Date

Prepared by:
Judy Higham, Administrative Assistant
Centre for Wildlife Ecology
4 April 2006.

11. APPENDIX II - PERFORMANCE MEASURES

Because this is not a direct restoration activity, but rather a project that fills information gaps to help prescribe restoration, the performance measures described in the BCRP performance measures table (in terms of square meters of habitat restored) are not directly applicable. However, the results from this work will be useful for Impact Mitigation, Habitat Conservation, Maintenance or Restoration of Habitat, and Habitat Development categories for harlequin ducks. All of these require an understanding of the habitat features that enhance suitability for harlequin ducks and, also, would benefit from information linking variation in habitat with harlequin duck productivity. Of the habitats listed in the performance measures table, the following would be affected by application of our work: Instream Habitat (both main stem and tributaries), Riparian, Reservoir Shoreline Complex, and Riverine.

12. APPENDIX III – CONFIRMATION OF BCRP RECOGNITION

During all presentations of the project we have displayed the BCRP logo on the opening slide of our PowerPoint presentations (Fig. 12.0.1) and explicitly noted that BCRP provides a portion of project funding.

Presentations:

Esler, D., R. C. Ydenberg, J. C. Bond, and S. V. LeBourdais. *Variation in Harlequin Duck Distribution and Productivity: Roles of Habitat, Competition, and Nutrient Acquisition*. Whispering Pine Clinton/ Indian Band, Kamloops, BC, April 2006. Oral Presentation.

Esler, D., R. C. Ydenberg, J. C. Bond, and S. V. LeBourdais. *Variation in Harlequin Duck Distribution and Productivity: Roles of Habitat, Competition, and Nutrient Acquisition*. Pemberton Wildlife Society, Pemberton, BC, March, 2006. Oral Presentation.

Esler, D., R. C. Ydenberg, J. C. Bond, and S. V. LeBourdais. *Variation in Harlequin Duck Distribution and Productivity: Roles of Habitat, Competition, and Nutrient Acquisition.* Lillooet Naturalist Society, Lillooet, BC, March 2006. Oral Presentation.

LeBourdais, S. V. and R. C. Ydenberg. *Aquatic Insect Availability and Breeding Harlequin Ducks*. Les Ecologiste Seminar, Simon Fraser University, BC, December 2005. Oral Presentationl.

Bond, J. C., D. Esler and K. A. Hobson. *Nutrient Acquisition and Allocation by Female Harlequin Ducks for Reproduction*. North American Sea duck Conference. Annapolis, MD, November 2005. Oral Presentation.

Bond, J. C., D. Esler and K. A. Hobson. *Nutrient Acquisition and Allocation by Female Harlequin Ducks for Reproduction*. American Ornithologists Union Meeting. Santa Barbara, CA, August 2005. Oral Presentation.

Bond, J. C., D. Esler , T. D. Williams, and R. C. Ydenberg. *Breeding Propensity of Harlequin Ducks: a Novel Approach using Radio Telemetry and Yolk Precursor Analysis*. Joint Pacific Seabird Group and Waterbird Society Conference. Portland, OR, January 2005. Oral Presentation.

LeBourdais, S. V. *Rainbow Trout and Harlequin Ducks: an example of Behaviourally Mediated Indirect Interactions.* Joint Pacific Seabird Group and Waterbird Society Conference. Portland, OR, January 2005. Poster Presentation.

Esler, D., R. C. Ydenberg, J. C. Bond, and S. V. LeBourdais. *Variation in Harlequin Duck Distribution and Productivity: Roles of Habitat, Competition, and Nutrient Acquisition*. Pemberton Wildlife Society, Pemberton, BC, December 2004. Oral Presentation.

Esler, D., R. C. Ydenberg, J. C. Bond, and S. V. LeBourdais. *Variation in Harlequin Duck Distribution and Productivity: Roles of Habitat, Competition, and Nutrient Acquisition.* Lillooet Naturalist Society, Lillooet, BC, April 2004. Oral Presentation.

Esler, D., R. C. Ydenberg, J. C. Bond, and S. V. LeBourdais. *Variation in Harlequin Duck Distribution and Productivity: Roles of Habitat, Competition, and Nutrient Acquisition.* Canadian Wildlife Service Seminar Series, Delta, BC, March 2004. Oral Presentation.

Figure 5.3.1 Example of Presentation Poster

Harlequin Duck Presentation

Title: Variation in Harlequin Duck Distribution and Productivity: the Roles of Habitat, Competition, and Nutrient Acquisition

Location: The Lillooet Friendship Centre

Date: Tuesday, March 21, 2006

Time: 7 pm

Tom Middleton 2005

BC HYDRO FISH & WILDLIFE
BRIDGE COASTAL RESTORATION PROGRAM

SIMON FRASER UNIVERSITY

Canadian Wildlife Service
Service Canadien de la faune

13. APPENDIX IV – JEANINE BOND THESIS

Nutrient Acquisition and Allocation Strategies for Reproduction by Female Harlequin Ducks

by

Jeanine C. Bond
Bachelor of Science, University of Victoria, 2000

THESIS
SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

In the
Department
of
Biological Sciences

SIMON FRASER UNIVERSITY

Fall 2005

13.1. Abstract

I analysed body mass variation and stable isotope signatures ($\delta^{15}N$, $\delta^{13}C$) of adult female Harlequin Ducks (*Histrionicus histrionicus*) on marine wintering areas and freshwater breeding streams in southern British Columbia to investigate when and where they acquire nutrients prior to reproduction and the sources of nutrients allocated to clutch formation. I found that female body mass on wintering grounds increased by 7% in the weeks before migration, irrespective of whether they were consuming their usual winter diet of intertidal invertebrates or superabundant spawn of Pacific herring (*Clupea pallasi*). However, stable isotope analyses revealed that freshwater nutrients, not marine, were allocated to eggs, and therefore, stored marine nutrients were likely used during other reproductive stages. I also estimated breeding propensity of Harlequin Ducks using a novel method combining yolk precursor analyses and radio telemetry, and estimated that 92% of females on streams initiated egg formation.

Keywords: Harlequin Duck, stored nutrient reserves, body mass, herring spawn, income breeding, reproductive investment, stable isotopes, breeding propensity, yolk precursors

13.2. General Introduction

13.2.1. Thesis Background

Birds have evolved various life history strategies to maximize lifetime fitness. A central tenet of life history theory is that trade-offs exist between components of fitness (Stearns 1992). Physiological trade-offs are thought to result through the allocation of a limited amount of energy among competing functions within an individual, such as reproduction and survival (Cam et al. 1998; Figure 13.2.1). Reproduction in birds requires a large investment of energy and nutrients (Carey 1996). Within the broad range of avian taxa, strategies for acquiring and allocating energy and nutrients for reproduction are variable, interspecifically and intraspecifically, and are likely influenced by factors such as body size, mode of development, predation pressure, climate, diet, and food availability (Moreno 1989). Further, these strategies affect migration strategies (Alerstram and Lindström 1990) and reproductive attributes including timing of breeding (Lack 1968), clutch size (King 1973), and incubation behaviour (Moreno 1989).

Nutrient acquisition strategies for meeting the nutritional requirements of reproduction can involve building stored nutrient reserves or increasing foraging in the local environment. The strategy of allocating stored nutrients, also termed endogenous reserves, to reproduction is known as 'capital' breeding, while using locally available food sources, also termed exogenous nutrients, to acquire energy without reliance on stored reserves is known as 'income' breeding (Thomas 1989, Jönsson 1997). Drent and Daan (1980) originated the concepts of capital and income breeding when considering clutch size determination. According to their definition, a capital breeder would base the decision to lay an additional egg on the absolute level of available capital relative to a critical threshold, whereas an income breeder would base the decision on the rate of nutrient accumulation from the local environment. The original and contemporary definitions of capital and income strategies differ in that Drent and Daan (1980) discuss the origin of information for decisions in a specific aspect of reproduction (clutch size) while more recent interpretations focus on the origin of resources in general for offspring production (Jönsson 1997).

Capital and income breeding have been considered extremes of a continuum ranging from high to low reliance on stored nutrients (Thomas 1989), although recent evidence suggests that sole reliance on stored nutrients for reproduction is rare (Meijer and Drent 1999). One example of a capital breeder is the Adelie Penguin (Pygoscelis adelie), which uses mostly endogenous reserves during reproduction, whereas the American Kestrel (Falco tinnunculus) is an example of an income breeders, using only nutrients available in the local environment (Meijer and Drent 1999). Many studies have also found intermediate approaches by various species (Meijer and Drent 1999, Gauthier et al. 2003). Jönsson (1997) considered the costs and benefits of each strategy from energetic and demographic perspectives. Income breeding can be considered beneficial when the energetic costs of nutrient storage are high, and when stores negatively influence flight performance and predator avoidance in such a way as to reduce survival or fitness. Capital breeding is considered beneficial when resources on breeding grounds are unpredictable or scarce, when predation risk on breeding grounds during foraging is high, or when time for reproduction is limited.

Many studies have investigated the role of nutrient reserves for reproduction, and therefore the extent of capital breeding, in waterfowl (see Alisauskas and Ankney 1992 for review). Most of these studies were initiated to consider nutritional effects on clutch size determination and timing of reproduction. For waterfowl, egg production is an energetically demanding stage because it involves the formation of many, large, energy-dense eggs in a short period of time (Alisauskas and Ankney 1992). Because waterfowl are diverse in morphology, distribution, behaviour, and diet, considerable interspecific variation exists in the degree of reliance on endogenous reserves for clutch formation (Alisauskas and Ankney 1992). For example, Common Eiders (Somateria mollisma) have been reported to rely heavily on endogenous reserves (Parker and Holm 1990) while Northern Shovelers (Anas clypeata) in Alaska use very little (MacCluskie and Sedinger 2000). Many waterfowl species appear to use moderate amounts of endogenous reserves, including Lesser Scaup (Aythya affinis; Esler et al. 2001), Canvasbacks (Aythya valisineria; Barzen and Serie 1990), and Ruddy Ducks (Oxyura jamaicensis; Tome 1984, Alisauskas and Ankney 1994). Esler and Grand (1994) demonstrated that the use of nutrient reserves also can vary intraspecifically. These studies have provided insights into the constraints on waterfowl reproduction and strategies for meeting those constraints, although these questions have seldom been addressed for sea ducks.

Sea ducks are thought to employ a life history strategy in which adult survival is emphasized and annual reproductive effort is low and variable relative to other waterfowl (Goudie et al. 1994). Based on this strategy, sea ducks would be expected to defer reproduction under scenarios of poor food availability or habitat quality (Goudie and Jones in press). However, this has been poorly documented in sea ducks, in part because of the difficulties associated with quantifying breeding propensity. Rates of nonbreeding, and the mediating role of nutrition, are significant data gaps that constrain understanding of sea duck productivity and population dynamics.

Population monitoring data indicate that, of the 17 sea duck species in the north Pacific Rim, at least 13 are reported to be declining (Goudie et al. 1994). Therefore, it is important to identify reproductive strategies of sea duck species to ascertain mechanisms by which productivity and recruitment may be limited. Further, knowledge of breeding strategies allows for informed population and habitat management.

13.2.2. Harlequin Duck Background

Harlequin Ducks (*Histrionicus histrionicus*) have a holarctic distribution, and on the west coast of North America, they range from Alaska to northern California. Pacific populations of Harlequin Ducks are of conservation concern, and there is evidence to suggest that recruitment in southern British Columbia is not compensating for annual adult mortality, and thus, productivity may be too low to sustain populations (Robertson and Goudie 1999, Smith et al. 2001, Rodway et al. 2003). Because of this concern, further investigation is needed to address knowledge gaps regarding reproduction in Harlequin Ducks.

Harlequin Ducks are small sea ducks that winter in marine environments and feed on a varied diet including amphipods, limpets, small crabs, fish roe, and other marine invertebrates (Vermeer 1983, Goudie and Ankney 1986). They are unusual among North American waterfowl because they use fast-flowing streams for breeding (Robertson and Goudie 1999). On these breeding streams, they are able to move swiftly in turbulent, white water and dive for invertebrate prey on rocky substrates (Robertson and Goudie 1999). The breeding range for those that winter in British Columbia extends inland to the Rocky Mountains. Like many other sea ducks, they exhibit low productivity, long lifespans, and delayed maturation (Goudie et al. 1994).

13.2.3. Study Area

The study area for this project included breeding sites on streams near the towns of Pemberton (50° 19'N, 122° 48'W) and Lillooet (50° 41'N, 121° 56'W) in the southern Coast Mountains of British Columbia, Canada (Figure 13.2.2). Specific study streams included sections of Cayoosh Creek, Seton River, Bridge River, Yalakom River, Ryan River, Rutherford Creek, Brandywine Creek, and Cheakamus River. Study sites on wintering areas were situated around the Strait of Georgia (49° 40'N, 124° 24'W) between Vancouver Island and the southern coast of mainland British Columbia (Figure 13.2.3). Specific study sites were located around Denman Island, Hornby Island, southern Quadra Island, Williams Beach, and Qualicum Bay.

13.2.4. Thesis Purpose and Outline

The purpose of this thesis was to investigate nutrient acquisition and allocation strategies used by Harlequin Ducks for reproduction, particularly clutch formation. These issues have never been addressed for this species and have important implications for understanding factors limiting productivity, and subsequently, have important population and habitat management ramifications. This thesis also contributes general knowledge about breeding propensity in Harlequin Ducks and appropriate methodology for quantifying this reproductive attribute. The chapters are written and organized in preparation for journal submission, and therefore, include some repetition. Co-authors are acknowledged in each of the data chapters while introductory and concluding chapters are written in the first person.

The first data chapter, Chapter Two, addresses nutrient acquisition prior to reproduction for Harlequin Ducks wintering in the Strait of Georgia, British Columbia. If Harlequin Ducks store endogenous reserves for subsequent investment in reproduction and especially clutch formation, it is important to determine where and when they build these nutrient stores in order to fully understand their nutrient acquisition strategy, and therefore, elucidate potential sources of constraints to nutrient acquisition. I use body mass measurements of adult females to determine the timing of nutrient acquisition and the relationship to Pacific Herring (*Clupea pallasi*) spawn events.

In Chapter Three, I investigate the sources of nutrients allocated to clutch formation. I use stable isotope analysis to determine whether Harlequin Duck eggs were composed of marine-derived nutrients, freshwater nutrients, or some combination of the two sources. By documenting the relative contribution of breeding and wintering site resources for meeting the nutritional and energetic demands of clutch formation, this chapter lends insight into the relative importance of breeding stream and coastal wintering site quality for Harlequin Duck productivity.

In Chapter Four, I investigate breeding propensity (the proportion of adult females on breeding streams that initiate egg production) and methodological influences on breeding propensity estimates. I employ a new technique combining yolk precursor analysis with radio telemetry to obtain accurate estimates of breeding propensity for Harlequin Ducks in southern British Columbia.

Finally, in Chapter Five, I draw conclusions and consider future directions, and then supplement the thesis with an appendix investigating migration costs between wintering and breeding study sites.

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Figure 13.2.1 Schematic demonstration of competing demands for allocation of nutrients in adult female birds.

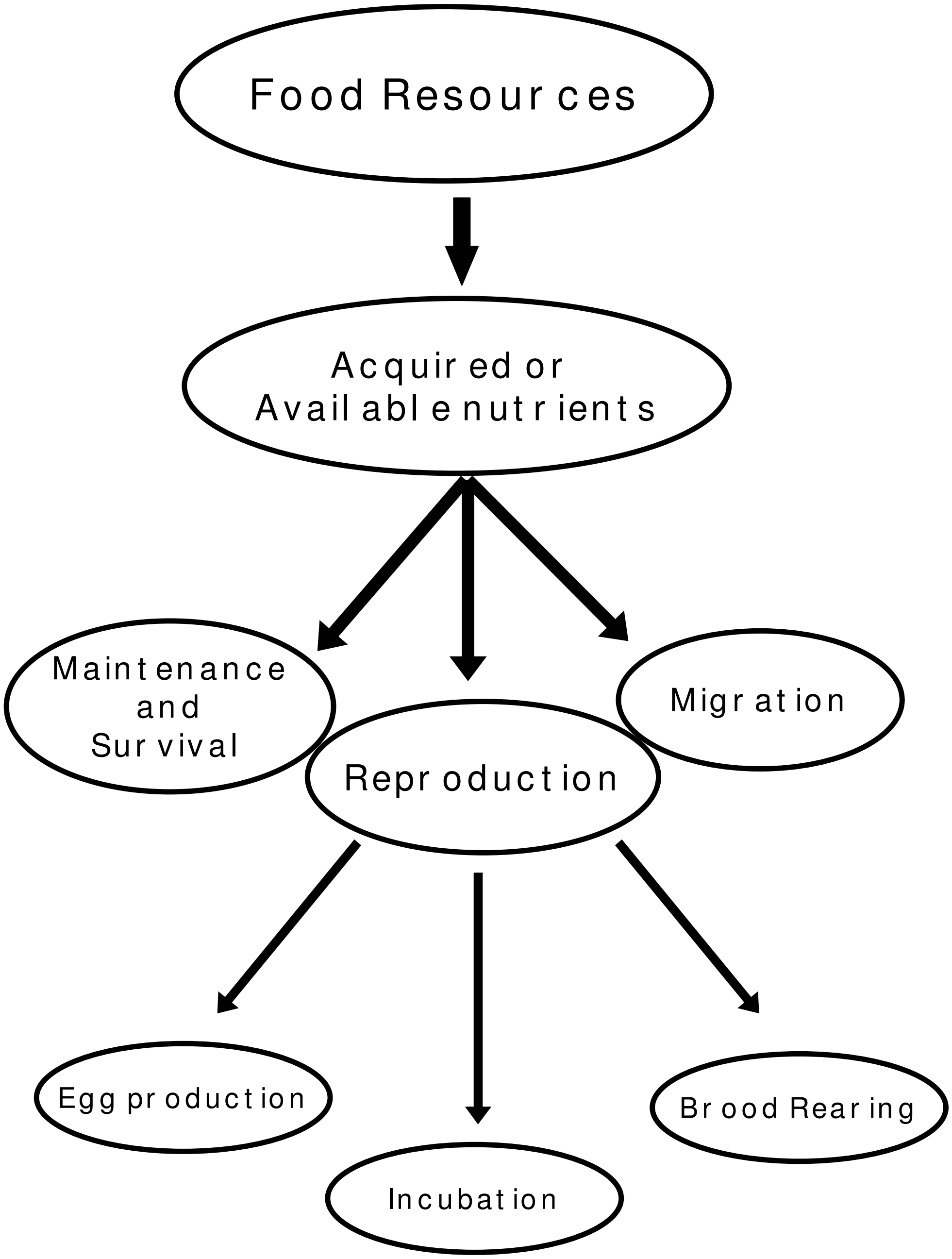


Figure 13.2.2 Map of breeding area study sites.

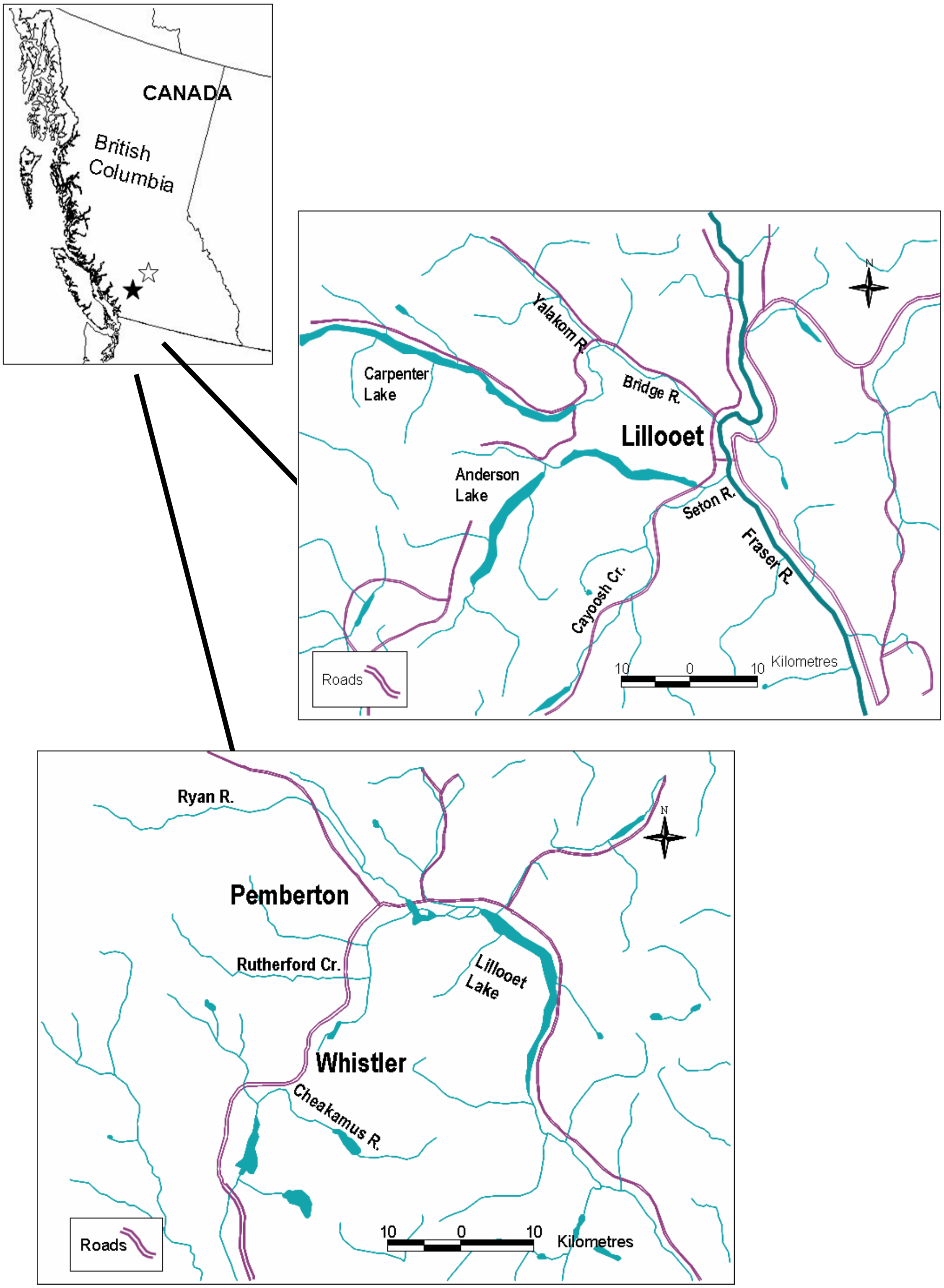
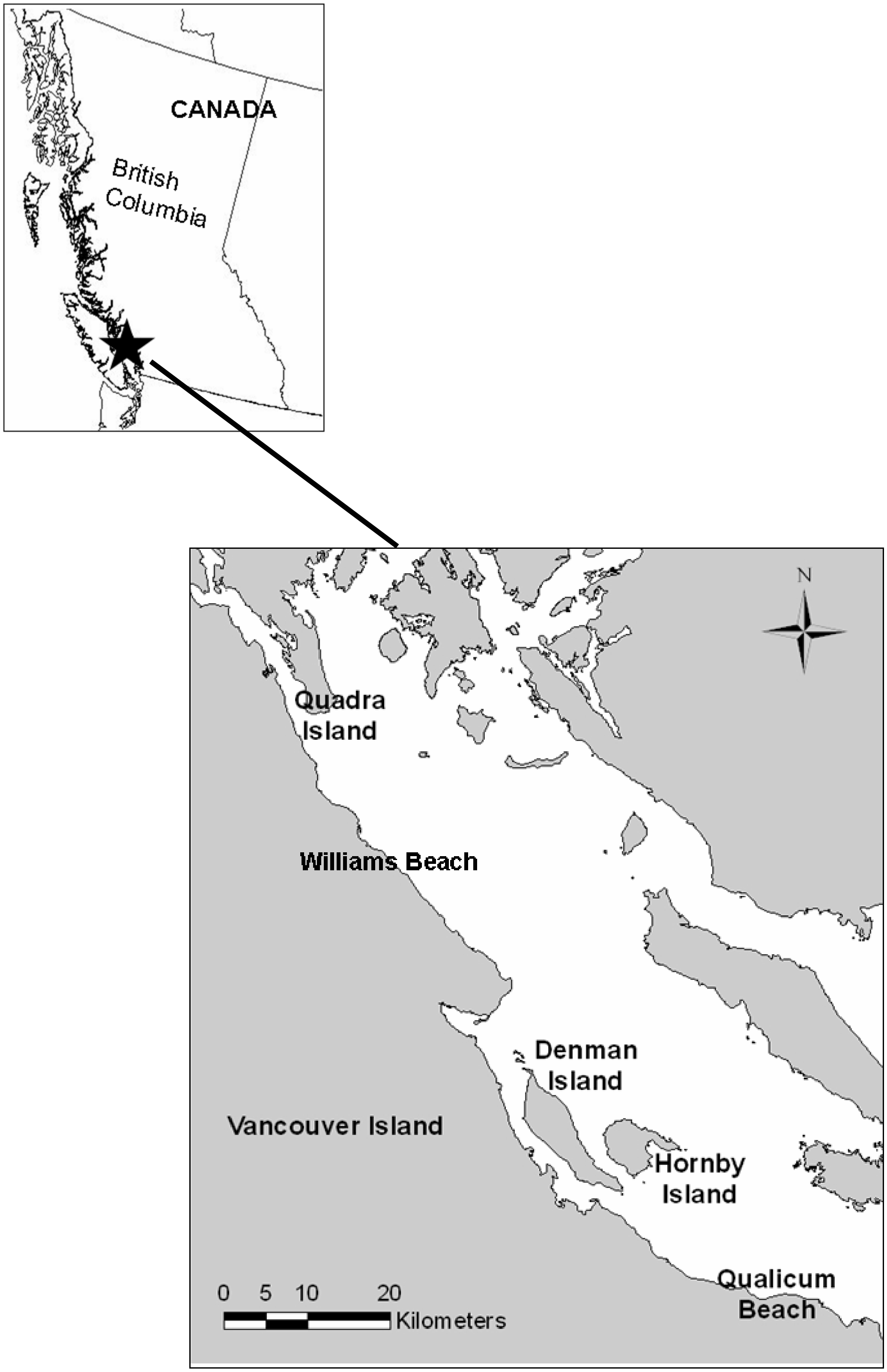


Figure 13.2.3 Map of wintering area study sites.



13.3. Nutrient Acquisition by Female Harlequin Ducks prior to Spring Migration and Reproduction: Evidence for Body Mass Optimization

Jeanine C. Bond[1]
Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6 CANADA

13.3.1. Abstract

We analysed variation in body mass of adult female Harlequin Ducks (*Histrionicus histrionicus*) on wintering sites in southern British Columbia, Canada, to investigate the chronology and location of nutrient acquisition prior to migration and reproduction. We found that female mass increased on average by 7% on coastal sites from late-winter to premigration; however, the chronology of mass gain varied depending on prey type. Females feeding on superabundant roe from spawning Pacific Herring (*Clupea pallasi*) became considerably heavier than prespawn measures and appeared to be heavier than females eating marine invertebrates, such as crabs, limpets, and snails, during the herring spawn period (March). By mid-April, prior to migration, females at all sites had similar body masses, with birds at sites without spawn increasing and those at spawn sites maintaining their earlier mass gain. Stable isotope analyses confirmed that birds at these different sites consumed very different diets. These results suggest that female Harlequin Ducks target an optimal premigratory body mass, regardless of access to a superabundant food source, and this body mass is likely shaped by the costs and benefits of nutrient storage for migration and reproduction.

13.3.2. Introduction

There is increasing recognition that cross-seasonal effects should be considered when investigating life history strategies and trade-offs (Tamisier et al. 1995, Gates et al. 2001, Boos et al. 2002, Webster et al. 2002), including those related to nutrient acquisition and allocation. Individuals carry over effects on condition from one season to the next, and these residual effects can influence demographic attributes such as reproductive success and annual survival (Webster et al. 2002). Seasonal variation in nutrient acquisition and allocation is commonly observed in birds as a result of differing energetic demands throughout the year. The relative use of stored nutrients (i.e., endogenous reserves) or dietary sources (i.e., exogenous nutrients) varies interspecifically during demanding stages such as migration and reproduction. The degree to which birds store energy and nutrients presumably reflects an adaptive

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[1] For submission to journals, authorship will include Daniel Esler.
Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6 CANADA .

strategy in which individuals maximize their fitness in relation to different selective pressures (Blem 1976, Moreno 1989, Stearns 1992).

Throughout the annual cycle, birds are thought to maintain optimal levels of endogenous reserves, not necessarily maximum, and this is considered a trade-off based on the costs and benefits of building and storing reserves (Lima 1986, Witter and Cuthill 1993). Benefits of storing nutrients include insulation, mechanical support, buoyancy, and most of all, access to energy (Witter and Cuthill 1993, Biebach 1996), while the costs of storing nutrients include mass-dependent predation risk from reduced flight agility (Lima 1986, Rogers 1987), mass-dependent foraging costs, and energy conversion inefficiencies (Witter and Cuthill 1993, Jönsson 1997). Decisions on how to balance these costs and benefits are further influenced by the environment in which the species resides.

In waterfowl, strategies of nutrient acquisition for migration and reproduction differ spatially and temporally for various species. For example, McLandress and Raveling (1981) found that Giant Canada Geese (Branta canadensis maxima) undergo considerable fattening before they leave wintering sites while Gauthier et al. (1992) determined that Greater Snow Geese (Chen caerulescens atlantica) store nutrients while on spring staging areas. Other species such as Ruddy Ducks (Oxyura jamaicensis; Tome 1984) and Greater Scaup (Aythya marila; Gorman 2005) appear to store nutrients after arrival on nesting areas. These temporal and spatial patterns of nutrient storage are likely affected by predictability and accessibility of exogenous food sources where predictable food supplies may reduce the need for endogenous stores (Jönsson 1997).

The extent to which Harlequin Ducks (*Histrionicus histrionicus*) build and use endogenous stores for migration and reproduction is unknown. If Harlequin Ducks store endogenous reserves for migration and subsequent investment in reproduction, it is important to determine where and when they build these nutrient stores in order to fully understand their nutrient acquisition strategy, and therefore, reveal potential sources of constraints to nutrient acquisition. Harlequin Ducks spend the winter in the marine environment generally consuming intertidal invertebrates such as snails, crabs, and limpets, and in spring, migrate to freshwater streams for nesting where they consume freshwater invertebrates (Robertson and Goudie 1999). Pacific Herring (Clupea pallasi) spawn is a key feature of the wintering habitat of Harlequin Ducks on the Pacific coast that could influence nutrient stores. For three to four weeks in late winter-early spring, herring roe is superabundant and some Harlequin Ducks are known to aggregate at herring spawn sites (Vermeer et al. 1997, Rodway et al. 2003). Rodway and Cooke (2002) determined that herring eggs are the principal prey for these aggregated ducks throughout the spawn period. The ecological implications of this food source have received little investigation, although there has been speculation on benefits to survival and/or reproductive potential (Rodway et al. 2003, Žydelis and Esler 2005).

To investigate timing of nutrient storage in Harlequin Ducks, as well as mediating effects of forage type, we measured body mass of captured adult female Harlequin Ducks in winter prior to spring migration. We also used stable isotope analyses to document diets of individuals in order to appropriately interpret the mass data. Our specific objectives were to determine (1) if females store nutrients on the wintering grounds prior to migration, and (2) the relative difference in amount or chronology of nutrient storage between females on herring spawn sites and those on nonspawn sites. For a species of concern like the Harlequin Duck (Robertson and Goudie 1999, Smith et al. 2001), strategies of nutrient acquisition for migration and reproduction can have important implications for understanding factors limiting productivity, and subsequently, can have important population and habitat management ramifications.

13.3.3. Methods

Study Locations and Capture Techniques

To evaluate body mass variation in relation to timing and occurrence of herring spawn, Harlequin Ducks were captured on marine wintering areas in the Strait of Georgia, British Columbia, at sites with and without spawn during three periods in 2004: prespawn (February 27 to March 5), midspawn (March 19 to 27), and postspawn (April 2 to 11). Capture locations were determined based on historical records of herring spawn occurrence (Fisheries and Oceans Canada 2004), and capture sites with spawn included locations around Hornby Island (49° 31'N, 124° 42'W), Denman Island (49° 32'N, 124° 49'W), and Qualicum Bay (49° 24'N, 124° 38'W) while nonspawn capture sites included locations around southeast Quadra Island (50° 12'N, 129° 15'W) and Williams Beach (49° 52'N, 125° 07'W).

We used a floating mist-net capture method modified for inshore use (Kaiser et al. 1995). Captured birds were immediately removed from the net, and then banded and weighed on an electronic balance (±1 g). We measured morphometric features including exposed culmen length and diagonal tarsal length to the nearest 0.01 mm, as well as wing chord (flattened and straightened) to the nearest mm. Age classes of females were determined by the depth of the Bursa of Fabricius (Mather and Esler 1999), and all females included in further analyses were after-third year (i.e., adults).

Sampling Methods and Laboratory Techniques

Some Harlequin Ducks move from their wintering sites to herring spawn sites and then return to their original wintering site, and because of this, we selected nonspawn sites at which few birds exhibited this movement (Rodway et al. 2003). However, to be sure that birds captured in nonspawn sites had not consumed any herring roe, we used stable isotope analysis to evaluate recent prey composition. The isotopic signatures of consumer tissues are related to their diets (DeNiro and Epstein 1978), and therefore, the stable isotope technique is ideal for identifying individuals that consume different food types. The heavy isotope of nitrogen (^{15}N) is preferentially incorporated into tissues of the consumer from the diet, which results in a systematic enrichment in the nitrogen ratio with each trophic level (Kelly 2000). For this study, we expected herring roe to have a more enriched nitrogen stable isotope value than marine intertidal invertebrates depredated by Harlequin Ducks, and we predicted that this difference would be reflected in the tissues of Harlequin Ducks consuming the different prey. We analysed female plasma because it indicates short-term diet information, i.e., within a few days, rather than cellular blood which may take up to a month to isotopically reflect a dietary change (Hobson and Clark 1992a; Hobson and Clark 1993, Bearhop et al. 2002).

A 1.5 ml blood sample was taken from the jugular veins of captured females using a heparinized 5.0 ml syringe with a 21-gauge needle. For a small number of females, a 1.0 ml syringe with a 24-gauge needle was used to take 0.5 ml of blood from the tarsal vein instead. Collected blood was transferred to a heparinized vial and stored on ice until the plasma was separated from cellular blood components using a centrifuge (within 12 h). These samples were transferred to separate vials and stored frozen. Also, following information provided by Rodway and Cooke (2002), we collected intertidal crabs, snails, limpets, and amphipods as food items making up the majority of Harlequin Duck winter diet, as well as herring roe for comparison.

Samples for stable isotope analyses were prepared at Simon Fraser University and then sent to the Department of Soil Sciences at the University of Saskatchewan for isotope ratio determination. The samples analysed in this study included plasma and marine diet items. Plasma samples were dried in a 60°C oven and ground to a fine powder with a mortar and pestle. The marine diet samples were rinsed with distilled water, removed from shells (for limpets and snails), dried and then powdered in the same fashion. Lipids were removed from the diet samples using a 2:1 chloroform:methanol solution (Bligh and Dyer 1959) and retrieved by evaporating off the solvent in a fume hood. The lipid-free, powdered invertebrate samples were treated with a few drops of a 0.1N HCl solution without rinsing to remove carbonates.

The nitrogen stable isotope signatures of samples were determined by loading 1 mg of each sample into tin cups and combusting them at 1800°C. Then the isotopic ratios were measured using continuous-flow isotope ratio mass spectrometry (CFIRMS). Analytical error for nitrogen isotope measurement was estimated to be 0.3 ‰. All isotope values per sample are expressed in delta (δ) notation, a ratio of the heavier to lighter isotope relative to a standard in parts per thousand. This ratio is written as:

$$\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where R is the corresponding ratio $^{15}N/^{14}N$. The standard for nitrogen is atmospheric nitrogen.

Statistical Methods

We used general linear models to evaluate variation in body mass of adult female Harlequin Ducks on marine areas in relation to spawn site status (spawn vs. nonspawn), period (prespawn, midspawn, and postspawn), and body size. A principal component analysis was conducted to create an index of body size for each individual based on tarsus, wing chord, and culmen measurements. This index, the PC_1 score, showed positive relationships with all morphometric variables and had an eigenvalue of

1.27, explaining 42.5% of the total original variance. PC_1 was included in a subset of candidate models (described below) to consider effects of body size on body mass and, if necessary, account for size-related variation when evaluating effects of sites and periods.

We employed an information-theoretic approach to model selection (Burnham and Anderson 2002), applying a set of biologically plausible combinations of explanatory variables as candidate models (Table 13.3.1). The assorted models represent different ways of grouping site status and period combinations, which is analogous to a two-way ANOVA with pairwise post-tests in a hypothesis testing statistical paradigm. We used the same model sets with and without PC_1 to allow consideration of body size effects. Because our dataset consisted of 80 females, Akaike's Information Criterion for small sample sizes (AIC_c) was calculated for each model (Table 13.3.1), which indicates the fit of the model given the data and set of models considered. We also calculated the differences between these values for each model in relation to the best-fitting model (ΔAIC_c) and the AIC_c weights (AIC_cW) for each model, which convey the relative support for each model in the candidate model set.

13.3.4. Results

Stable Isotope Results

We determined that nitrogen stable isotope values for herring roe and marine invertebrates were, as predicted, different and that after herring spawn commenced, birds captured on spawn sites had plasma isotope values that were more enriched than those at sites where spawn was unavailable (Figure 13.3.1). We estimated expected plasma values based solely on herring roe diet and mixed marine invertebrate diet by taking an average value for each diet and accounting for changes in isotope signature between prey and duck body tissues (i.e., discrimination or fractionation factors). The discrimination factor between Harlequin Duck plasma and diet has not been experimentally determined, so we applied a literature value of +3.3 ‰ determined for carnivorous species (Peregrine Falcon (Falco peregrinus), Hobson and Clark 1992b; Dunlin (Calidris alpina pacifica), Evans-Ogden et al. 2004). There was not perfect correspondence between the measured plasma isotope values and the predicted plasma values. This may have been a result of the applied discrimination factor or because we did not sample every possible invertebrate prey type, nor did we know the proportions of different invertebrate prey in the diet. Also, birds feeding primarily on herring spawn may also have consumed some marine invertebrates.

Despite these uncertainties, clear patterns are evident in the data. Plasma stable isotope values were similar for females on both sites prior to the occurrence of herring spawn. Once spawn commenced, stable isotope signatures changed dramatically at spawn sites, consistent with a switch to a more isotopically enriched diet, while isotope signatures on nonspawn sites did not change. Most importantly, there was no isotopic evidence that birds captured at nonspawn areas consumed spawn at any period, and therefore, we are confident that our body mass data accurately represent birds consuming roe and those consuming marine invertebrates. The isotope signatures for some females captured at spawn sites during the postspawn period are decreasing, which presumably is a reflection of birds switching back to consuming marine invertebrates as herring roe becomes less available.

Body Mass Analysis

We captured and measured 80 adult female Harlequin Ducks on wintering sites and found that period, site status, and body size had important effects on body mass. From our candidate set of models evaluating mass variation, the model best supported by the data (model 1, Table 13.3.1) was that which indicated that body mass differed between the following two groups: birds at both prespawn sites and at nonspawn sites during the midspawn period were in one group, and birds at midspawn spawn sites and both postspawn sites. An examination of the data (Figure 2.2) supports this model structure. This model, which included the body size parameter, was strongly supported with an AIC_cW of 0.628 and an R^2 of 0.41. The second best supported model (model 2) had a similar model structure, with the only difference being that data from the midspawn period at spawn sites were treated as a separate group; this model received less than half the support ($AIC_cW = 0.253$) of model 1. None of the remaining models received substantial support, including global models in which all periods and sites were treated as separate groups (models 6 and 14, with and without PC_1, respectively) and null models in which all data were treated as one group (models 10 and 17, with and without PC_1, respectively). These results strongly support the conclusions that body size explained important variation in the data and that body mass of females differed between prespawn and postspawn periods, but not between sites during those periods. There was more uncertainty surrounding mass dynamics during the midspawn period, although the high AIC_cW for models 1 and 2 combined (summed $AIC_cW = 0.881$) indicates that masses differed between sites during midspawn. Also, models in which midspawn data from both sites were together and either lumped with postspawn (model 4) data or alone (model 5), were not well supported with AIC_cW of 0.045 and 0.015, respectively.

To summarize, our analysis provided strong support for the conclusions that body mass (after accounting for body size) was similar between sites prior to spawn, birds on spawn sites increased mass substantially during the midspawn period while those on nonspawn sites seemed to maintain their prespawn mass, and masses were similar between sites during the postspawn period, due to increases in mass of birds from nonspawn sites and maintenance of previously gained mass by birds from spawn sites. The change in average body mass (± SE) between prespawn and postspawn periods, for both sites, was 40 ± 10 g, an increase of 7 ± 1.8 % (Figure 13.3.2). Although fewer females were captured during midspawn on nonspawn sites, there is an indication that the chronology of mass gain may depend on prey consumed (i.e., herring roe or marine invertebrates).

13.3.5. Discussion

Like many waterfowl, adult female Harlequin Ducks store endogenous nutrients on wintering areas prior to spring migration. Our data indicate that, despite differences in forage type and availability on herring spawn sites relative to nonspawn sites, females from both areas achieved a similar body mass prior to departure from wintering areas. This result suggests that females target an optimal premigratory body mass that balances the costs and benefits of nutrient storage, irrespective of exogenous nutrient availability.

Nutrient acquisition and storage prior to migration and reproduction can have significant fitness benefits. Storing energy for migration is important for sustained flights and reduces the need for stop-overs, which increases the speed of migration, and can buffer against food shortage in low quality stop-over sites (Biebach 1996). For reproduction, a growing body of evidence indicates that female waterfowl must attain some minimum threshold level of nutrient reserves to initiate egg production (Drent and Daan 1980, Alisauskas and Ankney 1994, Esler et al. 2001, Gorman 2005). Hence, arrival on breeding areas with higher levels of energy and nutrients can allow females to attain this breeding threshold faster, and therefore, nest earlier (Schultz 1991, Alisauskas and Ankney 1992). Numerous studies demonstrate that earlier nesting results in higher reproductive success, through larger clutch sizes, increased opportunity for renesting, and/or more favourable environmental conditions for broods (Perrins 1966, Rowe et al. 1994, Lepage et al. 2000).

These benefits of nutrient storage are countered by costs. Predation risk may be higher for heavier birds because of reduced manoeuvrability and ability to escape predators (Lima 1986, Rogers 1987). As well, heavier birds incur higher flight costs through increased wing loading, which is important for migrating birds (Kullberg et al. 2005). This may be especially prominent for ducks, which have relatively high wing loading. Also, for diving birds like the Harlequin Duck, higher fat levels associated with increased mass could increase buoyancy, and therefore, increase costs of foraging (Witter and Cuthill 1993). In light of these potential costs, Harlequin Ducks likely face a trade-off with the potential benefits of nutrient storage.

Our findings indicate that access to Pacific Herring spawn events may influence the chronology of nutrient storage, but it does not affect the absolute amount of nutrients acquired on wintering sites. Herring roe provides a superabundant food source on which Harlequin Ducks are known to aggregate and feed (Rodway and Cooke 2002, Rodway et al. 2003), and fish eggs are a high energy, lipid-rich diet item (Paul and Paul 1999). However, because female Harlequin Ducks can achieve the same premigratory body mass when feeding on intertidal invertebrates, we speculate that there may be benefits to aggregating on spawn sites beyond nutrient acquisition. These may include important social interactions as suggested by Rodway et al. (2003) or an increase in time spent in non-foraging behaviours due to reductions in feeding time (Rodway and Cooke 2001, Žydelis and Esler 2005). Also, Rodway and Cooke (2001) suggested that Harlequin Ducks foraging on herring spawn sites would face less predation risk because they tend to move to safer offshore roosting sites earlier than birds foraging on invertebrates.

Therefore, although there are not direct advantages to consuming herring roe and aggregating on spawn sites in terms of nutrient storage, birds may benefit in other ways, and this requires further investigation.

Many other seabirds are known to aggregate and feed at herring spawn sites (Haegele 1993, Vermeer et al. 1997, Sullivan et al. 2002), and it is unknown how their mass dynamics are influenced by herring spawn. Some species may rely more heavily on herring spawn for nutrient acquisition, such as species like scoters that deplete winter foods (Lacroix 2001), and hence may require spawn as a source of nutrients for spring hyperphagia. Also, high arctic nesting species such as the Steller's Eider (Polysticta stelleri) that aggregate on herring spawn prior to migration (Žydelis and Esler 2005) may depend on this food source for breeding on potentially food-limited sites. The proportion of a population that aggregates on herring spawn sites may be indicative of the population's dependence on spawn for meeting energetic costs (Vermeer et al. 1997), as illustrated by the fact that not all Harlequin Ducks in the Strait of Georgia aggregated during spawning events. Elucidating strategies for meeting the demands of migration and reproduction, including the role of herring spawn, are critical for informed management and conservation of bird species. As well, these strategies highlight the importance of considering cross-seasonal effects when managing populations.

13.3.6. Acknowledgements

We acknowledge BC Hydro Bridge Coastal Restoration Program and Environment Canada Science Horizons Program for financial support and the Centre for Wildlife Ecology at Simon Fraser University for logistical support. For assistance in the field, we thank E. Anderson, J. Bond, K. Bond, J. Harding, J. Heath, S. Iverson, S. LeBourdais, E. McClaren, K. Wright, and R. Žydelis. T.D. Williams, R.C. Ydenberg, and S.E. Jamieson provided useful comments on earlier drafts. Also, T.D. Williams provided laboratory facilities at Simon Fraser University. Thanks to K.A. Hobson, P. Healy, M. Benjamin, and M. Stocki for assistance with stable isotope analysis.

13.3.7. References

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Table 13.3.1 Candidate models describing variation in female Harlequin Duck body mass in relation to period (before herring spawn [pre], during herring spawn [mid], and following herring spawn [post]), site status (herring spawn site [S] and nonspawn site [N]), and a principal component score of morphometrics that indexes body size (PC_1).

Note: K is the number of parameters estimated in the model, AIC_c is Akaike's Information Criterion corrected for small sample sizes, ΔAIC_c is the difference in AIC_c relative to the best-fitting model, and AIC_cW is the AIC_c weight or model likelihood.

Model Rank	Candidate Model Structure	K	AIC_c	ΔAIC_c	AIC_cW
model 1	preN = preS = midN, midS = postN = postS + PC_1	4	551.6	0.00	0.628
model 2	preN = preS = midN, midS, postN = postS + PC_1	5	553.5	1.81	0.253
model 3	preN = preS = midN = postN, midS = postS + PC_1	4	556.9	5.25	0.046
model 4	preN = preS, midN = midS = postN = postS + PC_1	4	556.9	5.27	0.045
model 5	preN = preS, midS = midN, postS = postN + PC_1	5	559.2	7.52	0.015
model 6	preN, preS, midN, midS, postN, postS + PC_1	8	559.5	7.84	0.012
model 7	preN = preS = midN = postN = postS, midS + PC_1	4	564.8	13.16	0.001
model 8	preN = midN = postN, preS = midS = postS + PC_1	4	567.4	15.75	0.000
model 9	preN = preS = midN, midS = postN = postS	3	568.4	16.79	0.000
model 10	PC_1	3	568.7	17.09	0.000
model 11	preN = preS = midN, midS, postN = postS	4	570.3	18.64	0.000
model 12	preN = preS, midN = midS = postN = postS	3	572.3	20.67	0.000
model 13	preN = preS, midS = midN, postS = postN	4	574.5	22.88	0.000
model 14	preN, preS, midN, midS, postN, postS	7	577.1	25.48	0.000
model 15	preN = preS = midN = postN, midS = postS	3	577.8	26.11	0.000
model 16	preN = preS = midN = postN = postS, midS	3	584.8	33.13	0.000
model 17	preN = preS = midN = midS = postN = postS	2	589.5	37.82	0.000
model 18	preN = midN = postN, preS = midS = postS	3	590.1	38.41	0.000

Figure 13.3.1 Plasma nitrogen isotope ratios of female Harlequin Ducks captured on Pacific Herring spawn sites and nonspawn sites during the three periods corresponding to before, during, and after spawn.

> Note: Dotted line = expected plasma values based solely on herring roe. Dashed line = expected plasma values based solely on equal portions of several marine invertebrates (snail, crab, amphipod, and limpet). Discrimination factors were applied to create expected plasma values (see results).

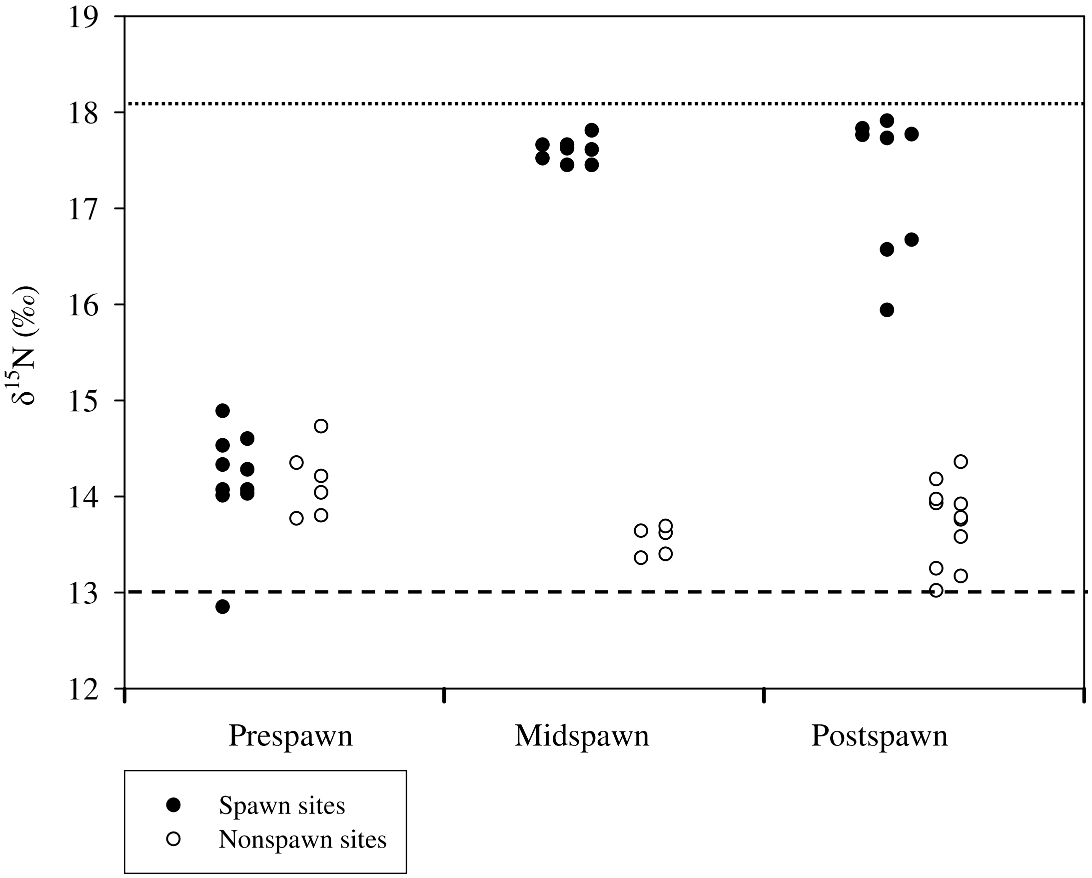
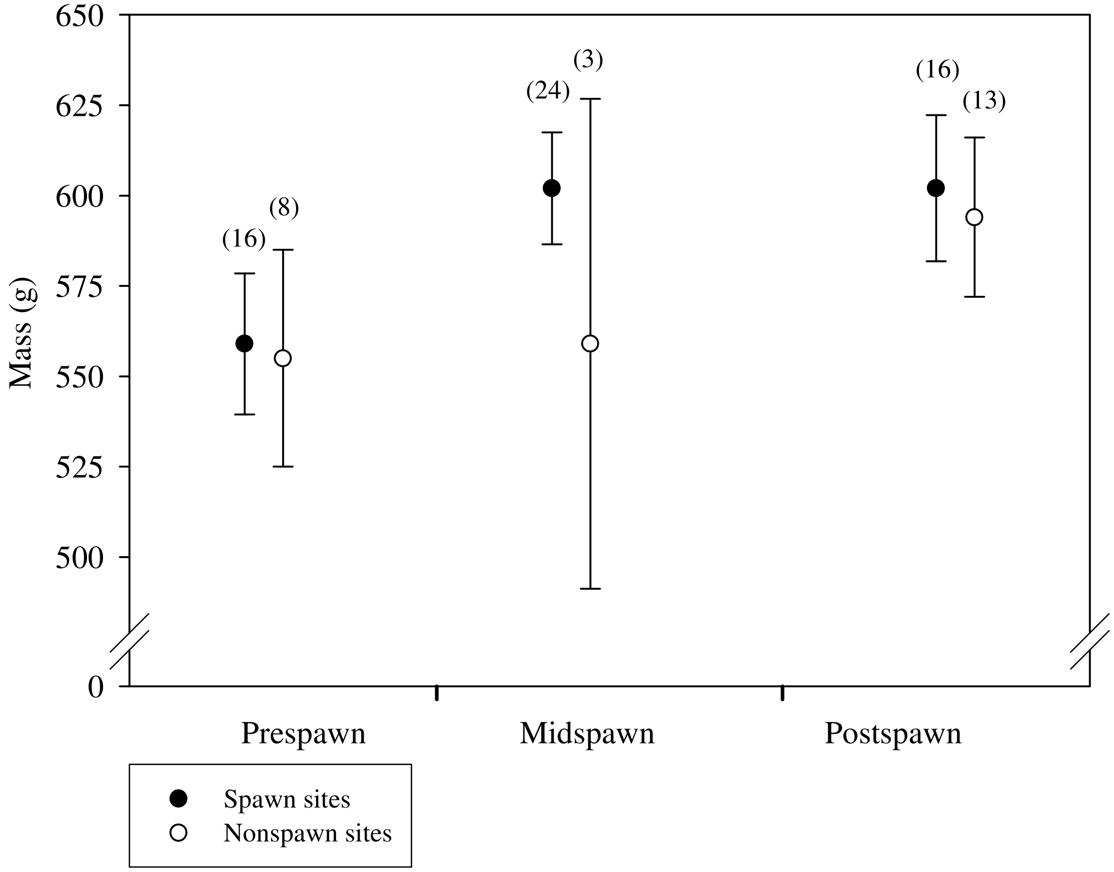


Figure 13.3.2 Mass (mean ± 95% CI) of adult female Harlequin Ducks on wintering sites with and without spawning Pacific Herring during prespawn, midspawn, and postspawn periods in the Strait of Georgia, BC.

Note: Sample sizes for each group are indicated in parentheses.



13.4. Isotopic Evidence for Sources of Nutrients Allocated to Clutch Formation by Harlequin Ducks

Jeanine C. Bond[2]
Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6 CANADA

13.4.1. Abstract

Waterfowl employ a broad array of strategies for acquiring energy and nutrients needed for egg formation, ranging from storage of endogenous reserves prior to arrival on breeding areas to complete reliance on exogenous food sources available at breeding sites. We used stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) to quantify the relative nutrient inputs to Harlequin Duck (*Histrionicus histrionicus*) eggs, and therefore, identify the strategy of nutrient acquisition and allocation used by females to meet demands of egg production. Harlequin Ducks migrate between isotopically distinct marine wintering grounds and freshwater breeding grounds, which facilitates the use of stable isotope signatures to track origins of nutrients. We found little evidence that endogenous reserves stored on marine wintering areas were allocated to clutch formation, with egg isotope signatures reflecting mostly freshwater nutrient sources. Therefore, Harlequin Ducks relied on food available on breeding streams for egg formation, and any reserves stored on marine areas were likely used during other energetically and nutritionally demanding stages.

13.4.2. Introduction

Animals maximize fitness through optimal resource use, which involves employing various strategies of nutrient acquisition and allocation throughout the annual cycle (Calow and Townsend 1981, Jönsson 1997). Egg production in birds can be an energetically and nutritionally demanding stage, particularly for precocial breeders like waterfowl that lay large clutches of energy-dense eggs (Alisauskas and Ankney 1992). Waterfowl exhibit an array of strategies for meeting demands of clutch formation. One strategy is to build nutrient stores prior to breeding that can be subsequently invested in reproduction. These stores are known as endogenous reserves, and use of these reserves for reproduction has been referred to as ‘capital’ breeding (Drent and Daan 1980, Jönsson 1997, Meijer and Drent 1999). Alternatively, reliance on locally available food sources, also known as exogenous resources, to acquire energy and nutrients for reproduction has been termed ‘income’ breeding (Drent and Daan 1980, Jönsson 1997, Meijer and Drent 1999).

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[2] For submission to journals, authorship will include Daniel Esler[1] and Keith A. Hobson [2].

[1] *Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6 CANADA*

[2] *Canadian Wildlife Service, 115 Perimeter Road, Saskatoon, SK, S7N 0X4 CANADA*

Nutrient acquisition and allocation for clutch formation by waterfowl spans a continuum of capital to income strategies, and can even be variable within species. Although strict capital breeding is now considered rare (Meijer and Drent 1999), some species such as Common Eiders (Somateria mollisma) have been reported to rely heavily on endogenous reserves for egg production (Parker and Holm 1990). Alternatively, Northern Shovelers (Anas clypeata) and Greater Scaup (Aythya marila) in Alaska rely almost entirely on dietary intake (MacCluskie and Sedinger 2000, Gorman 2005), and many species apparently use intermediate proportions of endogenous reserves for clutch formation, including Lesser Scaup (Aythya affinis; Esler et al. 2001), Canvasbacks (Aythya valisineria; Barzen and Serie 1990), and Ruddy Ducks (Oxyura jamaicensis; Tome 1984, Alisauskas and Ankney 1994). Also, Esler and Grand (1994) demonstrated that there can be intraspecific variation in endogenous reserve use. Identifying the nutrient allocation strategy for different species and populations offers insight into resource use and the suitability of differing habitats for meeting the requirements of reproduction. As well, in a conservation context, this information allows recognition of when and where nutritional constraints might be expressed, which can lead to important population and habitat management ramifications (Anteau and Afton 2004).

Traditionally, energetic strategies used by waterfowl during egg production have been inferred from carcass analysis of collected females (Alisauskas and Ankney 1992). With this method, the change in endogenous reserves relative to investment of nutrients into reproductive tissue can be interpreted as the maximum proportion of the clutch that could be derived from endogenous reserves. For example, if endogenous lipid reserves decline 0.5 of a gram for every gram of lipid used for egg production, no more than 50% of the egg lipid could be derived from endogenous reserves. However, it is unclear how much of the female’s reserves actually go into eggs, and how much are used for meeting her own energy requirements (Meijer and Drent 1999, Hobson et al. in press). This could result in an overestimation of nutrients transferred from endogenous reserves to eggs (Meijer and Drent 1999).

More recently, stable isotope analysis has been employed to directly trace nutrient allocation for reproduction (Hobson et al. 2000, Klassen et al. 2001, Gauthier et al. 2003, Hobson et al. in press). This method uses naturally occurring stable isotope signatures in the environment as a means of identifying nutrient sources for egg formation. The isotopic signatures of consumer tissues are related to their diets (DeNiro and Epstein 1978), and therefore, the stable isotope technique is ideal for identifying nutrients acquired from differing environments, either directly through diet or through tissues of laying females. Marine ecosystems are typically enriched in ^{13}C and ^{15}N relative to terrestrial or freshwater ecosystems (Michener and Schell 1994). Birds that migrate between wintering and breeding grounds that differ in isotopic composition, such as marine and freshwater, will have stored nutrients that differ isotopically from locally available nutrient sources (Hobson in press).

In this study, our objective was to identify the nutrient allocation strategy for clutch formation in Harlequin Ducks (*Histrionicus histrionicus*) by quantifying the relative inputs of nutrients from wintering sites and breeding sites into eggs using stable isotope analyses. Stable isotopes are particularly useful for addressing these issues because Harlequin Ducks winter in marine environments and breed along freshwater streams. In both areas, they feed on invertebrate prey (Robertson and Goudie 1999). On wintering areas, immediately prior to migration and reproduction, adult females increase in mass by 7% (Chapter Two), but it is unknown if these acquired nutrients are allocated to egg formation. We investigated the extent to which these acquired nutrients might be allocated to migration, and determined that only 2.6% of their wintering endogenous reserves would be used to fly to the breeding study site (Appendix). Hence, it is possible that females allocate some marine nutrients to egg production, and this information is important for understanding factors influencing reproductive performance.

13.4.3. Methods

Study Area and Capture Techniques

Harlequin Ducks were captured on breeding streams using mist nets from May 9 to 20, 2003, and from April 21 to May 20, 2004, in the southern Coast Mountains of British Columbia, Canada. The study area included streams near the towns of Pemberton (50° 19’N, 122° 48’W) and Lillooet (50° 41’N, 121° 56’W). Wintering ducks also were captured from February 27 to April 11, 2004, in the Strait of Georgia, British Columbia, using a floating mist-net capture method adapted for inshore ocean use (Kaiser et al. 1995). Captured birds were immediately removed from the net, and then weighed, banded, and assigned to an age class based on the depth of the Bursa of Fabricius (Mather and Esler 1999).

Sample Collection

Samples of blood were taken from captured wintering females for stable isotope analyses to represent endogenous marine nutrients. A 1.5 ml blood sample was taken from the jugular vein using a heparinized 5.0 ml syringe with a 21-gauge needle. For a small number of females, a 1.0 ml syringe with a 24-gauge needle was used to take 0.5 ml of blood from the tarsal vein instead. Collected blood was transferred to a heparinized vial and stored on ice until the plasma was separated from cellular blood components using a centrifuge (within 12 h). These samples were transferred to separate vials and stored frozen.

Also, a subcutaneous lipid biopsy was taken from each wintering female. Feathers in the area of lipid depots on the belly were parted using isopropyl alcohol and the site was prepped with Betadine solution. Using forceps, the skin was lifted and a small (~ 5 mm) incision in the skin was made with surgical scissors. Several milligrams of lipid in the region of the incision were removed with forceps. The incision site was sealed with veterinary-grade adhesive. Lipid samples were kept frozen until analysis.

In order to find nests for egg collection, each female captured on breeding streams was attached with a radio transmitter using a subcutaneous anchor and glue. The transmitters, made by Holohil Systems Ltd, were a six-gram RI-2B model with a motion-sensitive mortality sensor and a battery life of three to nine months. The transmitter was located in the small depression between the scapulae, dorsal to the approximate junction of the cervical and thoracic vertebrae. We monitored radio-tagged females at least once a week to locate nests, and we removed one egg at random from each discovered clutch. Clutches ranged from five to seven eggs. One egg was provided (by S. Freeman) for our study from the Skagit River (49° 00'N, 121° 05'W) in southern British Columbia. We also opportunistically collected two full clutches; in 2003, one female abandoned her nest due to rain and flooding, and in 2004, a female was depredated, leaving her clutch unattended. All collected eggs were hard boiled and then frozen (Gloutney and Hobson 1998).

Prey samples were collected from breeding streams to represent freshwater nutrient sources. Freshwater invertebrate larvae such as stoneflies, mayflies, and caddisflies were collected from each stream in the study area; these are the major diet items of Harlequin Ducks on streams (Wallen 1987, Wright et al. 2000). These samples were frozen in vials until analysis.

Laboratory Techniques

Samples for carbon and nitrogen stable isotope ratio analyses were prepared at Simon Fraser University and then sent to the Department of Soil Sciences at the University of Saskatchewan for isotope ratio determination. Samples were separated into lipids and nonlipid components, if necessary, because of potential differences in allocation of these nutrients to eggs. Samples analysed for this study included abdominal lipid (n = 18), cellular fraction of blood (n = 60), freshwater invertebrates (lipid [n = 5] and nonlipid [n = 9] components), lipid-free egg yolk (n = 23), egg yolk lipid (n = 23), and egg albumen (n = 23). Cellular blood samples were dried in a 60°C oven and homogenized by grinding to a fine powder with a mortar and pestle. Freshwater diet samples were rinsed with distilled water, dried, and then homogenized. Lipids were removed from the diet samples using a 2:1 chloroform:methanol solution (Bligh and Dyer 1959) and retrieved by evaporating off the solvent in a fume hood. The lipid-free, homogenized samples were treated with a few drops of a 0.1N HCl solution without rinsing to remove carbonates. Abdominal fat was subsampled and analysed directly. Eggs were separated into yolk and albumen easily because they were previously hard boiled. Albumen was dried and ground into a fine powder. The egg yolk was dried, and yolk lipid and lipid-free yolk were separated using the same extraction methods described above.

The carbon and nitrogen stable isotope signatures of samples were determined by loading 1 mg of each sample into tin cups and combusting them at 1800°C. Then the isotopic ratios were measured using continuous-flow isotope ratio mass spectrometry (CFIRMS). Analytical error for each isotope measurement was estimated to be 0.1 ‰ and 0.3 ‰ for carbon and nitrogen isotope measurements, respectively. All isotope values per sample are expressed in delta (δ) notation, a ratio of the heavier to lighter isotope relative to standards in parts per thousand. This ratio is written as:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The standard for carbon is PeeDee Belemnite (PDB) and for nitrogen the standard is atmospheric nitrogen.

Statistical Methods

To evaluate the relative contributions of source nutrients (marine or freshwater) to eggs, we used a single-isotope linear mixing model for carbon and for nitrogen (Phillips and Gregg 2001). We were only interested in considering two nutrient sources for the eggs so we did not look at both isotopes simultaneously, i.e., in a dual-isotope mixing model. Also, because lipid contains very little nitrogen, only carbon isotope values were used to model origins of this macronutrient. The two-endpoint linear mixing model can be formulated from the following mass balance equations for a mixture (M) and two sources (A and B) (Phillips and Gregg 2001):

$$\delta_M = f_A\delta_A + f_B\delta_B \qquad\qquad 1 = f_A + f_B$$

where δ is the mean isotopic signature and f is the proportion of the source found in the mixture. Then the mean proportion of source A in the mixture can be calculated as (Phillips and Gregg 2001):

$$f_A = \frac{\delta_M - \delta_B}{\delta_A - \delta_B}$$

For freshwater food sources, we used the mean lipid and nonlipid isotopic values (± SE) from the freshwater invertebrate samples collected in our study area (nonlipid: $\delta^{13}C$ = -25.4 ± 0.8 ‰, $\delta^{15}N$ = 2.2 ± 0.4 ‰; lipid: $\delta^{13}C$ = -29.7 ± 1.4 ‰). For endogenous marine sources, we used wintering tissues of cellular blood ($\delta^{13}C$ = -13.9 ± 0.1 ‰, $\delta^{15}N$ = 14.0 ± 0.2 ‰) for nonlipid samples and abdominal lipid ($\delta^{13}C$ = -19.7 ± 0.3 ‰) for lipid samples collected from the captured females. These body tissues do not appear to turnover quickly, and therefore, they represent an average winter diet (Hobson and Clark 1992a, Hobson 2005). We then investigated the relative contributions of these marine and freshwater sources to egg albumen, lipid-free yolk, and yolk lipid tissues.

A critical assumption implicit in the application of the stable isotope technique is that stable isotope concentrations of consumer diets can be related to those of consumer tissues in a predictable fashion (Hobson and Clark 1992b). The changes in isotope values from diet to tissue, also known as isotopic discrimination (or fractionation) factors, have been experimentally determined for various somatic tissues (Hobson and Clark 1992b, Bearhop et al. 2002) and for egg components (Hobson 1995). Although there is debate regarding the applicability of discrimination factors between species and between different tissues (Dalerum and Angerbjörn 2005), it has been recommended to use tissue-specific factors determined for closely related species with similar diets and habitats, in order to minimize errors associated with incorrect discrimination factors (Vanderklift and Ponsard 2003). Because Hobson (1995) is the only published report of discrimination factors between diet and egg tissues, we used his estimates for the carnivore model as being most similar to Harlequin Ducks. For exogenous sources, we used discrimination factors where carbon fractionates by 0 ‰ for yolk lipid and nonlipid and by +0.9 ‰ for albumen, and nitrogen fractionates by +3.4 ‰ for egg yolk nonlipid and albumen from diet to tissues. Discrimination factors for endogenous sources to eggs have not been experimentally determined, and so we followed Gauthier et al. (2003) and Schmutz et al. (in press) in using discrimination factors from the same carnivore model (Hobson 1995), assuming that mobilization of nutrients from somatic tissues is similar to a carnivorous diet.

The mixing model analyses calculated the mean contribution to eggs over the entire clutch because only one randomly chosen egg was analysed from each clutch. However, because we opportunistically collected two full clutches, we were also able to calculate intraclutch variation using a coefficient of variation and compare this to the variation between clutches.

13.4.4. Results

Of the 34 female Harlequin Ducks captured on breeding streams in the southern Coast Mountains of British Columbia, 22 were discovered on nests. We collected single eggs from 20 of those nests, complete clutches from the remaining two, and received a single egg from a nest on the Skagit River.

Female Harlequin Ducks allocated almost entirely freshwater nutrients to egg formation. From the carbon mixing model, we estimated that 100% (95% confidence interval = 83-100%) of the nutrients for egg albumen and lipid-free yolk were derived from breeding stream sources, and that 100% (95% confidence interval = 60-100%) of the nutrients for yolk lipid also came from freshwater nutrients (Figure 13.4.1). The nitrogen mixing model produced similar results but indicated a slight transfer of endogenous marine nutrients, especially for lipid-free yolk (89%; 95% confidence interval = 81-98%).

The conclusion that Harlequin Duck eggs are produced almost entirely from freshwater nutrients is supported by examination of plots showing isotopic signatures from the marine and freshwater biomes. Carbon and nitrogen isotope values for nonlipid components of eggs were clearly clustered with the values for freshwater invertebrates, and were distinct from the cluster of values for blood collected on wintering sites (Figure 13.4.2). Similarly, carbon values for yolk lipid matched those of lipid in freshwater invertebrates and were dissimilar from carbon isotope values of abdominal lipid collected from Harlequin Ducks on wintering areas (Figure 13.4.3).

We contrasted interclutch and intraclutch variation in stable isotope signatures, and found that variation within clutches was considerably smaller than variation between clutches (Figures 13.4.4 and 13.4.5). The interclutch coefficient of variation (CV) for egg yolk nonlipid was 18% and 9% for nitrogen and carbon, respectively. In contrast, intraclutch CVs for nitrogen and carbon were 4% and 3%, respectively, for clutch #1 and 2% and 1%, respectively, for clutch #2. Similarly, the interclutch CV for carbon in egg yolk lipid was 8%, compared to intraclutch CVs of 1% for each complete clutch. Even with the higher variation between clutches, the results are still strongly indicative of freshwater rather than marine contributions.

13.4.5. Discussion

Our stable isotope data indicate that Harlequin Ducks allocated little to no nutrients acquired on marine wintering areas to egg formation, and these results are similar for both protein and lipid components. Therefore, freshwater breeding site nutrient allocation is the predominant strategy of Harlequin Ducks for clutch formation in the southern Coast Mountains of British Columbia.

Because our results were based on a randomly chosen egg from each clutch, they represent the average strategy of nutrient allocation to egg production. There is some evidence to suggest, however, that there can be significant intraclutch variation in sources of egg nutrients. Both Barrow's Goldeneye (Bucephala islandica; Hobson et al. in press) and Redhead Duck (Aythya americana; Hobson et al. 2004) females allocated more endogenous stores to eggs laid early in the sequence than to later laid eggs. It has been speculated that endogenous nutrients unused during migration are invested in egg formation (Rohwer 1992, Hobson et al. in press) or that females can start egg production earlier if supplemented by some endogenous stores (Schultz 1991, Alisauskas and Ankney 1992). Our data do not support hypotheses of opportunistic marine endogenous transfer to eggs by Harlequin Ducks because variation within clutches is small and entirely within the freshwater range of isotope values. This suggests that values from a single egg per clutch for Harlequin Ducks are representative of each individual's strategy, and when pooled, allow appropriate inference about the average strategy of the population.

Some differences in isotope values were evident among clutches in our data. We suggest that this is not related to variation in strategies of nutrient acquisition and allocation among females, but rather, is due to differences in isotopic signatures across streams and freshwater diets. Other studies have found a lack of precision in freshwater endpoints (Hobson et al. 2004, Hobson et al. in press), and this is likely caused by different processes affecting each of the freshwater sources. In the study system, isotopic signatures between streams differed slightly and the exact prey composition of females' diets also likely differed, and these dissimilarities would lead to variation among eggs laid by different individuals. Despite variation in signatures among clutches, the egg components fall almost entirely within the isotopic range of freshwater stream invertebrates.

If female Harlequin Ducks use freshwater nutrients to form eggs, why do they store endogenous reserves on wintering grounds prior to migration (Chapter Two)? As shown in the Appendix, flights costs for Harlequin Ducks from the Strait of Georgia to our breeding study site near Lillooet are slight and would result in only a 2-3% reduction in body mass. It has been suggested that females may store nutrients to hedge against unfavourable conditions on breeding grounds when they arrive or they could be strategically storing limiting nutrients required for the physiological changes associated with reproduction (Rohwer 1992, Morrison and Hobson 2004). Another possibility is that stored nutrients could be used for the female's own maintenance during clutch formation or during subsequent stages of reproduction, such as incubation. Incubation in waterfowl can be a demanding stage of reproduction, especially because of reduced feeding associated with many incubation strategies (Afton and Paulus 1992). Nesting success has been related to body condition, where the depletion of endogenous reserves may lead to nest failure through nest abandonment or decreased nest attentiveness (Gloutney and Clark 1991, Arnold et al. 1995). Decreased nest constancy can leave the nest vulnerable to predation, and may also result in suboptimal egg temperatures for egg survival (Afton and Paulus 1992, Schmutz et al. in press). Therefore, the condition of females prior to incubation can be very influential to breeding success. In Harlequin Ducks, females are the sole incubators and are thought to take an abeyance from the nest once a day to feed and preen (Robertson and Goudie 1999). Hunt (1997) found that female Harlequin Duck mass decreased by 11% from laying to brood rearing, which indicates significant energy demands during incubation. Thus, it may be beneficial for females to store endogenous marine nutrients in order to meet these high energy requirements.

Harlequin Ducks may be simultaneously balancing demands of clutch formation and benefits of nutrient stores for incubation. Physiologically, it may be more efficient for females to convert exogenous, dietary nutrients directly to eggs rather than mobilizing endogenous reserves. The basis for this is that it would take more processing, with associated decreases in physiological efficiency, to allocate endogenous nutrients into eggs as opposed to currently ingested nutrients. If sufficient nutrients are available locally, then endogenous reserves built on wintering grounds could be used for female maintenance during laying and during incubation. Schmutz et al. (in press) determined that arctic-nesting geese used a mixed strategy of endogenous and exogenous resources for egg production, but also found isotopic evidence of significant endogenous marine reserve use during incubation. This suggests that these geese are ‘saving’ some endogenous resources for incubation and supplementing egg production with exogenous sources.

The capital/income classification would put Harlequin Ducks in the income breeder category because they use exogenous reserves for egg formation. However, the capital and income strategies, as they have become known, are in need of some clarification. The definitions have changed from their original meaning proposed by Drent and Daan (1980), which were related to timing of reproduction and clutch size determination. Now these terms are generally used to investigate energy and nutrient storage for reproduction (Stearns 1992, Jönsson 1997). In recent literature, reproduction has been replaced in this definition with egg production, with the justification that this is the most demanding stage especially for precocial birds. However, nutrients required for reproduction are those necessary for egg production and female maintenance (Meijer and Drent 1999, Schmutz et al. in press), and endogenous reserves may be used to varying degrees for the different stages of reproduction, not just egg formation. Meijer and Drent (1999) alluded to this by pointing out that it would be more correct to distinguish between ‘capital layers’ and ‘capital breeders’ because these breeding strategies are quite different. In the case of the Harlequin Ducks, they may be using marine endogenous reserves for incubation, but not egg formation. Therefore, when considering capital and income strategies, it is important to investigate how endogenous reserves may be used during the entire reproductive period.

We have demonstrated that the nutrient allocation strategy for clutch formation by Harlequin Ducks in the southern Coast Mountains of British Columbia involves mostly freshwater sources. Therefore, they are highly dependent on stream productivity and access to invertebrate food items for egg production, and this should be taken into consideration when altering or managing stream habitats. If females have reduced food levels on streams during the clutch formation stage, this may impede their ability to produce viable eggs, which could lead to consequences for population demographics. Because of current concerns regarding low productivity for Harlequin Ducks in southern British Columbia (Smith et al. 2001, Rodway et al. 2003), future research could investigate how food limitation on breeding streams may influence egg production. Previous work has linked diving duck productivity and food availability (Gardarsson and Einarsson 2004, but see Goudie and Jones in press), but more research is required to address the issue of food limitation and resultant effects on productivity in Harlequin Ducks.

13.4.6. Acknowledgments

We acknowledge BC Hydro Bridge Coastal Restoration Program and Environment Canada Science Horizons Program for financial support and the Centre for Wildlife Ecology at Simon Fraser University for logistical support. For assistance in the field, we thank C. Alec, E. Anderson, J. Bond, K. Bond, S. Boyd, S. Copeland, S. Freeman, J. Harding, J. Heath, S. Iverson, S. LeBourdais, E. McClaren, S. Smith, K. Wright, and R. Žydelis. Also, H. Nichol generously provided field housing near Pemberton. T.D. Williams, R.C. Ydenberg and S.E. Jamieson provided useful comments on earlier drafts. T.D. Williams provided laboratory facilities at Simon Fraser University. Thanks to P. Healy, M. Benjamin, and M. Stocki at the University of Saskatchewan assistance with stable isotope analysis.

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Figure 13.4.1 Percentage of Harlequin Duck egg components derived from nutrients acquired on freshwater breeding streams (± SE) based on mixing models analyses of carbon (C) and nitrogen (N) stable isotopes.

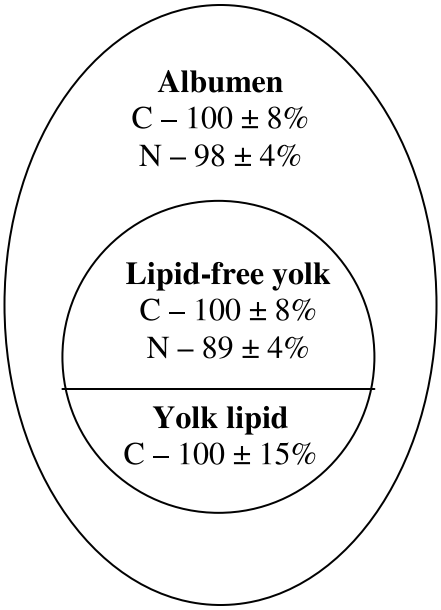


Figure 13.4.2. Lipid-free carbon and nitrogen stable isotope values for wintering blood, freshwater invertebrates, egg yolk, and egg albumen of Harlequin Ducks.

Note: discrimination factors applied to egg components (see methods).

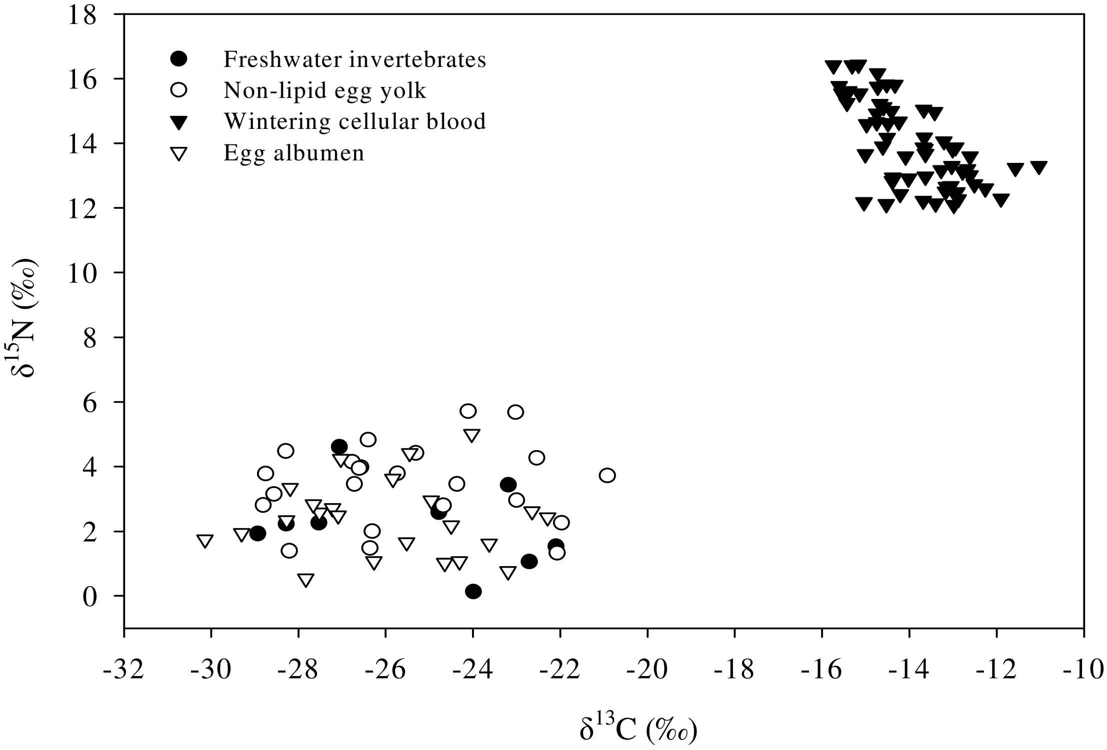


Figure 13.4.3 Carbon stable isotope values for lipid from freshwater stream invertebrates, and yolk lipid and winter abdominal lipid of Harlequin Ducks.

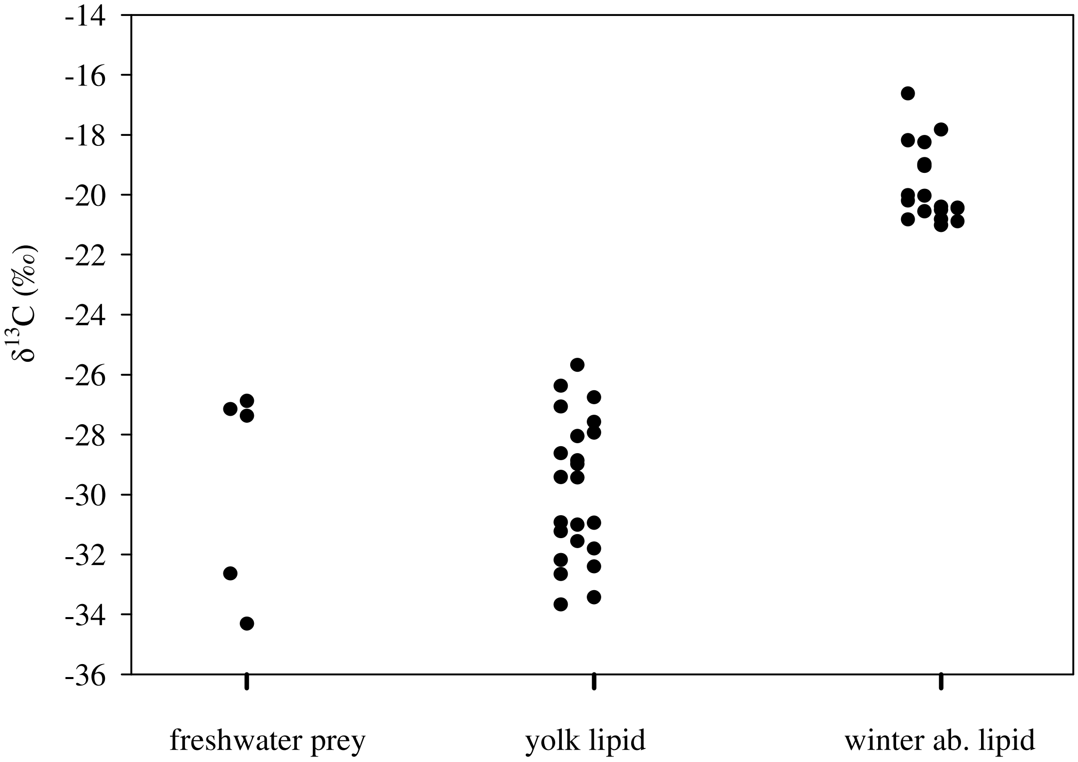


Figure 13.4.4 Interclutch and intraclutch variation in carbon and nitrogen stable isotope values for lipid-free egg yolk.

Note: The approximate marine stable isotope values for carbon and nitrogen are also shown (from wintering female blood samples).

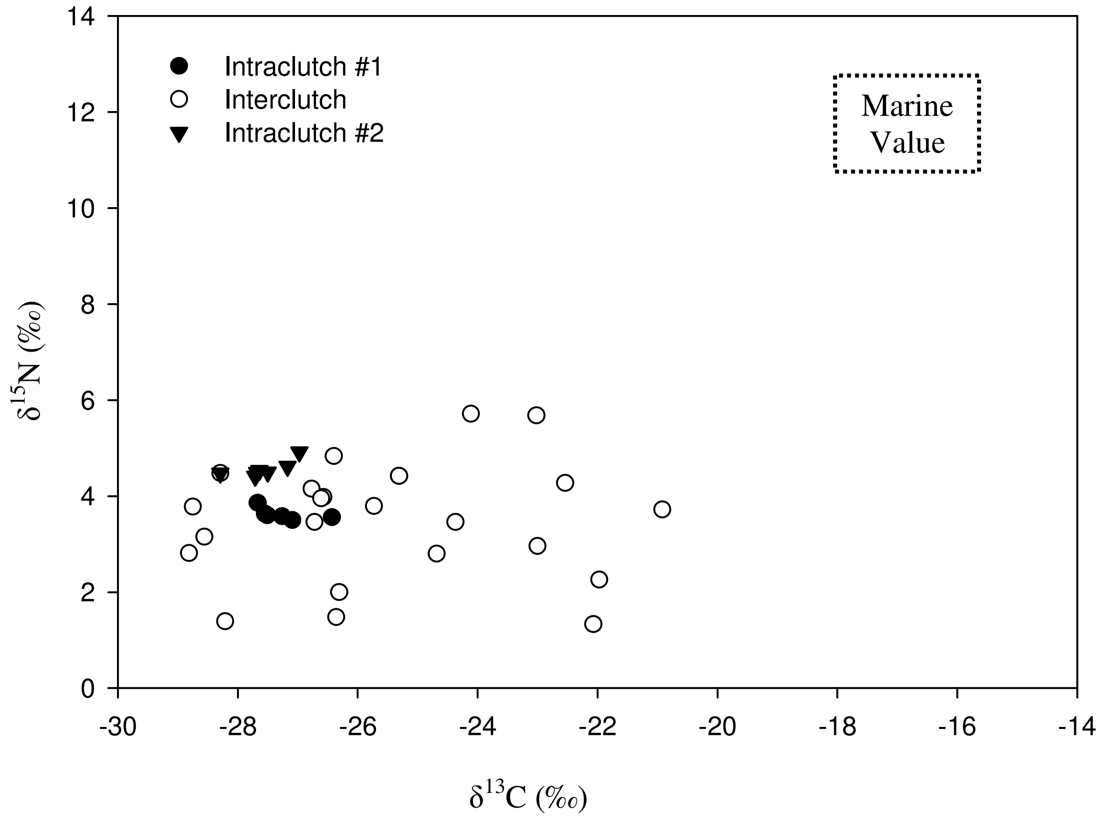
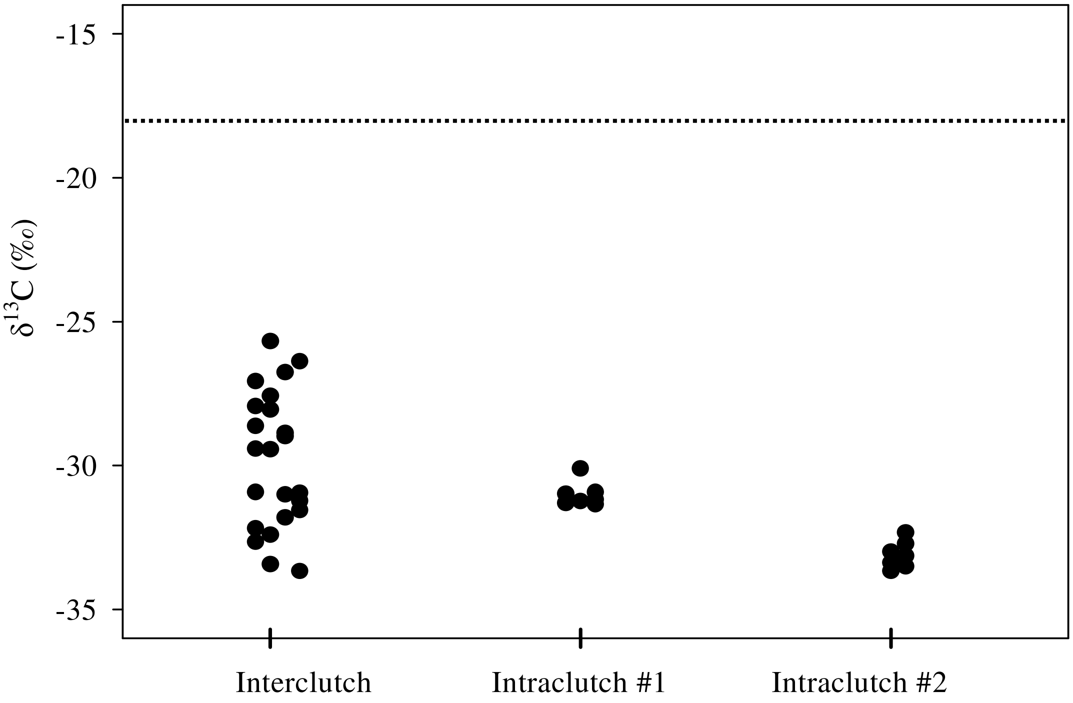


Figure 13.4.5 Interclutch and intraclutch variation for carbon stable isotope values of egg yolk lipid.

Note: Dashed line indicates approximate value of a marine signature from our samples of female abdominal lipid in winter.



13.5. Estimates of Breeding Propensity for Harlequin Ducks: a Novel Approach Using Yolk Precursors and Radio Telemetry

Jeanine C. Bond[3]
Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6 CANADA

13.5.1. Abstract

Breeding propensity, the proportion of reproductively capable females that initiate egg production, is an important trait when considering reproductive performance in birds. Unfortunately, appropriate methods for quantifying breeding propensity have not been available for many systems. A persistent problem when attempting to document rates of breeding propensity is that failed breeders, especially those that fail early, are difficult to distinguish from nonbreeders, and this can lead to underestimates of breeding propensity. Female Harlequin Ducks (Histrionicus histrionicus) have been speculated to show high rates of deferred breeding, although no study of this species has been able to apply an appropriate method to address this issue. We employed a novel approach combining information from radio telemetry and yolk precursor (vitellogenin and very-low-density lipoprotein) analyses to quantify breeding propensity of adult female Harlequin Ducks. Using both methods, we estimated that breeding propensity of females that migrated to breeding streams was 92%, the highest estimate reported to date. In our study, telemetry misclassified breeders that failed early (21%), and yolk precursor analyses misclassified breeders captured outside of the egg formation period, although this was rare (3%). These data can lend insight into life history strategies and potential sources of constraints on productivity of Harlequin Ducks. Further, these methods can be applied to other species to derive accurate estimates of reproductive effort.

13.5.2. Introduction

Intermittent or deferred breeding in birds is a widespread phenomenon, and estimates of nonbreeding rates have indicated that this behaviour can be extensive in some populations, especially in seabirds (Coulson 1984, Cam et al. 1998). This nonbreeding by sexually mature individuals is often viewed in the context of life history theory as a trade-off between current and future reproductive potential (Stearns 1992, Chastel et al. 1995, Golet et al. 1998). In this way, nonbreeding has been proposed as an adaptive strategy for long-lived species under certain conditions (Wooller et al. 1989). Proximate factors suggested to influence rates of nonbreeding include body condition (Drent and Daan 1980, Coulson 1984, Johnson et al. 1992) and inter-individual variation in quality

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[3] For submission to journals, authorship will include Daniel Esler and Tony D. Williams.
Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6 CANADA

(Mills 1989, Cam et al. 1998). It is likely that rates of nonbreeding are affected by multiple causes, and that individual state, as well as external factors such as food shortage or severe environmental fluctuations, are both influential (Cam et al. 1998).

Overall reproductive success is the product of success across a series of reproductive stages including breeding propensity, which we define as the proportion of females that initiate the egg formation process (the inverse of nonbreeding). The literature is replete with studies of rates of avian reproductive performance at most stages, such as nesting success and brood survival; however, relatively speaking, breeding propensity has been poorly documented. This data gap represents a significant shortcoming in our understanding of avian breeding biology. Without adequate estimates of breeding propensity, overall reproductive performance cannot be determined. Also, documentation of breeding propensity allows consideration of the stages and mechanisms by which reproductive effort may be constrained (Cam et al. 1998). For example, low rates of breeding propensity may indicate poor habitat conditions, such as poor food availability or low nest site availability, while poor nesting or brood success may be a result of high predation rates or inclement weather. We argue that breeding propensity is an important attribute to quantify when investigating avian reproductive success, and unfortunately, studies of breeding propensity have been constrained in part by a lack of appropriate tools.

Sea ducks have been hypothesized to be an avian taxon that exhibits relatively high rates of nonbreeding (Goudie et al. 1994); however, research in this area has been limited and has focused mainly on eiders (Coulson 1984, Quakenbush and Suydam 1999). For Harlequin Ducks (Histrionicus histrionicus), a cryptic-nesting sea duck, there has been a general assumption that some proportion of females on breeding streams are nonbreeders, although data to support or refute that assumption are few and, we argue, methodologically flawed. Reported rates of breeding propensity are highly variable (18-88%), as are the methods employed to obtain them (Table 13.5.1). For example, Bengtson (1971) and Bruner (1997) defined nonbreeders as those females seen in flocks on streams during the nesting period. Hunt (1997) classified nonbreeders as those females active midday when breeding hens were presumed to be on their nests; he also inferred breeding status of captured females based on the presence of a brood patch, wide pelvis, or egg in the abdomen. Crowley (1999) classified captured females as breeders or nonbreeders based on brood patch and cloacal attributes. Most recently, MacCallum and Godslave (2000) and Smith (2000) used telemetry to follow radio-marked birds to determine nesting status. All of these approaches have methodological constraints, a primary one being that most of these cannot distinguish between true nonbreeders, i.e., those females that do not initiate clutch formation, and females that fail early in the egg production or incubation stages. Also, attributes such as brood patches and oviductal eggs may not be apparent if females are captured early in reproduction (McFarlane Tranquilla et al. 2003b). Thus, estimates of proportions of nonbreeding females likely include some proportion of failed nesters and late nesters, and hence breeding propensity can be underestimated (Robertson and Goudie 1999, McFarlane Tranquilla et al. 2003a).

In this study, we apply a novel approach combining radio telemetry and yolk precursor analyses to quantify breeding propensity in Harlequin Ducks. Plasma yolk precursors, vitellogenin (VTG) and yolk-targeted, very-low-density lipoprotein (VLDLy), are produced in the avian liver and become elevated as estrogen concentrations increase during reproduction (Deeley et al. 1975, Chan et al. 1976). VTG and VLDLy are the primary sources of egg yolk protein and lipid, respectively (Wallace 1985, Walzem 1996), and therefore, are highly correlated with egg production. Yolk precursors have been demonstrated to be reliable indices of reproductive status in European Starlings (Sturnus vulgaris; Challenger et al. 2001), Marbled Murrelets (Brachyramphus marmoratus; Vanderkist et al. 2000, McFarlane Tranquilla et al. 2003a), and Greater Scaup (Aythya marila; Gorman 2005). Using a blood sample, it is possible to nondestructively determine if individual females are in the process of egg formation at the time of capture. Radio telemetry allows us to infer breeding propensity by monitoring behaviour to determine the proportion of females found on nests. By using both these methods on the same set of female Harlequin Ducks, we were able to compare the efficiency of each for estimating breeding propensity and to derive an overall estimate of breeding propensity that accounts for misclassification of breeding status by both methods.

13.5.3. Methods

Study Area and Captures

Harlequin Ducks were captured on breeding streams using mist nets from May 9 to 20, 2003, and from April 21 to May 20, 2004, in the southern Coast Mountains of British Columbia, Canada. The study area included streams near the towns of Pemberton (50° 19'N, 122° 48'W) and Lillooet (50° 41'N, 121° 56'W). Captured birds were immediately removed from the net, and then weighed, banded, and assigned to an age class based on the depth of the Bursa of Fabricius (Mather and Esler 1999).

Radio Telemetry

Each captured female had a radio transmitter attached using a subcutaneous anchor and glue. The transmitters, made by Holohil Systems Ltd, were a six-gram RI-2B model with a motion-sensitive mortality sensor and a battery life of three to nine months. The transmitter was located in the small depression between the scapulae, dorsal to the approximate junction of the cervical and thoracic vertebrae. We monitored radio-tagged females at least once a week (usually several times a week) to determine if each female was detected on a nest. We classified those on nests as breeders, and those not on nests as putative nonbreeders. Some individuals were also categorized as unknown, if their radio signal was lost during the nesting period.

Yolk Precursor Analyses

A 1.5 ml blood sample was taken from the jugular veins of captured females using a heparinized 5.0 ml syringe with a 21-gauge needle. For a small number of females, a

1.0 ml syringe with a 24-gauge needle was used to take 0.5 ml of blood from the tarsal vein instead. Collected blood was transferred to a heparinized vial and stored on ice until the plasma was separated from cellular blood components using a centrifuge (within 12 h). Plasma from the blood samples was analysed for yolk precursor concentrations of vitellogenin (VTG) and total very-low-density lipoprotein (VLDL – both generic and yolk-targeted). Following Mitchell and Carlisle (1991), diagnostic kits for vitellogenic zinc and total triglycerides were used as indices of concentrations of VTG and VLDL, respectively. Intra-assay and inter-assay coefficients of variation for VTG were 3.2% and 13.0% (n = 6), and for VLDL were 5.1% and 4.3% (n = 5), respectively. Also, blood samples were analysed from females captured on wintering grounds in the Strait of Georgia, British Columbia, to determine a baseline, nonbreeding value for the yolk precursors (n = 16).

Although both yolk precursors are correlated with egg production, VTG has been shown to be a more accurate and reliable indicator of reproductive status than VLDL (Vanderkist et al. 2000, Gorman 2005). Therefore, VTG was considered first for determining whether or not females were captured during egg production. Because threshold or cut-off levels for this determination have been variable (see discussion), we categorized individual females into one of three categories based on VTG results: egg-producing, non-egg-producing, and unknown. The unknown category included those females whose VTG concentration fell within a range that we considered uncertain. The lower limit of this uncertain zone was the mean VTG + 3SD of our wintering females (0.44 µg/mL; recommended by McFarlane Tranquilla et al. 2003a), which is low compared to other values in the literature. The upper limit for the unknown category was the highest cut-off value reported in the literature (Gorman 2005, 1.4 µg/mL; Figure 13.5.1). Any individuals with VTG values higher than 1.4 µg/mL were considered egg producers (and hence breeders) and those below 0.44 µg/mL were categorized as non-egg producers and putative nonbreeders. If an individual was categorized as unknown based on VTG level, the VLDL value was then used to evaluate status. As with VTG, VLDL values also were used to categorize these birds as egg producers, non-egg producers, or unknown with the lower limit defined as mean VLDL + 3SD for our wintering females (3.66 mg/mL) and the upper limit of 5.2 mg/mL from published literature (Gorman 2005). If a female was classified as unknown for both VTG and VLDL, then her overall status using yolk precursors was considered unknown.

Breeding Propensity Determination

Our summary dataset for estimation of breeding propensity consisted of classifications of breeder, putative nonbreeder, or unknown for each individual for each of our two methods, using yolk precursors as a direct measure of egg production and radio telemetry to infer egg production from birds detected on nests. We estimated a putative breeding propensity for each method individually as simply the proportion of individuals that were classified as breeders, excluding those classified as unknown from the calculation. Because we were using two methods to estimate breeding propensity, we also calculated a misclassification rate for each method, which was the proportion of birds that were incorrectly classified as a putative nonbreeder when it was known to produce eggs based on the other method. We then estimated the probability of incorrectly designating an individual as a nonbreeder when using both methods, by multiplying the misclassification rates for each method. This estimated the proportion of birds that were truly breeders, but that were captured before the onset of rapid follicle growth and their nest failed before telemetry methods confirmed incubation. An overall estimate of breeding propensity was the proportion of individuals confirmed as a breeder by either method plus the estimate for the proportion misclassified as a nonbreeder by both methods.

13.5.4. Results

Over the two years of this study, 34 female Harlequin Ducks were captured and attached with radio transmitters. We determined that the age class of all captured females was after-third year (i.e., breeding age adults). Five females were captured and monitored in both years.

The two methods we applied produced different estimates for breeding propensity. Yolk precursor analyses showed that of the 34 females, 25 were producing eggs when they were captured (Figure 13.5.1). Five were not producing eggs, two were classified as unknown because their values fell within the uncertain zone for both yolk precursors, and two had blood samples that were unusable for analyses. Therefore, we estimated a putative breeding propensity based solely on yolk precursors to be 83% (95% confidence interval = 69 - 97%; Table 13.5.2). Our telemetry efforts resulted in detection of 22 females on nests, eight females that were never found on nests, and four whose status was unknown (due to loss of radio signal or mortality); therefore, putative breeding propensity using telemetry was 73% (95% confidence interval = 57 – 89%). Using both data types combined, three females on breeding streams were designated as putative nonbreeders, one was unknown, and 30 (91%; 95% confidence interval = 81 – 100%) were confirmed to have initiated egg production. However, this estimate does not include those breeding females that could have been missed by both methods.

Misclassification rates differed by method. If using telemetry alone, we would have misclassified 17% of egg producers as nonbreeders (Table 13.5.2). Of the 30 females categorized by telemetry, five putative nonbreeders were known to be breeders based on yolk precursors (Figure 13.5.2). These five egg producers presumably failed early during the nesting phase, before they could be detected via telemetry. Yolk precursor analysis was less likely to misclassify breeders as putative nonbreeders. Of the 30 birds with yolk precursor data indicating their breeding status, only one (3%) was classified as a putative nonbreeder based on yolk precursors but was subsequently confirmed to produce eggs based on telemetry (Figure 13.5.2). This was a late-nesting bird that presumably was captured prior to rapid follicle growth. Our estimate of the proportion of individuals misclassified by both methods, derived by multiplying misclassification rates of each method used independently, was low (1%), indicating that it was unlikely for both methods to miss a breeding bird. Our final estimate of breeding propensity (proportion of known breeders by either method plus the estimate of misclassification by both methods) was 92%.

13.5.5. Discussion

By applying a new approach, we estimated breeding propensity of adult female Harlequin Ducks in southern British Columbia to be 92%. This result is surprisingly high considering that these ducks are long-lived species that have many potential breeding attempts, and are thought to be quick to defer breeding in order to increase survival and lifetime reproductive success (Stearns 1992, Goudie et al. 1994). The Common Eider (Somateria mollissima), another long-lived sea duck, has estimates of breeding propensity averaging around 75% with incidents of as low as 45% (Coulson 1984). As well, the breeding propensity of Greater Snow Geese (Chen caerulescens atlantica) has been reported to be around 57% on average (Reed et al. 2004). Our data, showing over 90% of adult female Harlequin Ducks on breeding streams initiating clutch formation, possibly indicates that their life history strategy is not as extreme as previously suggested or that the years of this study were favourable for reproduction. We note that our estimate does not include those females that may decide to defer breeding prior to migration and remain on wintering areas. Applying these methods across a range of conditions for Harlequin Ducks will give a clearer, more accurate view of breeding propensity, and hence, life history strategies.

As discussed by Cam et al. (1998), the criterion used to distinguish between breeding and nonbreeding individuals is an important methodological choice that is likely to influence study results and conclusions. Although our comparatively high estimate of breeding propensity could be a site or year effect, we suggest that it is more likely a function of the methods used. Yolk precursor analysis is a direct measure of egg production while most other methods, including radio telemetry, attempt to infer breeding status from behaviour later in the breeding cycle. Yolk precursors, however, can also misclassify individuals and we suggest that it is the combination of this method with another confirming incubation that provides the best estimates of breeding propensity.

Using two methods directed at different phases of the reproductive cycle is also useful in that it allows estimation of misclassification rates by each method, and calculation of an estimate of overall misclassification. It should be recognized that when using yolk precursor analyses, the blood sample is only a snapshot of the condition of a female at the time she was caught. If the female is caught during ovarian follicle development, her status as an egg producer will be evident because yolk precursor levels increase quickly in association with onset of rapid follicle growth and remain high until laying is complete (Challenger et al. 2001, Gorman 2005). However, if a female is caught outside of the egg production stage, yolk precursors will not distinguish nonbreeders from those that will initiate egg formation later or have already completed egg laying. Therefore, captures for yolk precursor sampling should be targeted for the period when females are expected to be producing eggs. Our estimate of misclassification when using yolk precursors was surprisingly low (3%), indicating that our captures were well timed. In most situations, we would expect higher rates of misclassification using yolk precursors, as it seems unlikely to catch all females during the egg production phase; in these situations, a second method for estimating misclassification rates using yolk precursors would be particularly important.

One aspect of the yolk precursor analyses that could be refined is the definition of cut-off levels to distinguish egg-producing from non-egg-producing females. These have been defined by various authors in different ways. For example, McFarlane Tranquilla et al. (2003a) and Peery et al. (2004) used the mean of their known nonbreeding samples plus three standard deviations as the maximum non-egg-producing concentration of VTG in the plasma of Marbled Murrelets (0.96 µg/ml and 0.64 µg/ml, respectively), while Vanderkist et al. (2000) used two times the highest known nonbreeding value for the same species (0.52 µg/ml for VTG). These intraspecific differences in cut-off levels could create different estimates of breeding propensity, although presumably not dramatically different because yolk precursor dynamics, especially those of VTG, generally lead to a clear signal differentiating birds at different stages. Gorman (2005) determined that a VTG value of 1.4 µg/ml correctly classified the most female Greater Scaup as egg-producing or non-egg-producing individuals. This indicates that there are also interspecific differences in appropriate cut-off levels to consider. The physiological causes of this interspecific variation have not been formally investigated and leads to questions about applicability of broad threshold values. Because determination of a distinct cut-off level can be somewhat arbitrary, we recommend using similar methods to ours, in which intermediate values can be categorized as uncertain with respect to breeding status.

Another potentially important factor when estimating breeding propensity, which has been overlooked by some investigators, is determination of age class. Our estimate applies strictly to after-third-year females because ample evidence exists to suggest that young birds are more likely to defer breeding within a given year than older, more experienced birds and young birds are also known to prospect (Johnson et al. 1992). Therefore, inclusion of young birds can lead to underestimates of breeding propensity. For example, Perfito (1998) estimated Harlequin Duck breeding propensity to be 50% but when she removed subadults from the calculation, the estimate became 74%. Although this is presumably still an underestimate due to methodological constraints, it illustrates the importance of accounting for age class when considering mechanisms affecting breeding propensity and applying estimates to population models.

We reiterate that accurate estimates of breeding propensity are important for determining factors that influence reproductive success and productivity. Knowledge of the factors influencing reproduction is vital to managing populations. A high proportion of females that do not initiate egg formation may be indicative of a physiological influence such as poor food availability while a high proportion of females that do not complete incubation may indicate external factors such as high predation pressure. Peery et al. (2004) included the proportion of breeders when considering limiting factors, such as food, nest sites, or predation, on Marbled Murrelet populations. Also, Gardarsson and Einarsson (2004) have linked food availability with productivity of several diving ducks in Iceland. Goudie and Jones (in press) recently suggested that productivity of Harlequin Ducks is limited by predation rather than food based on activity budgets and breeding propensity estimates. Monitoring breeding propensity could indicate chronic or sporadic influences on reproductive success, and if we had an indication of the proportion of birds committing to each stage in the breeding chronology, we may be able to identify mechanisms responsible for low productivity and recruitment.

13.5.6. Acknowledgements

We acknowledge BC Hydro Bridge Coastal Restoration Program and Environment Canada Science Horizons Program for financial support and the Centre for Wildlife Ecology at Simon Fraser University for logistical support. For assistance in the field, we thank C. Alec, E. Anderson, J. Bond, K. Bond, S. Boyd, S. Copeland, J. Harding, J. Heath, S. Iverson, S. LeBourdais, E. McClaren, S. Smith, K. Wright, and R. Žydelis. Also, H. Nichol generously provided field housing near Pemberton. R.C. Ydenberg and S.E. Jamieson provided useful comments on earlier drafts. Thanks to K. Gorman and K. Salvante for assistance with laboratory analysis.

13.5.7. References

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Table 13.5.1 Historical Harlequin Duck breeding propensity estimates and methods.

Region	*Year of Study*	*Breeding Propensity (%)*	*Method*	*Reference*
Iceland	1965-1969	**70-85**	Proportion of females in flocks during June and July	Bengtson and Ulfstrand 1971
Iceland	1970	**18**	Proportion of females in flocks during June and July	Bengtson and Ulfstrand 1971
Alaska	1979-1980	**50-53**	Brood patch and behavioural observations	Dzinbal 1982
Alaska	1991-1992	**74-86**	Examination of cloaca and brood patch; egg in abdomen	Crowley 1999
Wyoming	1985-1986	**38**	Mass of captured females	Wallen 1987
Oregon	1995-1996	**49**	Repeat observations of females in single or mixed-sex groups	Bruner 1997
Washington	1996-1997	**74**	Multiple captures checking for brood patch presence	Perfito 1998
Alberta	1997-1999	**52**	Telemetry and observational data	MacCallum and Godslave 2000
Alberta	1997-1999	**88**	Telemetry	Smith 2000

Table 13.5.2 Breeding propensity (with 95% confidence intervals) as determined using yolk precursor analyses and radio telemetry, and the probability of misclassification using each method (see methods).

Method	Breeding Propensity	n	Misclassification Rate
Yolk Precursors (YP)	83% (69 – 97%)	30	3%
Telemetry (T)	73% (57 – 89%)	30	17%
Both (YP & T)	91% (81 – 100%)	33	1%

Figure 13.5.1 Yolk precursor data for breeding propensity determination.

The symbols on this figure show how each individual is classified based on the yolk precursor cut-off criteria and grey areas are zones of uncertainty (see methods). Note two individuals only had values for VTG, and therefore, are not shown.

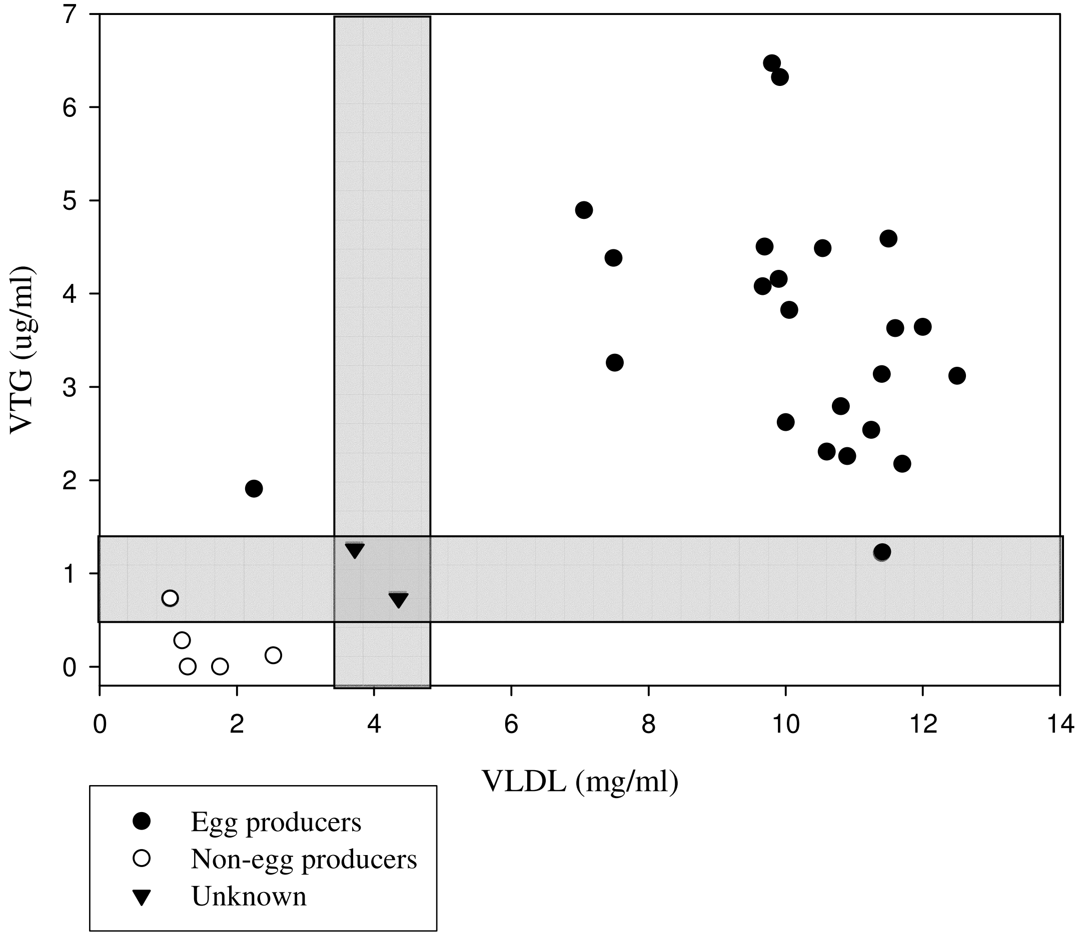
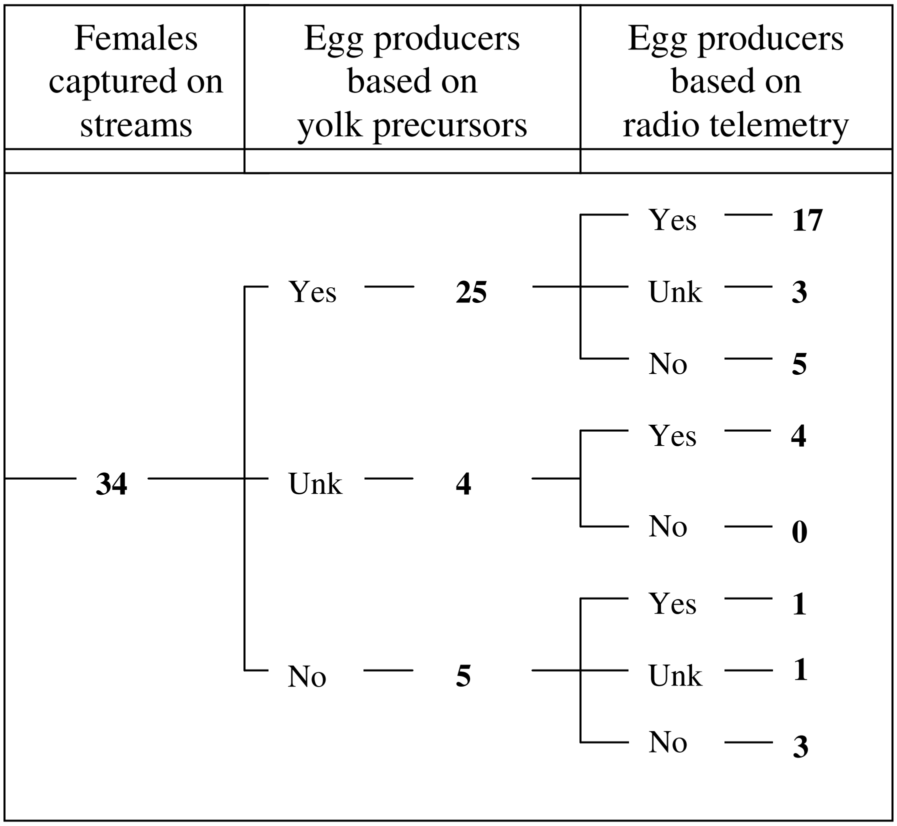


Figure 13.5.2 Of the 34 females captured on breeding streams, this figure shows the distribution of samples indicating breeding activity at two different points in the reproductive cycle (i.e., yolk precursors measure egg production and radio telemetry measure incubation), and how these two methods work in conjunction to determine the number of females that commit to clutch formation.



13.6. General Conclusions and Future Directions

13.6.1. Conclusions

Reproduction in waterfowl is considered an energetically demanding stage and strategies for acquiring and allocating nutrients to meet these demands varies. Current concerns regarding low productivity and recruitment of Harlequin Ducks (Histrionicus histrionicus) in southern British Columbia (Smith et al. 2001, Rodway et al. 2003) highlight the need for research improving our knowledge of breeding requirements for this species. In this thesis, I investigated nutrient acquisition and allocation strategies of adult female Harlequin Ducks, and specifically examined (1) nutrient storage on wintering grounds prior to migration and reproduction, with particular focus on the role of herring spawn, (2) nutrient allocation to clutch formation and the relative contributions from marine and freshwater sources to egg components, and (3) breeding propensity of females on freshwater breeding streams in southern British Columbia. These studies provide novel insights into Harlequin Duck reproductive ecology, which have important implications for addressing conservation concerns surrounding low productivity.

I found that body mass of adult female Harlequin Ducks in the southern Strait of Georgia, British Columbia, increased by 7% prior to migration on wintering grounds (Chapter Two). This mass gain occurred regardless of whether females were consuming intertidal invertebrates or herring spawn, although there was a suggestion that diet did correspond to differences in chronology of mass gain. Those females consuming herring roe increased in mass several weeks before those that were feeding on a mixed intertidal invertebrate diet. Females on all sites had similar body masses prior to migration, which suggests that there was a targeted, optimal premigratory body mass, presumably shaped by the costs and benefits of nutrient storage. Therefore, consumption of herring roe rather than marine invertebrates does not necessarily confer advantages in terms of nutrient storage although there may be other aspects of aggregating at spawn sites that are important such as social interactions (Rodway et al. 2003).

I examined allocation of these endogenous marine nutrients by using stable isotope analyses to identify sources of nutrients for clutch formation (Chapter Three). By analysing Harlequin Duck eggs, I determined that freshwater, not marine, nutrients were allocated to eggs for both protein and lipid. This indicates that Harlequin Ducks are highly dependent on stream invertebrates during egg formation. Therefore, in a conservation context, factors that influence availability of invertebrates might be expected to have effects on Harlequin Duck reproductive performance. Although marine nutrients are not used for egg production, they are likely used for migration (Appendix) and potentially during other stages of reproduction. This offers a novel perspective on classification of species along a capital to income breeding continuum (Drent and Daan 1980, Meijer and Drent 1999). If considering egg production (the reproductive phase for which the ‘capital’ and ‘income’ labels have usually been applied for waterfowl), these females would be considered strict income breeders. However, my work demonstrates that female Harlequin Ducks store nutrients that may be subsequently invested in other reproductive phases – a capital strategy, but at an unexpected point in the reproductive cycle. These findings corroborate those of other waterfowl studies (e.g., Gorman 2005) that indicate that pre-reproductive nutrient acquisition is important and even limiting, irrespective of the strategy of nutrient acquisition and allocation for clutch formation.

In Chapter Four, I estimate breeding propensity of adult females on breeding streams using yolk precursor analysis and radio telemetry. Yolk precursors (vitellogenin and yolk-targeted, very-low-density lipoprotein) are highly correlated with egg production, and have been demonstrated to be reliable indices of reproductive status in birds (European Starlings (Sturnus vulgaris), Challenger et al. 2001; Marbled Murrelets (Brachyramphus marmoratus), Vanderkist et al. 2000; Greater Scaup (Aythya marila), Gorman 2005). The combination of yolk precursors and radio telemetry is a novel approach that avoids biases associated with using these methods singly, and I estimated that 92% of females on streams produced eggs. This is the highest estimate reported to date for Harlequin Ducks, presumably due in part to methodological limitations of other studies. Breeding propensity estimates are important for assessing reproductive effort and the approach that I employed offers a useful, noninvasive method that can be applied to other species.

13.6.2. Future Directions

This information on reproductive strategies of Harlequin Ducks can be an impetus for future research. One important avenue would be to address specific mechanisms that may limit productivity, especially the possibility of food limitation (Gardarsson and Einarsson 2004, Goudie and Jones in press). Because my thesis research has demonstrated that females rely almost exclusively on freshwater nutrients for egg production, directed research evaluating how limitation of these freshwater nutrients may influence productivity would be useful. Also, with the improved methods of assessing breeding propensity, investigators may directly consider how food limitation affects a female's probability of producing eggs.

While conducting this research, I found that the stable isotope signatures of adipose tissue in breeding females were highly variable, but tended to declined toward more freshwater values with time spent on breeding streams. This relationship is hard to interpret because the change toward more freshwater signatures could represent (1) use of marine nutrients and storage of freshwater nutrients, (2) simply storage of freshwater nutrients without using stored marine lipid, or (3) turnover. Further research investigating the mechanism responsible for changes in adipose tissue isotope values would be useful for interpretation of endogenous and exogenous lipid allocation to female maintenance and egg formation.

Another fruitful area of investigation could be to evaluate how nutrient acquisition and allocation strategies vary depending on migration strategy and breeding location. Harlequin Ducks winter in fairly large congregations and then disperse to breeding sites that range from just a few kilometres to hundreds of kilometres away from wintering areas (Robertson and Goudie 1999). Migration distance and geographic variation in breeding sites may influence an individual female's strategy for storing and allocating nutrients, and this information would provide a more complete picture of population-level strategies for nutrient acquisition and allocation. Also, comparative studies could be developed to investigate these relationships for Harlequin Ducks on the East Coast of North America as well as Greenland and Iceland.

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13.7. Appendix[4]:
Flight Costs for Harlequin Duck Migration

Purpose

The goal for this appendix was to evaluate how much of the acquired endogenous marine nutrients (Chapter Two) female Harlequin Ducks (Histrionicus histrionicus) would allocate to migrate from wintering grounds in the Strait of Georgia (49° 40'N, 124° 24'W) to breeding streams near Lillooet (50° 41'N, 121° 56'W) in the southern Coast Mountains of British Columbia, Canada. I investigated this by estimating flight costs and comparing those costs to the estimated level of endogenous stores that females acquired prior to migration.

Methods and Results

I estimated costs of migration using Flight Program 1.15 available at http://www.bio.bristol.ac.uk./people/pennycuick.htm. As per the instructions, I input required variables, and let the program set the default values for most other variables. I entered body mass as the average premigratory (i.e., postspawn) female mass (0.6 kg) from my data (Chapter Two). Wing span (0.685 m) and wing area (0.0295 m^2) were calculated from photographs of extended wings of female Harlequin Ducks (D.Esler, unpublished data) using one-centimetre grids (Pennycuick 1989) and then standardized using the average wing chord measurement from my captured birds. Great-circle distances, which include earth curvature, were used between Hornby Island, in the Strait of Georgia, and Lillooet (235 km) to approximate migration distances from wintering grounds to breeding grounds in this study. Based on these input values, I used the Flight Program to calculate change in overall body mass.

These migration flight cost calculations revealed that a female travelling from Hornby Island to Lillooet would lose approximately 16 grams or 2.6% body mass. This is an approximate value although this result is not particularly sensitive to reasonable changes of input values (i.e., changes in initial mass +/- 20 g produces similar flight cost results). Given the migration distance, estimated changes in body mass were fairly consistent across a range of input values.

Conclusions

In general, Harlequin Ducks are comparatively short-distance migrants (Smith and Smith 2003) and are presumed to make fast, direct flights between wintering and breeding grounds (Robertson and Goudie 1999). It appears that females travelling to the Lillooet area to breed only use 2-3% of their body mass to fly from the Strait of Georgia to this breeding site, and that they store more marine endogenous nutrients during spring hyperphagia (7% increase in body mass; Chapter Two) than they need for

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[4] This appendix was created to publish important findings that supplement interpretation of results and conclusions of this thesis, but that do not clearly fit in the established chapters.

migration. Therefore, one might predict that females travelling to Lillooet to breed may allocate some marine nutrients to reproduction (see Chapter Three).

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14. APPENDIX V – SUNNY LEBOURDAIS THESIS

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

by

Sunny V. LeBourdais
Bachelor of Science, University College of the Cariboo, 2001
Bachelor of Education, University of British Columbia, 2001

THESIS
SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

In the
Department
of
Biological Sciences

SIMON FRASER UNIVERSITY

Summer 2006

14.1. Abstract

I investigated factors affecting the availability of insect prey for harlequin ducks (*Histrionicus histrionicus*) breeding on streams in southwestern British Columbia. I measured benthic insect availability and harlequin duck breeding density on eight rivers in each of two years (2003 and 2004). I estimated the density of fish in each of these river systems using data collected by local utilities and government agencies. I found that aquatic insect availability was strongly and negatively associated with flow variability. Comparing rivers, harlequin duck density was positively associated with the availability of aquatic insects in both years of the study, and higher food availability in 2004 coincided with enhanced breeding success. I found a negative relationship between the densities of breeding harlequin ducks and fish. The evidence suggests that this relationship arises because insects are less available as prey for harlequin ducks in fish-bearing streams, rather than because fish reduce insect densities by consuming them. Availability drops because insects behave in ways that reduces their vulnerability to fish predators. The interaction between harlequin ducks and fish is thus indirect, and mediated by insect behaviour. These findings support the hypothesis that the introduction of fish such as trout into previously fishless rivers negatively affects harlequin duck breeding success. Such introductions have been widespread, and 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.

14.2. 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 14.2.1). 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.

14.2.1. 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.

14.2.2. Study Area

Data were collected from eight stream reaches in the Southern Coastal Mountains surrounding the communities of Lillooet and Pemberton BC, Canada (Figure 14.2.2).

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.

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.

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.

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.

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.

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).

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).

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

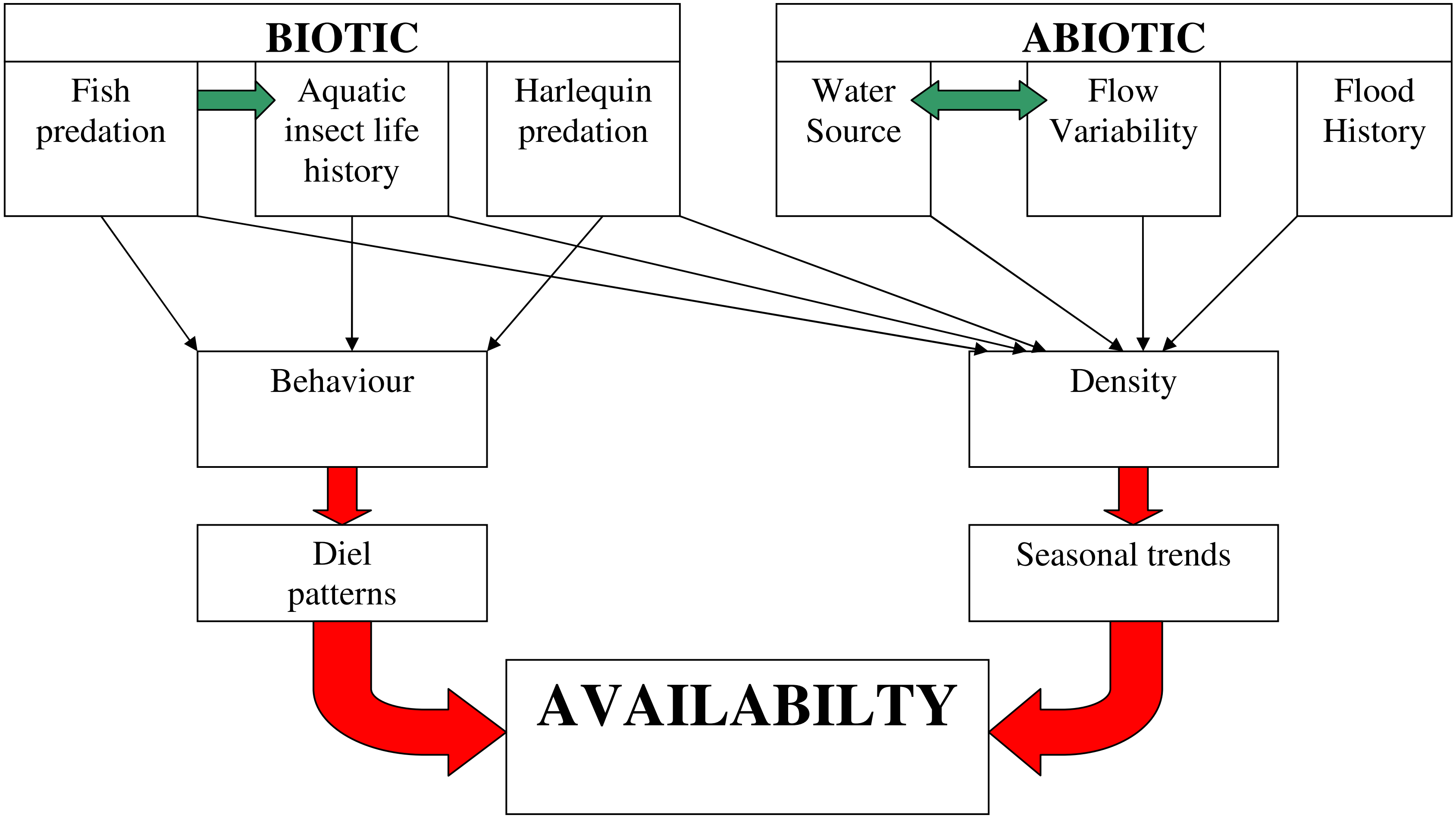
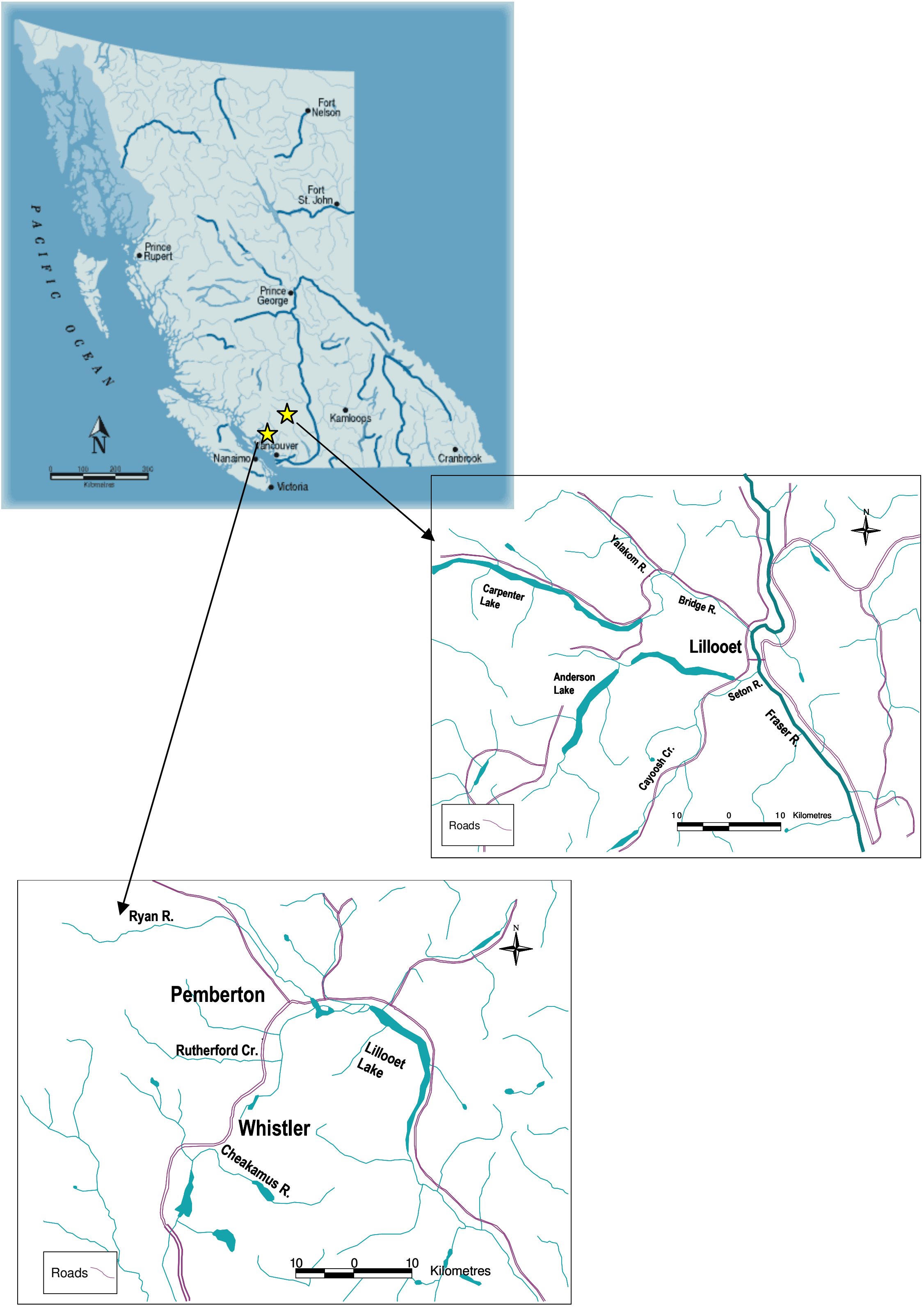


Figure 14.2.2 Map of British Columbia, Canada with inset maps of study rivers.



14.3. Variation in Aquatic Insect Communities and Relationships with Harlequin Duck Distribution.

14.3.1. 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.

14.3.2. 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.

14.3.3. Methods

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

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.

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.

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.

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 $p > 0.10$.

14.3.4. Results

Flow variability differed greatly between rivers (Figure 14.3.1). 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 14.3.2). 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 14.3.3), 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 14.3.4). 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 14.3.5). 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: $y = 9.02 (x) + 0.06$).

14.3.5. 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 14.3.1 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.

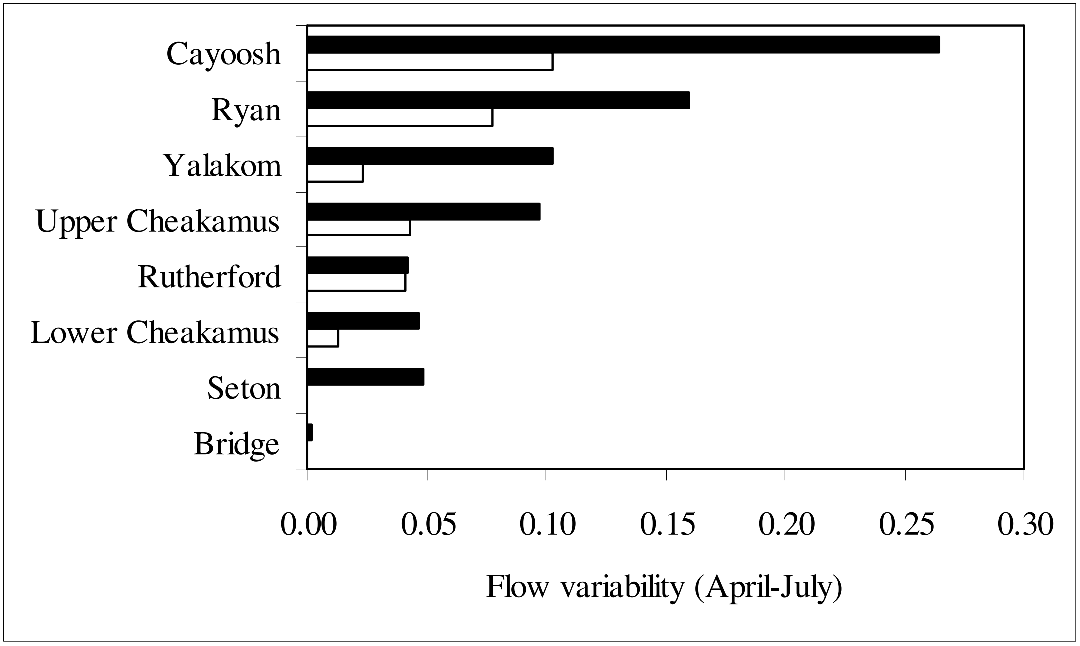


Figure 14.3.2 Aquatic insect availability and flow variability of Cayoosh Creek (∆), Cheakamus River (*), Seton River (○), Ryan River (+) and Yalakom River (□).

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 ($r^2 = 0.87$).

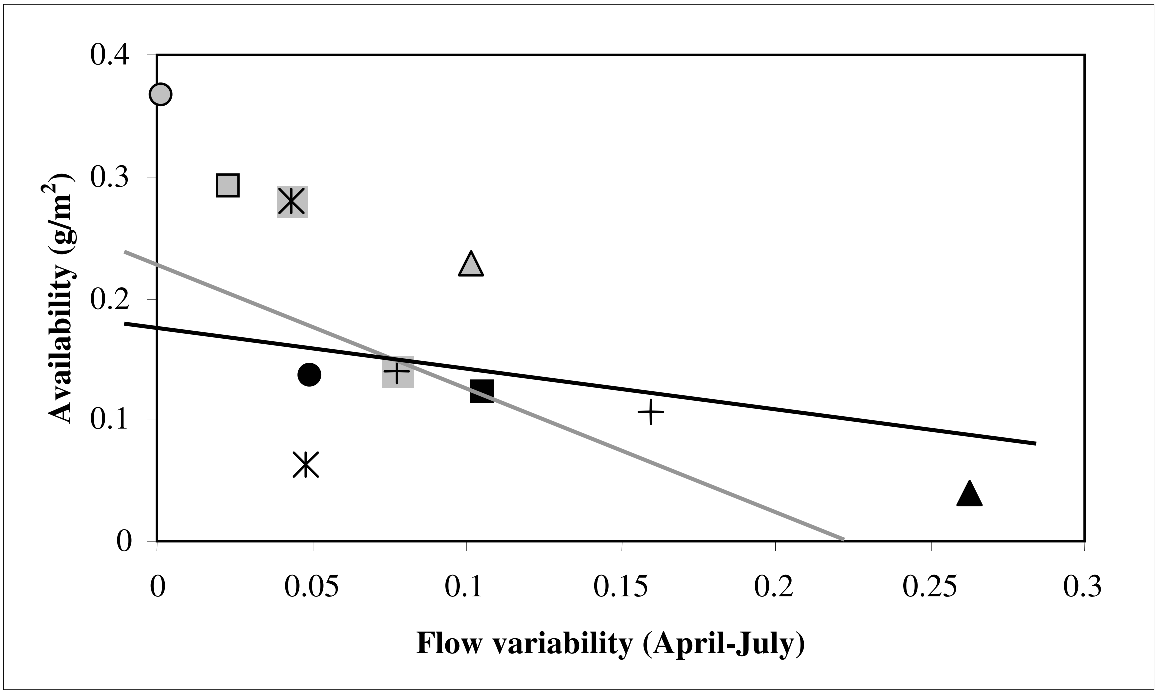


Figure 14.3.3 Mean aquatic insect availability (+/- 95% CI) measured in 2003 and 2004.

The point closest to y axis represents Rutherford Creek, which was measured only in 2004. Dotted line represents 1:1 ratio.

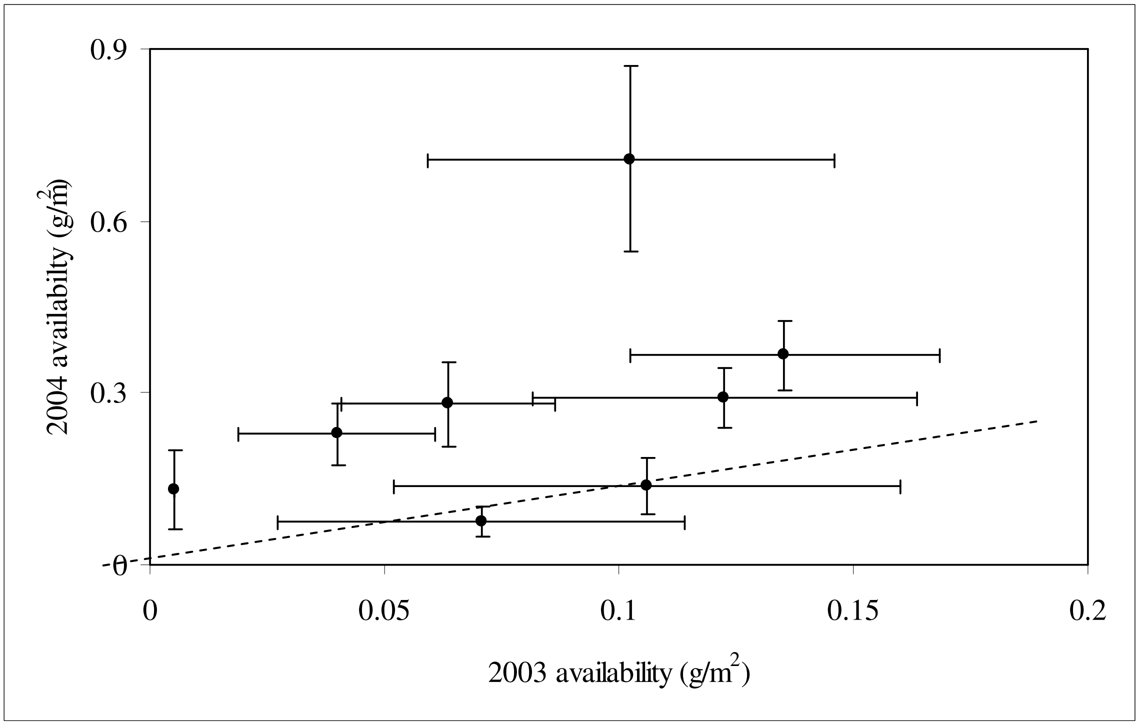


Figure 14.3.4 Aquatic insect densities of rivers measured in study during the 2003 and 2004.

Each point represents a river's mean aquatic insect availability (Error bars are 95% CI). Black bars are 2003, grey bars are 2004.

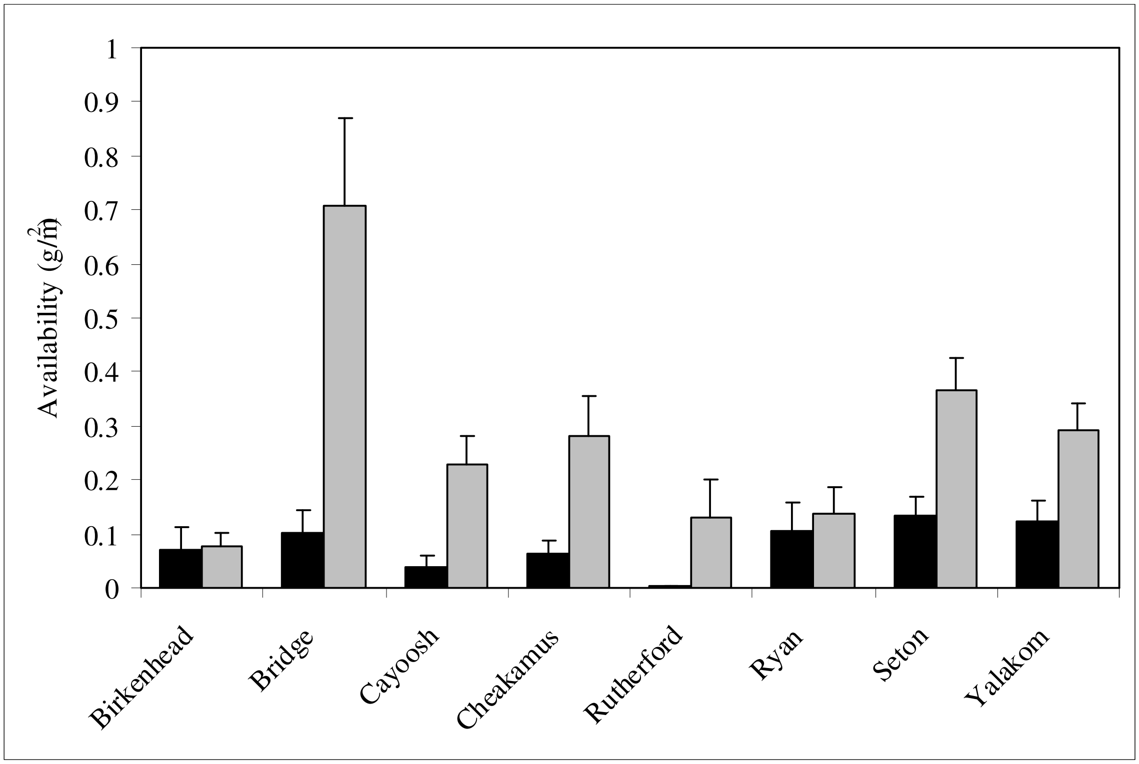
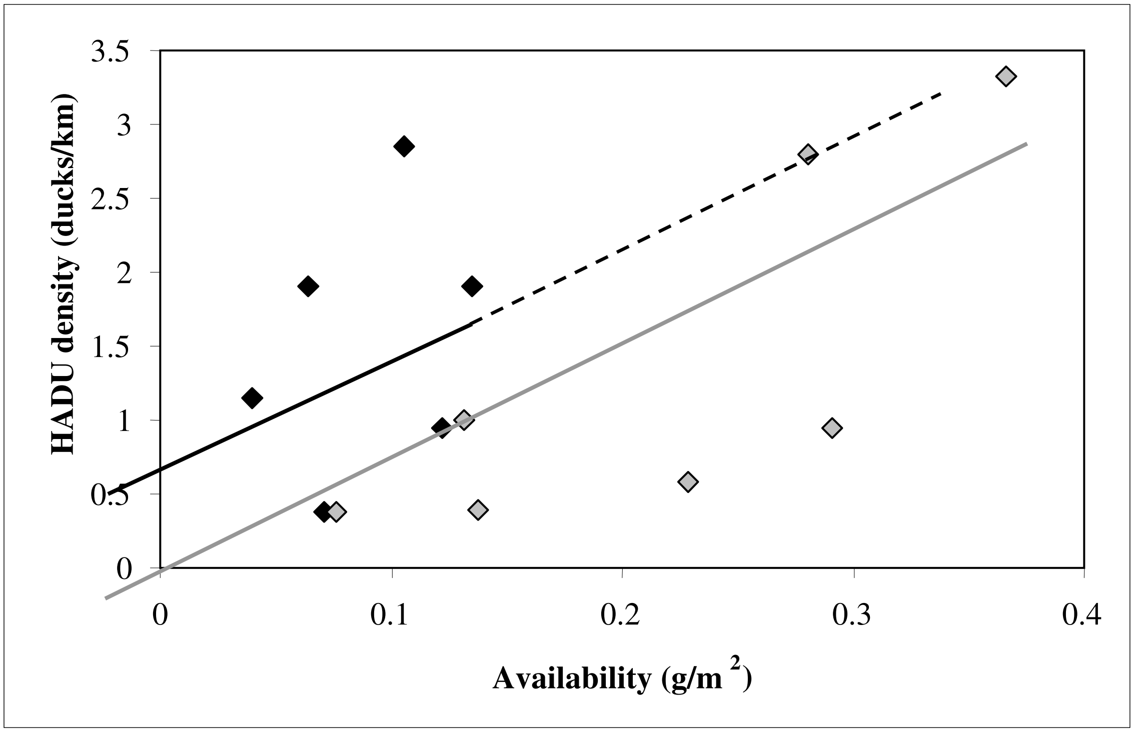


Figure 14.3.5 Aquatic insect and harlequin duck availabilities for 2003 (black), and 2004 (grey) (r2 = 0.46).

Line equations, 2003: y = 9.02 (x) + 0.72, 2004: y = 9.02 (x) + 0.06. Dotted line for 2003 extrapolated beyond data.



14.4. The Influence of Fish on Harlequin Duck Prey Availability on Breeding Streams.

14.4.1. 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.

14.4.2. 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.

14.4.3. Methods

Aquatic insect sample method

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

Aquatic insect sample regime

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

Harlequin duck survey

Methods for harlequin duck survey were described in Chapter 2.

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.

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 coefficients 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.

14.4.4. Results

Aquatic insect communities differed between river reaches in overall availability (Figure 14.4.1) and in the relative composition of functional feeding groups (Figure 14.4.2). 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 14.4.2).

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 14.4.3) 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 14.4.3). 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 14.4.4).

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 14.4.1). 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 14.4.1).

14.4.5. 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 unpublished data) 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 14.4.1 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 14.4.1 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.

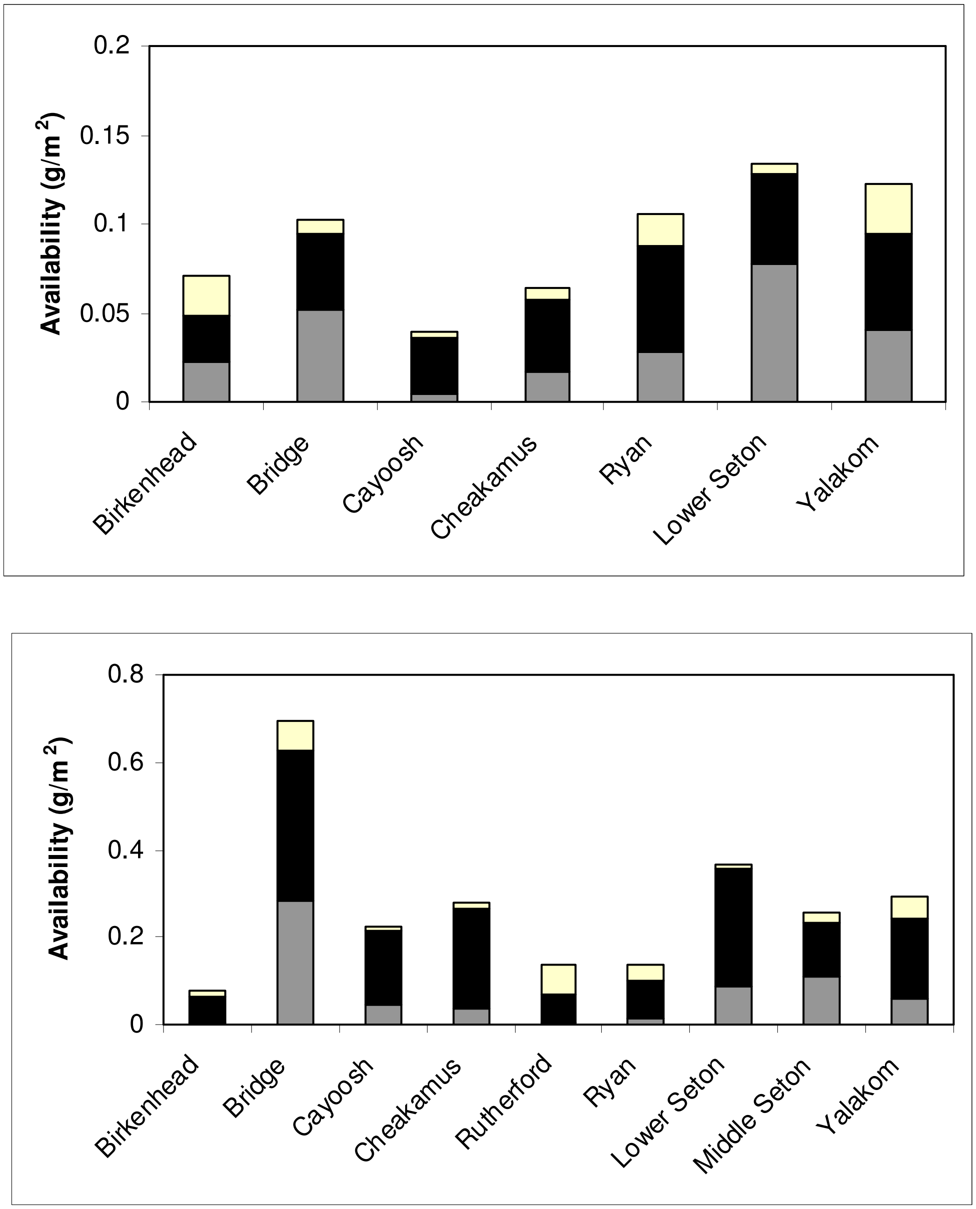


Figure 14.4.2 Functional feeding group composition of studied river reaches in 2003 (top) and 2004 (bottom).

Predaceous aquatic insects (☐), grazing aquatic insects (■), filter-feeding aquatic insects (▨). Predaceous and grazing aquatic insects are mobile.

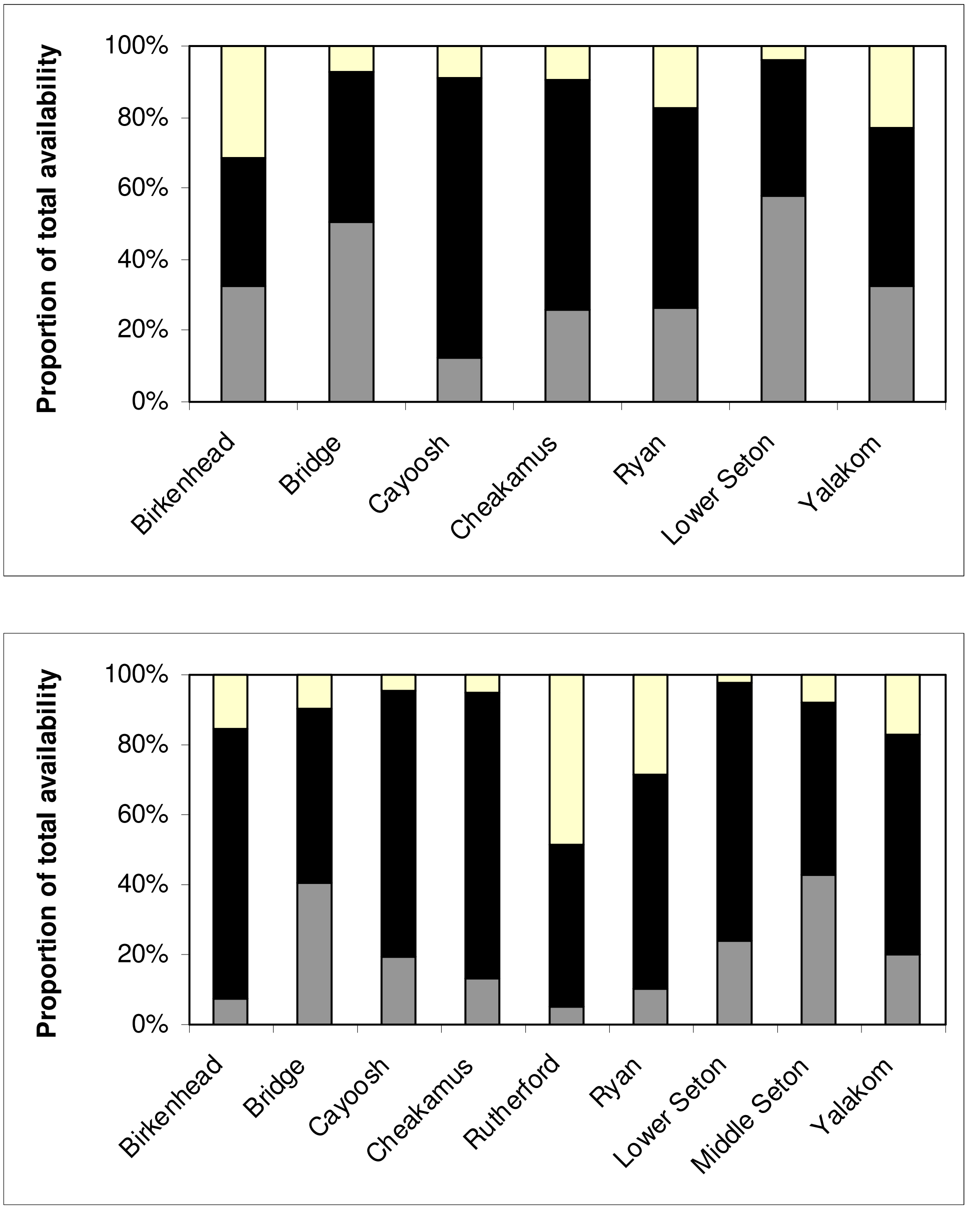


Figure 14.4.3 Harlequin duck density versus total fish rating (using fish rating scheme #1).

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.

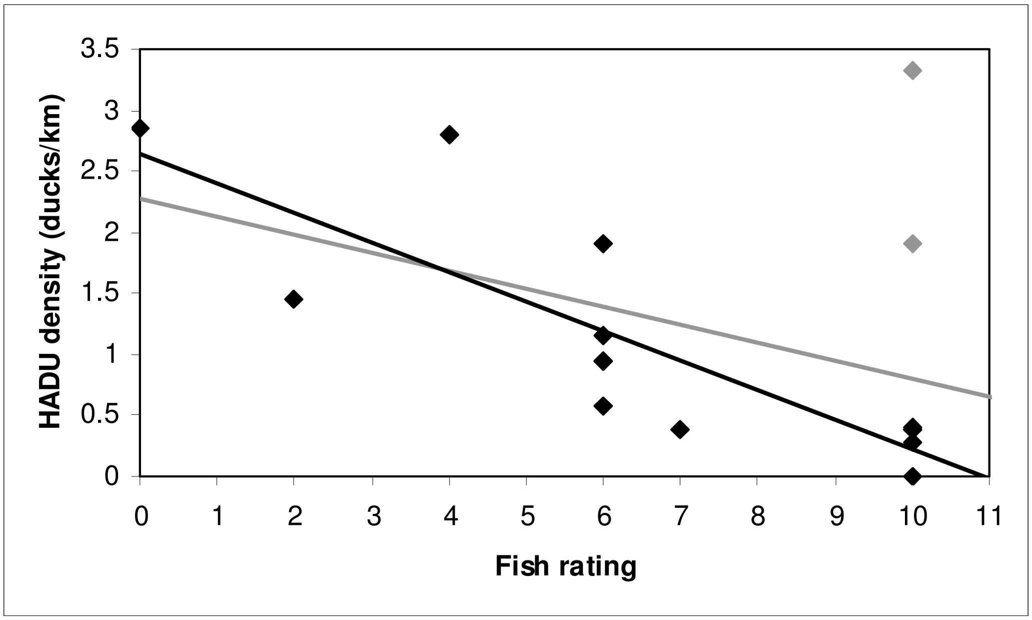
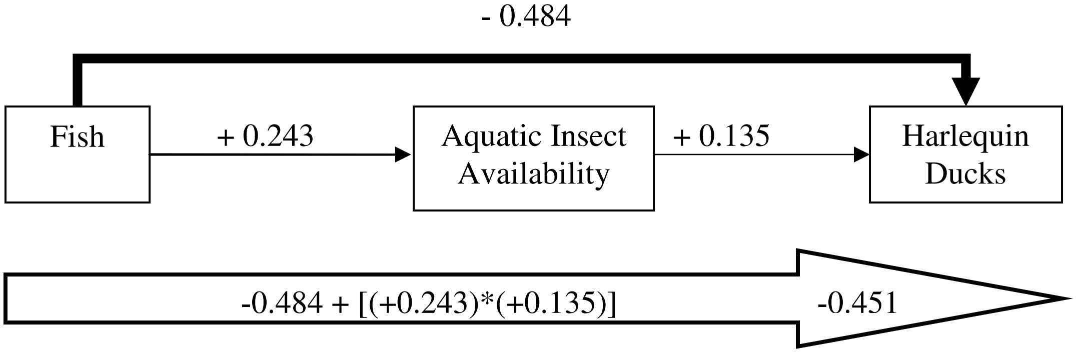


Figure 14.4.4 Path diagram of interactions between fish and harlequin ducks depicting the correlation as a sum of the two separate paths calculated as a product of their standardized partial regression coefficients. Results are from path analysis using fish rating scheme #1. Arrow widths are proportional to their contribution to the total interaction.



14.5. General Conclusions, Recommendations, and Future Directions

14.5.1. 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).

14.5.2. 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.

14.5.3. Future Directions

This thesis was motivated by studies revealing low productivity in harlequin duck populations along the British Columbia coastline. The results provide some 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. Further refinement and testing of this hypothesis will require a number of initiatives. First, we need a better assessment of whether the current level of productivity is low enough to have caused harlequin duck population decline. In order to examine this question demographic modelling of existing data should be completed to explore the stability of the population. Background research, surveys and mapping work could be completed to estimate the impact of fish introduction on prey availability on harlequin duck breeding streams. Researching the fish status and harlequin duck use on stream reaches could also be conducted to further test the hypothesis that a BMII exists between harlequin ducks and fish. This would entail identifying stream reaches that are fishless, or have low densities of fish in a watershed area used by harlequin ducks and measuring their harlequin duck densities. This project would predict that harlequin duck use on these reaches would be high and would have high densities of ducks. For example, the upper Birkenhead reach in our study system has low use by fish with duck use lower on the river, therefore I would predict high densities of harlequin ducks on the upper reach. Finally, some experimental work will be needed to evaluate whether fish introductions lower the suitability of streams for harlequin duck breeding. This could 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 removal 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 a long enough study period taking into consideration harlequin duck site fidelity.

14.5.4. Reference List

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14.6. 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

14.6.1). These rating systems were used to calculate a fish rating for each river reach (Table 14.6.2). 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 14.6.1) (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 14.6.3) (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 14.6.3) (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 14.6.2) (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 14.6.3) (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 14.6.1) (FISS 2006). Benthic feeding species include: mountain whitefish, and suckers (Figure 14.6.3) (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 14.6.3) (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 14.6.2) (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 14.6.1) (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 14.6.3). 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 14.6.1) (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 14.6.2) (Lister and Beniston 1995). Benthic-feeding species in this reach include: mountain whitefish, sculpin, sucker, and longnose dace (Figure 14.6.3) (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 14.6.1) (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 14.6.2) (Conlin 1994). Benthic-feeding species noted are: sculpin, mountain whitefish, and longnose Dace (Figure 14.6.3) (FISS 2006; Komori 1997).

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Table 14.6.1 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 14.6.2 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 14.6.3 Fish rating according to rating system #1 for each of the studied river reaches.

River Reach	Anadromous spawning of salmonids		Coho escapement level relative rating		Rainbow trout level relative rating		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 14.6.1 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).

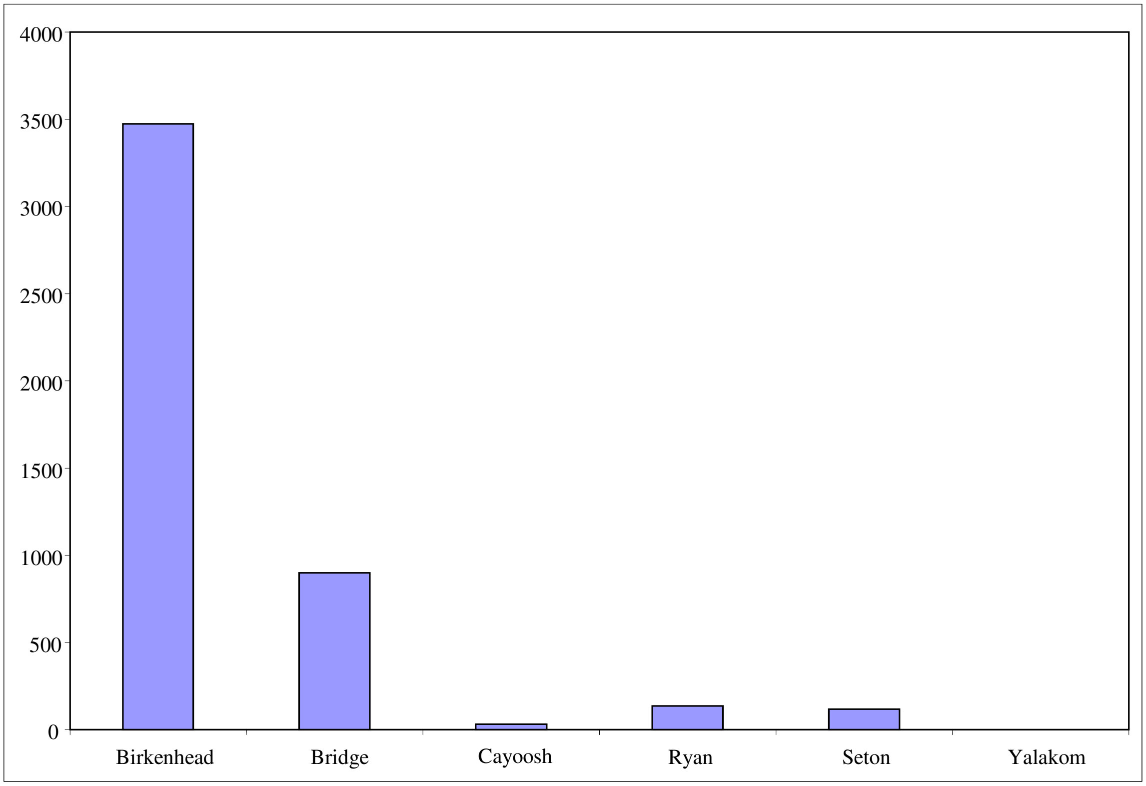


Figure 14.6.2 Rainbow trout density estimates. All estimates include both fry and parr.

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.

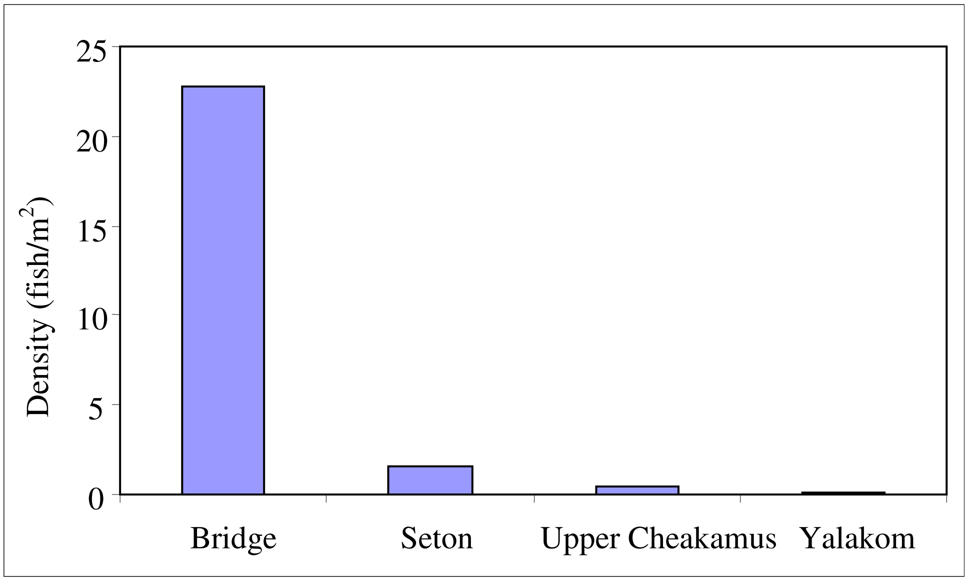
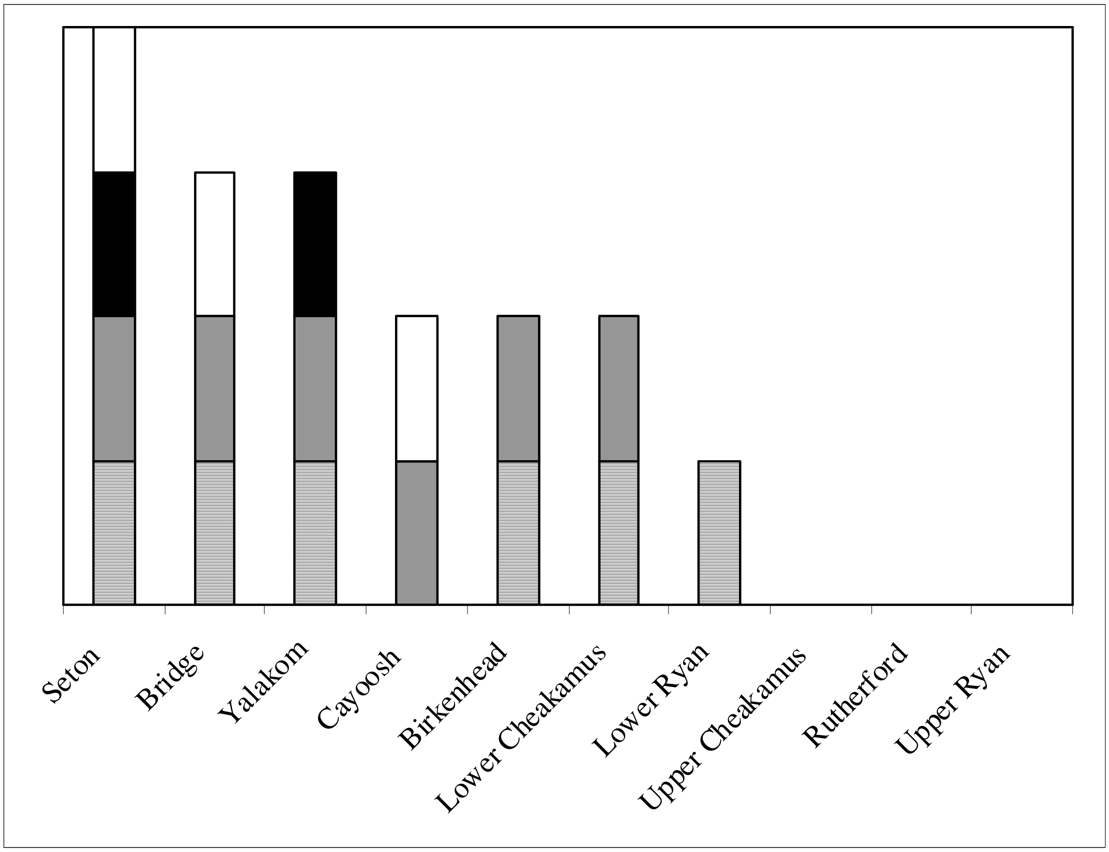


Figure 14.6.3 The presence/absence of benthic-feeding species.

Sculpin (▤), mountain whitefish (▨), dace (■), sucker (☐).



14.7. 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 14.7.1). Ephemerellids from this system increased their activity at night relative to full sunlight and dusk conditions (Tables 14.7.1 and 14.7.2). 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 14.7.3). 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 14.7.3).

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 14.7.1 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 14.7.2 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 14.7.3 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 14.7.1 Visibility measures from predator odour experiment.

Day (☐), Dusk (▨), Night (■). Error bars are 95% CI.