

Fish and harlequin ducks compete on breeding streams

S.V. LeBourdais, R.C. Ydenberg, and D. Esler

Abstract: We investigated interactions among harlequin ducks (*Histrionicus histrionicus* (L., 1758)), fish, and their shared aquatic insect prey. We measured flow variability, benthic aquatic prey abundance, fish presence, and breeding density of harlequins on eight rivers in the Southern Coast Mountain Range in British Columbia, Canada, in 2003 and 2004. Rivers with lower flow variability had higher abundance of aquatic insects. Densities of harlequins and fish presence on the rivers were both significantly and positively related to insect abundance, but path analysis revealed a strong negative correlation between them. We interpret this as an indirect interaction between harlequins and fish mediated by anti-predator behaviour of insects in the presence of fish, which reduces insect availability, rather than as a reduction in the abundance of aquatic insects through consumption by fishes. We hypothesize that the ongoing and widespread introduction of fish into historically fishless waters throughout North America may have contributed to the current low productivity and recruitment measured in populations of harlequins by reducing quality of breeding habitat.

Résumé : Nous étudions les interactions entre les arlequins plongeurs (*Histrionicus histrionicus* (L., 1758)), les poissons et les insectes aquatiques qu'ils utilisent conjointement comme proies. Nous avons mesuré la variabilité du débit, l'abondance des proies aquatiques benthiques, la présence de poissons et la densité des arlequins plongeurs en reproduction dans huit rivières de la chaîne de montagnes de la côte sud de la Colombie Britannique, Canada, en 2003 et 2004. Les rivières à débit moins variable ont de plus fortes abondances d'insectes aquatiques. Il y a une relation significative et positive entre les densités des arlequins plongeurs et la présence de poissons, d'une part, et l'abondance des insectes, d'autre part, mais une analyse des coefficients de direction montre une forte corrélation négative entre ces deux variables. Nous interprétons ce phénomène comme une interaction indirecte entre les arlequins plongeurs et les poissons qui s'explique par le comportement anti-prédateur des insectes en présence des poissons, ce qui réduit la disponibilité des insectes, plutôt que par une réduction de l'abondance des insectes aquatiques à cause de la consommation par les poissons. Nous posons l'hypothèse selon laquelle les introductions courantes et répandues de poissons dans des eaux historiquement sans poissons dans toute l'Amérique du Nord peuvent avoir contribué à la productivité et au recrutement faibles mesurés actuellement chez les populations d'arlequins plongeurs en réduisant la qualité des habitats de reproduction.

[Traduit par la Rédaction]

Introduction

Many North American sea duck populations have been declining over recent decades (Goudie et al. 1994). In eastern North America, numbers of harlequin ducks (*Histrionicus histrionicus* (L., 1758)) were reduced to fewer than 1500 birds by 1990, and the eastern population was consequently listed as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). This was downgraded to a Species of Special Concern in 2001, owing to population stability and a marginal increase in numbers (COSEWIC 2006). The western population is listed as a Species of Special Concern, as a Sensitive Species throughout the northwestern states of the United States, and is on the Yellow List in both British Columbia and Alberta (Rob-

ertson and Goudie 1999). Surveys of age ratios of harlequins wintering in the Strait of Georgia have detected recruitment rates that appear too low to sustain the population (Smith et al. 1999, 2001; Rodway et al. 2003), given estimated rates of survival. The conservation status of this species requires a fuller understanding of the reasons for the observed low recruitment.

Harlequins spend the majority of the year in marine environments, where they feed on a variety of invertebrates in the intertidal zone including crabs, amphipods, and gastropods. In April or May, breeding individuals move to inland sites on clear, fast-flowing rivers, where they feed on a wide variety of aquatic insects (Robert and Cloutier 2001) found on the substrate surface and under smaller cobbles (McCutchen 2002). Prey availability in streams might have important effects on harlequin productivity, as the energy from consumed stream insects are used by females for forming clutches (Bond et al. 2007) and for raising young (Gardarsson and Einarsson 2004). Stream prey abundance has been hypothesized to affect breeding propensity (Bengtson and Ulfstrand 1971) and productivity of breeders (Gardarsson and Einarsson 1994, 2004), although the role of variation in food abundance has been debated (Goudie and Jones 2005).

Prey abundance can be affected by several factors. Abiotic stream features, such as flow variability, can influence

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both aquatic insect abundance and community structure (Hildrew and Giller 1994; Allan 1995; Giller and Malmqvist 1998). A variety of stream-dwelling fish species also prey on these insects and competition between fishes and waterfowl has been hypothesized. For example, Eadie and Keast (1982) showed that common goldeneyes (*Bucephala clangula* (L., 1758)) and yellow perch (genus *Perca* L., 1758) had high dietary overlap, and that their densities in small lakes were negatively related. Goldeneyes increased their use of lakes after fish were removed, providing direct evidence for competition (Eriksson 1979). Dietary overlap and size selective predatory predation with fish has been linked to reduced amounts and size of preferred prey (amphipods) in the diets of spring migrating lesser scaup (*Aythya affinis* (Eyton, 1838)) (Strand et al. 2008). In another example, competitive interactions between red-necked grebes (*Podiceps grisegena* (Boddaert, 1783)) and fishes resulted in niche separation; grebes used relatively fish-free reed bed areas in lakes, where aquatic insect densities were 5–10 times greater (Wagner and Hansson 1998).

We considered competition with fish as a potential mechanism by which prey availability to harlequins might be reduced and their breeding productivity affected. If fish presence has a detrimental effect on breeding distribution or productivity of harlequins, the mechanism for this competition is likely indirect, mediated by effects on the shared prey resource. A growing body of literature has been devoted to describing and contrasting the various means of competition by way of indirect interaction. In a density-mediated indirect interaction (DMI), Werner and Peacor (2003), an initiator (in our case, fish) reduces by consumption the density of a resource (the transmitter; here insects) shared with and thereby affecting a third species (the receiver; here harlequins). In a trait-mediated indirect interaction (TMI), prey individuals alter physiological, developmental, morphological, and (or) behavioural traits in ways that make them less available to the receiver (Werner and Peacor 2003; Bolnick and Preisser 2005; Preisser et al. 2005). TMIs are widespread when interactions involve predators, because of the powerful effects of predator intimidation (Lima and Dill 1990; Werner and Peacor 2003; Bolnick and Preisser 2005; Preisser et al. 2005). Prey may shift habitats, change activity levels, or alter their foraging schedule and behaviours to reduce predation risk (Soluk and Collins 1988; McIntosh and Townsend 1994). Predation risk posed by fishes has been shown to lower the daytime activity level and increase refuge use in several families of aquatic insects (Bechara et al. 1993; Culp and Scrimgeour 1993; McIntosh and Peckarsky 1996). TMIs have been found to account for as much as 93% of the total predator effect in aquatic ecosystems (reviewed by Preisser et al. 2005).

In this paper we evaluate competition between harlequins and fish through their shared aquatic insect prey and how it may be affecting breeding habitat quality for harlequins.

Materials and methods

Study area

We studied the abundance of insects, fishes, and harlequins in eight rivers in the Southern Coastal Mountains, British Columbia, near the communities of Lillooet and

Pemberton, including the Bridge River, Yalakom River, Cayoosh Creek, Seton River, Birkenhead River, Cheakamus River, Rutherford Creek, and Ryan River (Fig. 1; for detailed descriptions see LeBourdais 2006).

Sampling of aquatic insects

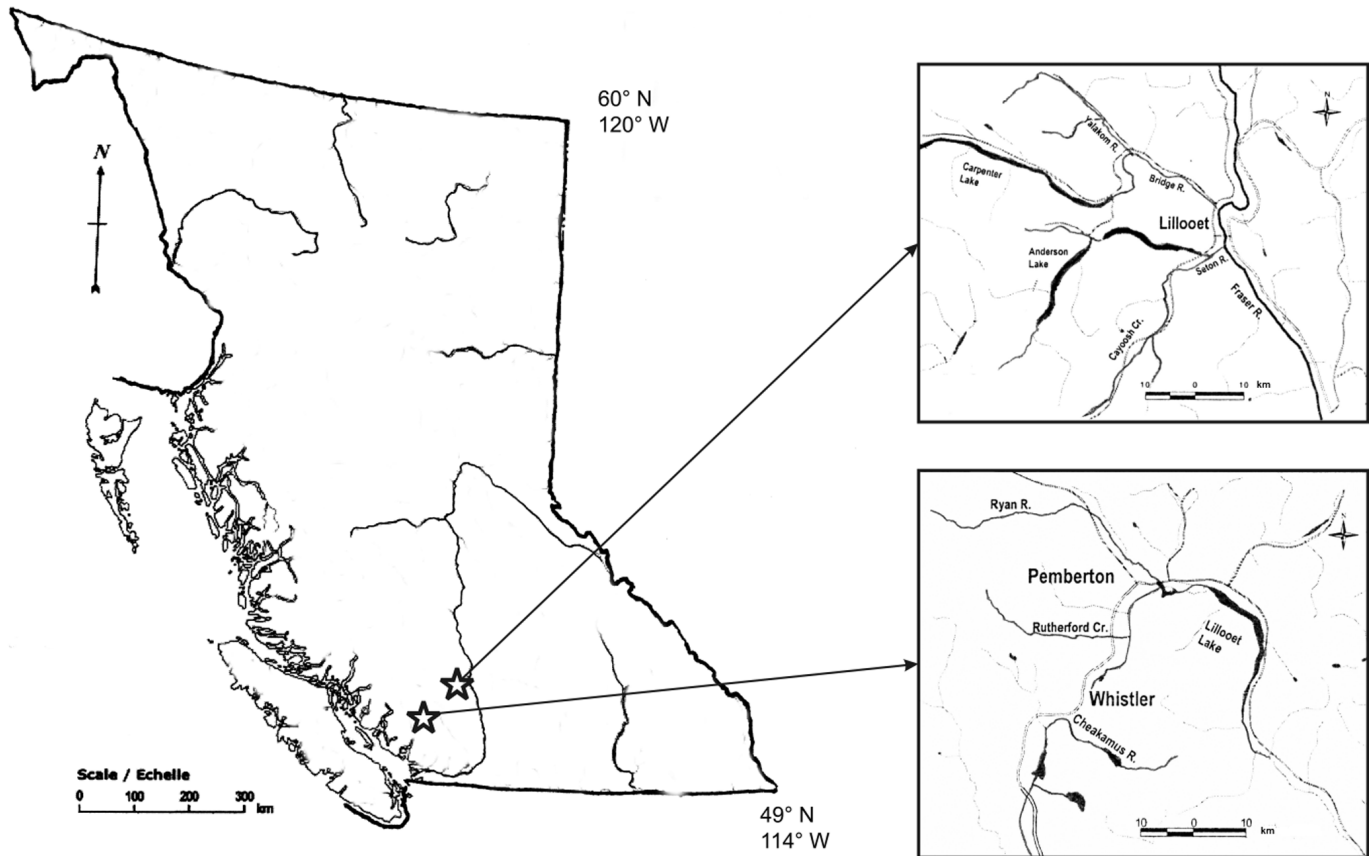
Aquatic insects consumed by harlequins on breeding streams are poorly quantified using conventional sampling methods. Surber and Hess methods (Surber 1937; Welch 1948) are difficult to use owing to the coarseness of the substrate in streams used by harlequins, while kick sampling is time consuming, poorly controls the volume of benthos sampled, and includes animals located deep in the substrate that would be unavailable to harlequins. We measured the abundance of aquatic insects using the “five-rock” method (see McCutchen 2002; McCutchen and Ydenberg 2004). This method reveals patterns of aquatic insects similar to kick sampling but is superior in its ability to sample aquatic insects on the substrate surface and thus available to harlequins.

Each sample consisted of five approximately hand-sized cobbles, randomly selected from the river substrate at each sample site. Successive rocks in a sample were collected moving upstream to minimize disturbance to insects. A fine-mesh aquatic D-net was positioned downstream of each rock as it was picked up, and the aquatic insects on all surfaces of the rock were scrubbed from the rock and into the net. The volume of each rock was estimated (to the nearest 25 mL) by water displacement in a large graduated cylinder, and the surface area (cm²) was calculated as surface area = $13.875 \times \log(\text{volume} \times 3.603)$ (McCutchen 2002). Insects from each sample were placed together in a labelled vial and stored in 90% ethanol for later counting and identification. Samples were dried for 24 h at 30 °C and weighed to the nearest microgram. The abundance of prey was expressed as a density (mg/m²), calculated as the total dry mass of aquatic insects divided by the total surface area of the rock substrate.

Five-rock samples were collected on seven 5 km reaches during the 2003 and 2004 breeding seasons (May–August). Sample stations were established at 500 m intervals with a randomly selected starting site, as well as wherever harlequins were encountered. At each sampling station three five-rock samples were collected (one at the station marker, one 10 m downstream, and one 10 m upstream). In July 2003, five-rock samples were taken at 10 m intervals along 150 m reaches of the Yalakom River, Seton River, and Cayoosh Creek. In 2004, samples were collected on eight reaches located on four rivers surrounding Lillooet, British Columbia (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 over the course of the breeding season of harlequins. Samples at specific stations were not taken when the spring freshet disallowed access to the stream substrate owing to water depth and velocity.

Together these procedures yielded a total of 271 five-rock samples on seven rivers in 2003 (missing Rutherford Creek)

Fig. 1. Map of British Columbia, Canada, with inset maps of study rivers.



and 467 five-rock samples on eight rivers in 2004. These five-rock samples were used to calculate a mean availability measurement on each river. A mean of 39 (SD = 11) samples in 2003 and 58 (SD = 19) 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.

Daily (2003 and 2004) readings of water levels were obtained from the Water Survey of Canada for the Yalakom, Cayoosh, Seton, and Cheakamus rivers; from BC Hydro for the Bridge River; and from Summit Power for the Ryan River. We obtained records from Cloudworks Energy for Rutherford Creek in 2000 and 2001, but records were not available for 2003 and 2004. No data regarding water levels were available for the Birkenhead River. Variability in river levels was calculated as the variance of daily river levels from 1 April to 1 July, which encompassed the study period.

Harlequin surveys

Harlequin surveys were conducted along 5 km reaches of each river during the prebreeding period (30 April – 23 May in 2003, 4–26 May in 2004). Surveys were conducted following the standard harlequin duck survey protocol outlined in the Provincial Resource Inventory Committee Standards (B.C. Ministry of Environment, Lands and Parks 1998). Each survey team consisted of at least two observers. Harlequin density was calculated as the number of ducks divided by the length of the surveyed reach. Seven of the eight rivers were surveyed in each year; Rutherford Creek was not surveyed in 2003 and the Yalakom River was not surveyed in 2004.

Fish indices

Data on the fish species in each of the rivers were obtained from reports by government ministries, companies, and organizations, along with personal communication with local biologists and personal observations. Sources and data are fully documented in LeBourdais (2006) and summarized here in Table 1. From these sources we were able to compile data on all of the study rivers by nine categories of fish species: (1) spawning by anadromous salmonids (steelhead, chinook, coho); (2) number of spawning coho salmon (*Oncorhynchus kisutch* (Walbaum, 1792)); (3) the densities of fry and parr of resident rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)); (4) the presence of bull trout (*Salvelinus confluentus* (Suckley, 1859)) and dolly varden (*Salvelinus malma* (Walbaum in Artdi, 1792)); (5) the presence of coastal cutthroat trout (*Oncorhynchus clarkii clarkii* (Richardson, 1836)); (6) the presence of mountain whitefish (*Prosopium williamsoni* (Girard, 1856)); (7) the presence of sucker (family Catostomidae) species; (8) the presence of sculpin (family Cottidae) species; and (9) the presence of longnose dace (*Rhinichthys cataractae* (Valeciennes in Cuvier and Valenciennes, 1842)). Spawning salmon (categories 1 and 2) do not feed in fresh water; however, the product of their spawning activities (i.e., fry) do feed on aquatic insects while in the freshwater environment. Trout (categories 3, 4, and 5) feed mostly on stream drift, and are piscivorous if large enough. Species in the last four categories (6–9) are benthic feeders.

The methods used in collecting these data vary somewhat and cannot easily be standardized. We scored the data for

Table 1. Fish rating for each of the study river reaches.

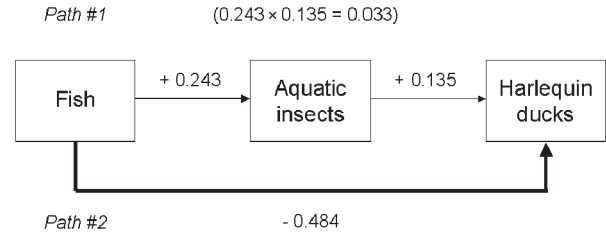
River reach	Presence [†]									Fish rating (points)
	Relative rating of levels*			Dolly varden or bull trout			Cutthroat trout	Sucker	Dace	
	Anadromous spawning of steelhead, coho, and chinook [†]	Coho escapement	Rainbow trout	Dolly varden or bull trout	Cutthroat trout	Sucker	Dace	Whitefish	Sculpin	
Birkenhead	Yes	High	Moderate	Yes	Yes	No	No	Yes	Yes	10
Bridge	Yes	Moderate	High	Yes	No	Yes	No	Yes	Yes	10
Cayoosh	Yes	Low	Low	Yes	No	Yes	No	Yes	No	6
Lower Cheakamus	No	None	Moderate	Yes	Yes	No	No	Yes	Yes	6
Upper Cheakamus	No	No	Low	Yes	No	No	No	No	No	2
Rutherford	No	None	Low	Low	No	No	No	No	No	2
Upper Ryan	No	None	None	No	No	No	No	No	No	0
Lower Ryan	Yes	Low	Moderate	Yes	Yes	No	No	Yes	Yes	7
Seton	Yes	Low	Moderate	Yes	Yes	Yes	Yes	Yes	Yes	10
Yalakom	Yes	None	Low	Yes	No	No	Yes	Yes	Yes	6

Note: See text for binomials of fish species.

*Points rating scheme: high = 3, moderate = 2, low = 1, none = 0.

[†]Points rating scheme: yes = 1, no = 0.

Fig. 2. Path diagram of interactions between fish and harlequin ducks (*Histrionicus histrionicus*) depicting the correlation as a sum of the two separate paths calculated as a product of their standardized partial regression coefficients. Path #1 represents a possible density-mediated indirect interaction (DMII) between fish and ducks, while path #2 represents a possible trait-mediated indirect interaction (TMII). Results are from path analysis using fish rating index #1. Arrow thicknesses are proportional to their contribution to the total interaction.



each river in each of the nine fish categories on either 2 point (presence or absence) or 4 point scales (absent, low, moderate, or high abundance). When 4 point scales were used, the abundance measures in the original reports corresponding to points on the 4 point scale varied by an order of magnitude or more. Measures of coho escapement and rainbow trout density had obviously been given priority in most of the reports and were generally well-quantified. The fish rating index employed here used 2 point (presence or absence) scales for all categories, except for coho escapement and rainbow trout density, which were assigned 4 point scales. The overall fish rating simply summed the scores in all nine categories. The index could thus range from 0 (no fish at all) to 13 (scores of 1 or 3 in all categories).

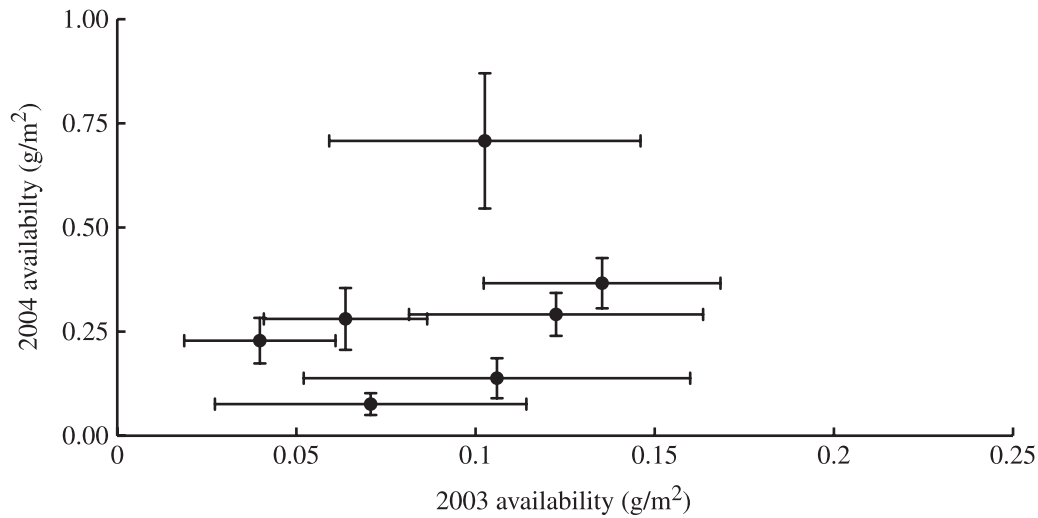
We used various combinations of 2 and 4 point scales across the nine categories to derive six other indices. The results obtained were very similar to those reported below for the above fish rating index, and we report only those results here. Full details are given in LeBourdais (2006).

Statistics

All analyses were run in JMP IN (academic) version 4.0.4 (SAS Institute Inc., Cary, North Carolina) utilizing a significance level of $p = 0.05$. The aquatic insect abundance data were examined for outliers. The Bridge River was deemed an outlier and omitted from analyses testing the relationships involving insect abundance. This point had exceptionally high insect abundance for 2004, exceeding by twofold the next highest observation, and falling more than 5 SD from the mean. We presume that the extraordinarily high insect density is due to the re-establishment of the reach below the Terzaghi dam, following the initiation of a permanent flow release in August 2000 from the Carpenter Reservoir. Harlequins (and other riverine birds) are currently recolonizing the river; more were seen in 2004 than in earlier years on this reach, and bird use increased in each year following the initiation of the permanent flow (Walton and Heinrich 2004, 2005).

Differences in insect abundance among rivers were tested using a one-way ANOVA for each year of the study. We compared insect abundance between the 2 years using a Student's t test for each river. We compared flow variability between years with a paired t test. Relationships between

Fig. 3. Mean aquatic insect availability measured in 2003 and 2004. Bars are 95% confidence intervals. Rutherford Creek was measured only in 2004 and is not represented here. Differences between rivers are highly significant within each year (separate one-way ANOVAs, $p < 0.001$).



flow variability and aquatic insect abundance, and between harlequin density and insect abundance, were examined using ANCOVAs, with year as a co-variate. Model selection in the ANCOVAs was performed using backward selection, removing factors with $p > 0.10$.

Relationships among aquatic insect abundance, harlequin density, and the presence of fish were examined using path analysis (Fig. 2; Mitchell 2001). By assessing the strength of hypothesized interactions between variables, path analysis can evaluate the strength of interactions in a community (Wootton 1994; Englund and Evander 1999). We constructed a path diagram to discern between the two hypothesized competitive relationships between fishes and harlequins.

Competition between fishes and harlequins will be evident through the negative overall correlation between harlequin density and fish index (sum of path #1 and path #2). Fishes and harlequins might compete by consuming and so lowering the density of aquatic insects, reducing abundance (DMII, path #1). This would be supported by a negative correlation between insect abundance and both fish index and harlequin density, as these predators would consume and thereby reduce the density of insects. Fish also could interact with harlequins indirectly through their effect on prey behaviour, reducing insect availability (TMII). This would be evident as a negative correlation between harlequin density and value of the fish index (path #2), in coordination with a positive correlation between fish index, harlequin density, and insect density (path #1). This would mean that both fish and harlequins are inhabiting areas with higher aquatic insect densities; however, harlequins and fish are not using the same reaches. If this effect is present, it presumably occurs because the presence of fish depresses the availability of insects for ducks, where insects move to locations where they are less available to harlequins (e.g., the underside of larger rocks; McCutchen 2002).

The overall correlation between the fish rating index and harlequin density is the sum of standardized regression coefficients for path #1 and path #2. The correlation on path #1

is the product of the standardized partial regression coefficients of (i) the fish index on aquatic insect abundance and (ii) aquatic insect abundance on harlequin density. These correlation coefficients are measures of the relative strength of these pathways.

Results

Aquatic insect abundance varied among rivers ($p < 0.001$ in both years; Fig. 3), with approximately a fourfold range among rivers in 2003 and a fivefold range in 2004. Abundance was overall greater in 2004 in all reaches measured, with significant increases on the Bridge River, Cayoosh Creek, Cheakamus River, Seton River, and Yalakom River (all $p < 0.0001$). The overall mean abundance was 0.19 g/m^2 (range $0.04\text{--}0.71 \text{ g/m}^2$, $n = 14$).

Flow variability differed greatly between rivers (Fig. 4). 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 Terzaghi 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 (matched pairs, $t_{[6]} = -2.415$, $p = 0.052$) and rivers retained their ranking relative to one another. The absolute magnitude of the difference between years was greatest in the most variable rivers.

There was a negative relationship between aquatic insect abundance and flow variability (Fig. 5). The relation held not only when comparing rivers, but also when comparing years, as the overall decrease in flow variability in 2004 was accompanied by an overall increase in aquatic insect abundance. Both factors (flow variability, $F_{[1,6]} = 9.23$, $p = 0.0229$; year, $F_{[1,6]} = 5.71$, $p = 0.0541$), as well as the inter-

Fig. 4. Flow variability for rivers in the study area. Variability is the calculated variance of daily river level from 1 April to 1 July. Solid bars represent 2003 and shaded bars represent 2004. Rutherford Creek variability measures are for 2000 and 2001. There are no river level data for Birkenhead River.

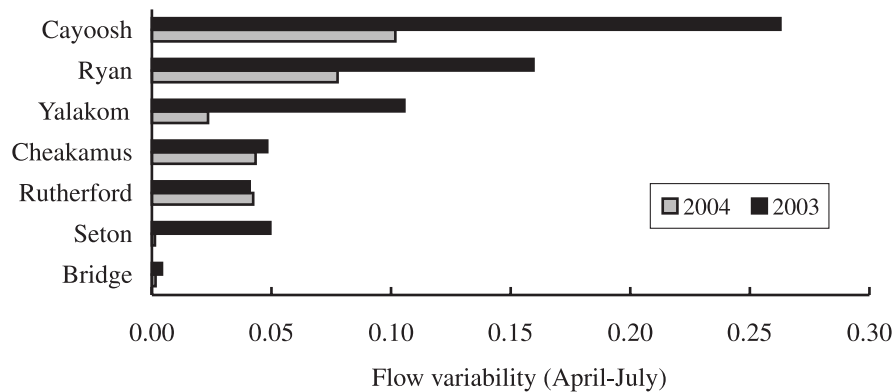
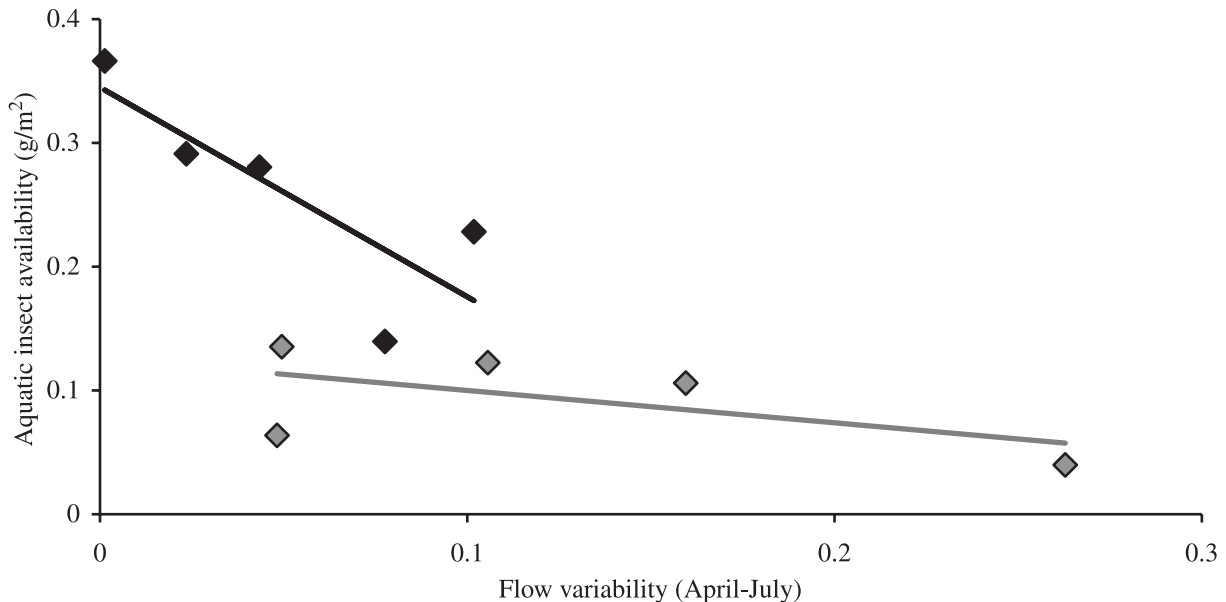


Fig. 5. Aquatic insect availability and flow variability of study rivers. Solid diamonds represent 2003 and shaded diamonds represent 2004. The sample size (n) is 10, with Rutherford Creek and Birkenhead River excluded from the sample owing to missing data. Bridge River was excluded as an outlier (see text for an explanation). The model $r^2 = 0.87$.



action term (year \times flow variability, $F_{[1,6]} = 5.00$, $p = 0.0668$) were significant factors. The model had an overall r^2 of 0.87.

The mobility of species in the insect community indicates how readily they are able to respond to predation danger by moving to less accessible locations, and thus forms part of the assessment of the hypothesized indirect interactions. The composition of the aquatic insect communities differed somewhat between rivers, with predaceous insects composing 15.1% (range 2.1%–48.6%, $n = 16$) and grazing insects composing 58.6% (range 35.8%–81.6%, $n = 16$) of the total biomass. The community was therefore largely (mean 73.7%, range 42.0%–95.1%, $n = 16$) composed of mobile aquatic insects. Filter-feeding aquatic insects composed 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.

Aquatic insect abundance and harlequin density were positively related with both abundance ($F_{[1,10]} = 8.48$, $p =$

0.0155), and year ($F_{[1,10]} = 4.75$; $p = 0.0542$) explaining significant variation in harlequin density ($r^2 = 0.46$; Fig. 6). Slopes of the linear relationship between harlequin density and insect abundance did not differ between years (interaction term is not significant; $t_{[9]} = 0.162$, $p = 0.875$), but the relationship was significantly elevated in 2003 (i.e., more harlequins per unit insect density in 2003), as one would expect if the overall abundance of food was lower.

The mean fish index value was 7.1 (SE = 0.8, range = 0.0–10.0, $n = 16$). The mean density of harlequins was 1.23 ducks/km (SE = 0.26 ducks/km, range = 0.00–3.33 ducks/km, $n = 16$). Path analysis revealed a negative overall correlation between fish and harlequins of -0.451 (data shown on Fig. 7), which is the sum of the negative relationship between fish index and harlequin density (path #2, standardized partial correlation coefficient = -0.484), and the product of the two smaller, positive relationships between fish index and aquatic insects (standardized partial

Fig. 6. Aquatic insect availability and density of harlequin ducks (*Histrionicus histrionicus*). Solid diamonds represent 2003 and shaded diamonds represent 2004. The model $r^2 = 0.46$. Abundance on Rutherford Creek was measured only in 2004 and Bridge River was excluded as an outlier.

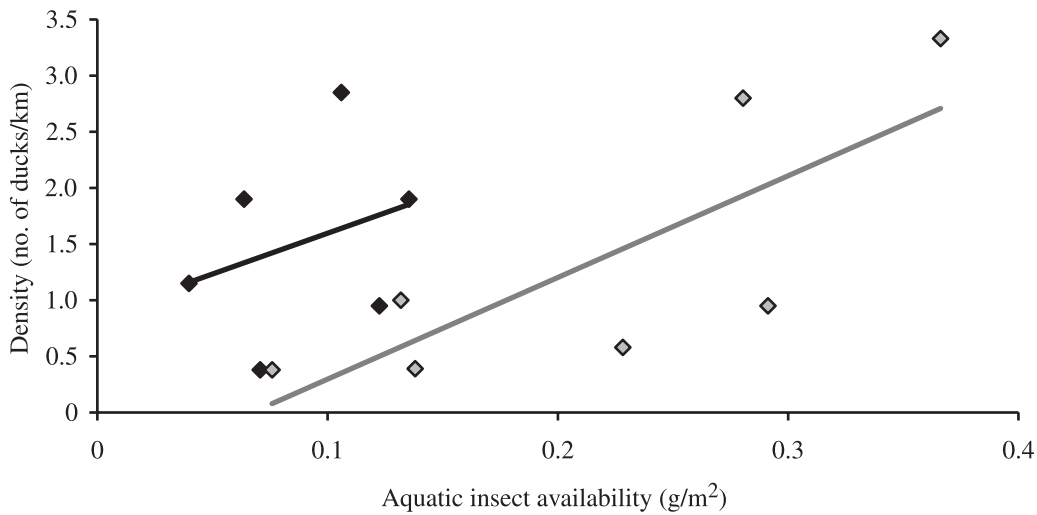
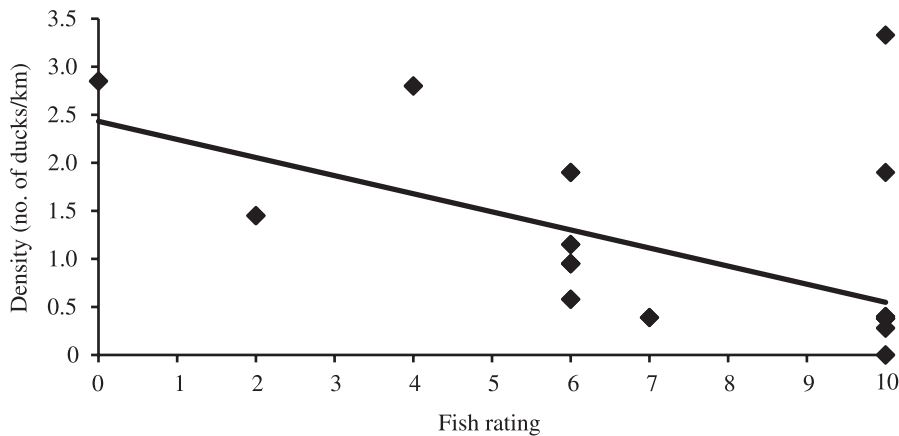


Fig. 7. Density of harlequin ducks (*Histrionicus histrionicus*) in relation to fish index. The model $r^2 = 0.18$.



correlation coefficient = 0.243), and aquatic insects and harlequins (standardized partial correlation coefficient = 0.135; product 0.033; Fig. 2).

Discussion

Our results show (i) that there was significant variation in abundance of aquatic insects among the rivers we studied, with lower abundance on rivers with more variable flow; (ii) that both the fish rating index and harlequin density were positively associated with our measure of insect abundance; but (iii) the fish index and harlequin density were strongly and negatively associated with each other. The path analysis supported the hypothesis that competition may exist between these species, as a result of the fishes effect on insect availability to harlequins. These findings support our hypothesis that the presence of fish lowers the quality of streams and rivers for breeding by harlequins.

Predation risk from fish has been shown to reduce the daytime activity level and increase refuge use in many different families of aquatic insects known to be consumed by breeding harlequins. For example, the presence of the mot-

tled sculpin (*Cottus bairdi* Girard, 1850) reduced the amount of time the stonefly *Agneta capitata* (Pictet, 1841) spent on the sides and tops of rocks, and decreased the amount of time spent moving on the substrate (Soluk and Collins 1988). A substantial portion of the aquatic insect community in our study consisted of grazing and predatory aquatic insects, which are highly mobile, and thus could accommodate a TMII between fish and ducks.

The literature records diverse effects of fish predation on aquatic insect density, with some studies showing strong effects and others showing little or no effect (Dahl and Greenberg 1996). Grazing aquatic insects experience the largest effects of fish predation compared with other groups because they feed on periphyton on the substrate surface (Kohler and McPeck 1989; Rosenfeld 2000). 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 accounted for 93% of the total predator effect (Preisser et al. 2005). In a study with the mayfly *Baetis bicaudatus* Dodds, 1923, Peckarsky and McIntosh (1998) found that the reduced growth rate owing to increased predator avoidance

behaviours accounted for a greater proportion of the reduction in biomass than did direct losses to consumption.

But could these effects be large enough to account for the reduction in recruitment measured in The Strait of Georgia, which no longer compensates for normal adult mortality? Harlequins wintering in the Strait of Georgia breed throughout the western cordillera, but because the breeding density is low, impacts localized at one or even a few breeding areas seem unlikely to be able to account for low productivity in the entire population. The breeding range has no obvious widespread large-scale impacts, and has relatively low human population, especially in mountain areas where harlequins breed. In fact, large areas appear pristine, and most breeding studies show normal or good local breeding success (e.g., Hunt and Ydenberg 2000).

Although much of the western cordillera appears pristine, there have been widespread introductions of fish, especially of rainbow trout, including the harlequin breeding streams in our study area (Conlin 1994; Griffith 1994; Krzesinska 1995; Stockwell 2002). Although the rainbow trout is endemic to western North America, there are many streams and lakes that it could never naturally colonize because of geographic barriers. It has, however, been subsequently introduced (as have other species) into many of these previously fishless waters. Many of these introductions, which were sanctioned, sponsored, and vigorously promulgated by state and provincial agencies, in addition to numerous enhancement programs, continue to present day. A large number of unrecorded and accidental introductions must have occurred as well.

Rainbow trout have been introduced to at least 82 countries (Horne and Goldman 1994), and are considered a major threat to biodiversity and to conservation efforts (Cambray 2003). This is because the addition of new species may have large effects when they exploit resources already being used by other species, and the introduction of even low densities of non-native predators into novel areas can cause a response in the entire prey populations (Kohler and McPeck 1989; Townsend 1996; Werner and Peacor 2003; Preisser et al. 2005). For example, the widespread introduction of brown trout (*Salmo trutta* L., 1758) across New Zealand since the 1860s has resulted in the displacement of native galaxiid fish species and has caused fixed antipredator behaviours to evolve in the siphonurid mayflies (McIntosh and Townsend 1994).

We suggest that the widespread introduction and enhancement of fish populations into historically fishless reaches of western North America could have caused a reduction of food available to harlequins, resulting in reduced quality of many breeding locales. In the Maligne River system, trout and char were successfully stocked into Maligne Lake in the 1920s. 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 a subsequent reduction in use by breeding harlequins has been hypothesized to be the result of this introduction (McCutchen 2002). Within our study area several successful stocking efforts have resulted in rainbow trout residing in previously fishless, the breeding reaches of harlequins. The effects of these introductions may also have contributed to range contraction of harlequins that has occurred in the northwestern United States (Robertson and Goudie 1999). The pervasive

nature of this impact and its potential negative effect on productivity and recruitment could be contributing to population decline for harlequins in western North America.

Fish introduction throughout North America may be contributing to widespread population declines in many species of waterfowl. It has been shown that spring migrating lesser scaup have reduced their use of their preferred amphipod prey owing to a reduction in amphipod availability in the presence of fish predation (Anteau and Afton 2006; Strand et al. 2008). In the Western Boreal Forest wetlands, the introduction of brook stickleback (*Culaea inconstans* (Kirtland, 1840)) resulted in the reduction of predaceous invertebrates, which act as a major food source to mallard (*Anas platyrhynchos* (L., 1758)) ducklings (Hornung and Foote 2006). The reduction in prey availability owing to extensive fish introduction may result in the overall decline to breeding success for waterfowl now forced to share their breeding and migrating grounds.

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