

# Fish and harlequin ducks compete on breeding streams

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**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 actuellement

ité des habitats de reproduction.

## 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*

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 (cm<sup>2</sup>) 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/m<sup>2</sup>), 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)

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.

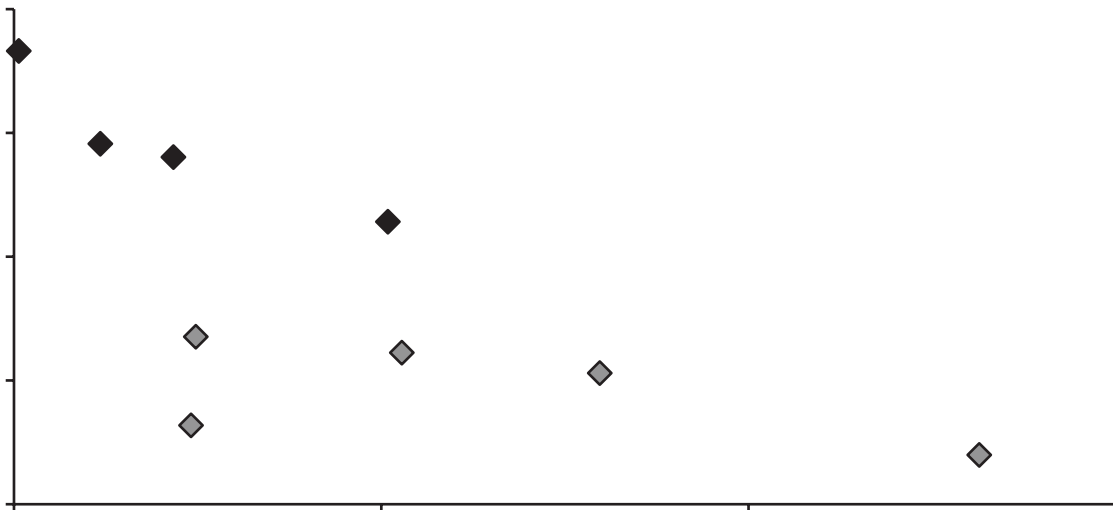
### Fish indices

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 Artedi, 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

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

flow variability and aquatic insect abundance, and between



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

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 dif-

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 suc-



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