

# Aggregative response of Harlequin Ducks to herring spawning in the Strait of Georgia, British Columbia

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**Abstract:** We determined the scale of aggregative response of Harlequin Ducks (*Histrionicus histrionicus*) to seasonally and locally superabundant prey at Pacific herring (*Clupea pallasii*)

more realistic models admit that individuals may suffer movement costs and be constrained by imperfect information (Stephens and Krebs 1986; Kennedy and Gray 1997). Such costs may limit access to superabundant food supplies and may mean that some individuals lose access to the resource when its availability changes.

The Pacific herring (*Clupea pallasii*) is an important prey species for marine birds in southern British Columbia (Hay et al. 1989), and consumption of herring eggs is intense during spawning periods. Herring spawn mainly in protected intertidal and shallow subtidal waters in late winter and spring (Grosse and Hay 1988). Large spawns can be many kilometres long, with depositions of  $10^6$  eggs/m<sup>2</sup> or more — the equivalent of 2–3 kg/m<sup>2</sup> of eggs. Spawning is usually a conspicuous event: the water turns milky white from milt and the activity may attract thousands of marine mammals and seabirds to feed on both spawning fish and spawned eggs. Aggregations of 50 000 – 300 000 waterbirds, mostly gulls (*Larus* spp.), sea ducks, and other diving species, have been observed at annual herring spawning events in British Columbia (Campbell et al. 1990; Haegele 1993).

Other than counts of bird aggregations and dietary data showing consumption of spawn (Haegele 1993; Vermeer et al. 1997; Rodway and Cooke 2002), there is little detailed information on the use of herring spawn by any marine bird species. This is surprising given that herring spawning is such a conspicuous event. Also, the high energy content of eggs may provide substantial benefits by increasing survival rates and fuelling migration and reproduction (Munro and Clemens 1931; Bayer 1980; Vermeer 1981). Therefore, the consequences for marine birds of the recent spatial and temporal contraction of spawning (Hay and McCarter 1999), and the periodic fisheries-related collapse of herring stocks, are unknown. Sea ducks in the North Pacific Ocean are the focus of recent management concern (Goudie et al. 1994), and there is a need for studies of marked birds to determine how individuals use spawn and the proportion of total populations that use it, whether movements to herring spawning sites are part of the migration to the breeding grounds, and whether access to spawn increases survival rates and breeding success. In this paper we examine the use of herring spawn by Harlequin Ducks (*Histrionicus histrionicus*) in the Strait of Georgia, British Columbia.

Our specific objectives were to determine (i) if Harlequin Ducks aggregate at herring spawning grounds, and if so, at which locations, (ii) the proportion of the Harlequin Duck wintering population that uses spawn, (iii) the origin of aggregating birds and the distances over which they move, (iv) the duration of individuals' stay at spawning sites, (v) whether moving to herring spawn is part of the migration to the breeding grounds or simply a shift in winter habitat use, and (vi) annual consumption of herring spawn by Harlequin Ducks in the northern Strait of Georgia.

## Methods

### Direct counts

The study was conducted throughout the northern Strait of Georgia and at White Rock (Fig. 1) during the winter and spring of 1998–2001, at Hornby Island during spawning (March) in 1995–1997, and at Hornby Island and the adja-

cent Vancouver Island shore in March 2002. Numbers of Harlequin Ducks wintering in the study areas were determined during a complete survey of the northern Strait of Georgia and White Rock conducted during the winter (November–February) in 1999–2000 (Rodway et al. 2003; M.S. Rodway, unpublished data). Repeated counts at sampling areas that were accessible by road were used to determine changes in numbers of birds before (January and February), during (March), and after (April) herring spawning. The occurrence and timing of herring spawning were determined during our shoreline surveys, complemented by data from Fisheries and Oceans Canada (DFO 2002).

Counts of small flocks of Harlequin Ducks were straightforward and are likely quite accurate because we did not conduct counts in compromising weather or sea conditions and birds generally were close to shore. Large flocks that aggregated at Hornby Island during spawning were more difficult to count and numbers were usually estimated by counting by 10s. In 1998–2001, we calculated the maximum flock size for these aggregations by averaging repeated estimates made at the time the flock was judged to be at its largest. Sample sizes for these mean counts were thus the number of estimates made of the same flock. Standard deviations for these maximum counts indicate the variation in our estimates and should not be misconstrued as indicating variation in the numbers of birds present. In 1995–1997 and 2002, only one estimate was made of maximum numbers at Hornby Island during spawning in each year.

### Population estimates from mark–recapture analyses

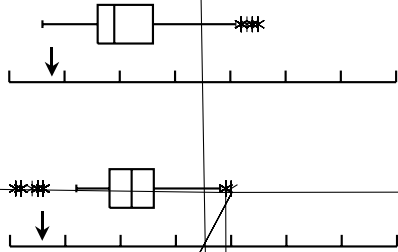
Since 1993, about 3500 Harlequin Ducks have been captured during their postbreeding moult in the Strait of Georgia or on their breeding streams. Beginning in 1994, captured birds were leg-banded with two-digit alphanumeric colour bands and standard U.S. Fish and Wildlife Service (USFW) metal bands. Birds captured in 1993 received colour bands without an identifiable code. Nasal tags with unique colour–shape combinations were also put on 457 birds in 1997–2000. The main coastal banding locations have been Hornby Island, Comox, Campbell River, Quadra Island, and White Rock (Fig. 1). Since 1995, and especially from 1998 to 2001, a great effort has been made by numerous persons to resight marked birds on Hornby Island during herring spawning (Fig. 2). Harlequin Ducks spend more time hauled out on shoreline rocks at this time, and there is a high probability of a banded bird being identified if it is present (see below).

Maximum counts at Hornby Island during spawning did not indicate the total numbers of birds moving there for herring spawn because there was a turnover of birds due to variation in when individuals arrived and how long they stayed. We followed Jolly (1965) to estimate this total population ( $\hat{N}_t$ ) during each annual spawning period,  $t$ , using the relationship

$$\hat{N}_t = \frac{\hat{M}_t}{\hat{\alpha}_t} \cdot 2.8 \text{ (probability)}$$

where

where  $m_t$  is the number of marked birds actually resighted, which was simply the number of banded individuals identified, and  $u_t$  is the number of marked birds present but not resighted. We could not estimate  $u_t$  using conventional mark-recapture methods (Seber 1982) because we were unable to assume that individuals not sighted at time  $t$  but sighted after time  $t$  were actually present at Hornby Island at time



ible at close range. Unreadable colour bands included those that were too worn to allow their alphanumeric code to be read, those without a code, and those that birds had lost. We then compared  $B_w$  with our estimate of  $u_r$ . These two measures should be similar if most readable bands were being identified.

**Movement of birds**

Movements of birds to herring spawning sites were determined through resightings of marked individuals. Two of us (M.S. Rodway and H.M. Regehr) spent much of the winter in 1998–1999 and 1999–2000 identifying marked birds throughout the northern Strait of Georgia. We combined data from those 2 years to determine where birds wintered that came to feed on herring spawn in the spring, what proportion of these wintering populations moved to spawning sites, and how this proportion related to the distance birds had to travel. The high cost in labour and time of collecting these data made it impractical to obtain enough data to be able to estimate annual movement probabilities among all our study locations using multistratum mark–recapture analyses (Brownie et al. 1993). We were able to directly estimate parameter values typically obtained from capture–mark–recapture analyses in order to answer these questions, but were unable to determine error rates associated with these values. However, the proportional values generated are comparable among areas and with future data using analyses of frequencies.

We estimated the numbers of birds moving to location A from wintering area C:

$$[1] \quad \hat{N}_{C \rightarrow A} = N_C \left( \frac{m_{C \rightarrow A}}{m_C R_A} \right)$$

where  $N_C$  is the total number of wintering birds at location C, determined during our winter surveys,  $m_C$  is the number of marked individuals identified at location C during the winter,  $m_{C \rightarrow A}$  is the number of marked individuals identified at location C during winter that were identified at location A during spawning, and  $R_A$  is the probability of resighting a marked bird at location A during spawning.

$$R_A = \frac{m_A}{\hat{M}_A - B_w \hat{M}_A}$$

where  $m_A$  is the number of banded birds identified at location A,  $\hat{M}_A$  is the total number of birds predicted to have bands at location A, and  $B_w$  is the proportion of bands that were unreadable (see above). At all locations other than Hornby Island,

$$\hat{M}_A = N_A \hat{\alpha}_A$$

where  $N_A$  is the total number of birds present and  $\hat{\alpha}_A$  is the proportion of birds with bands at location A, which we determined at each location as described above for Hornby Island. We had to subtract  $B_w \hat{M}_A$  from  $\hat{M}_A$  in the above equation to calculate  $R_A$  because  $\hat{\alpha}_A$  included bands that were not readable. We could not use this method at Hornby Island because the number of bands identified was higher than the number predicted, owing to birds moving through the area. At Hornby Island,

$$\hat{M}_A = m_A + u_A$$

where  $u_A$  is the number of marked birds present but not resighted, and is calculated as described above.

Equation 1 gives an accurate estimate of the total number of birds moving only if banded and unbanded birds are equally likely to move. We determined whether this was so by comparing, at each wintering location, the proportions of birds with bands in winter and during spawning. Proportions should remain the same if banded and unbanded birds were moving with equal probability. We also compared proportions of birds with bands at Hornby Island during winter and spawning to estimate the proportion of birds that were coming from marked populations.

**Distance travelled**

The distance from each location to Hornby Island that birds had to travel was taken as the shortest path over water between the midpoint on the northeast shore of Hornby Island and the midpoint of the respective location. Distances were measured to the nearest kilometre on a 1 : 80 000 scale marine chart.

**Duration of stay**

We subtracted the dates of first and last sightings (+1) in March and April to obtain the number of days that individuals were present at Hornby Island during spawning. We calculated duration of stay only for birds marked with nasal tags because they were the most readily identified. We confined our analysis to 1999 and 2000, when we had large

samples of birds marked with nasal tags and our resighting efforts spanned the spawning period (Fig. 2). We identified nasal-tagged birds that were winter residents on Hornby Island in those 2 years, and separated residents from immigrants in the analyses. Two-way ANOVA was used to test for differences between years and between residents and immigrants. Tolerance for Type I error was set at 5%. Values are given as the mean  $\pm$  SD.

### **Consumption of spawn**

The proportion of bands that were unreadable ( $B_u$ ) was 15.1% ( $N = 152$ ) and 15.8% ( $N = 133$ ) in 2000 and 2001, respectively. Using these proportions and the number of banded birds identified (Table 3) we calculated that 126 and 88 birds present at Hornby Island during spawning had bands that were unreadable in 2000 and 2001, respectively. These estimates of the number of bands that were unreadable were only slightly lower than the estimates made using regression analysis of the number of banded birds that were present but not identified ( $u_i$ ) in 2000 and 2001 (Table 3). This increased our confidence that most marked birds with readable bands present on Hornby Island during spawning were identified in those years and, by extension, in other years.

### Origin of birds aggregating for spawn

The majority of marked birds seen at Hornby Island during spawning in 1999 and 2000 came from nearby wintering areas at Denman Island, Comox, Qualicum, and Baynes Sound (Table 4). Some marked birds travelled 64 km from Quadra and Cortes islands in the north, and a single bird travelled 150 km from White Rock in the south (Fig. 1). Estimated numbers of birds coming from marked populations made up 68% of the numbers of birds present at Hornby Island for spawn. On Hornby Island, birds that wintered on the south and west sides moved to the northeast side during spawning more frequently (58% of known banded birds,  $N = 53$ ) than the reverse (12%,  $N = 82$ ;  $\chi^2_1 = 32.6$ ,  $P < 0.001$ ).

There were also movements to areas other than Hornby Island during spawning (Fig. 1). We calculated resighting probabilities ( $R_A$ ) during spawning of 48% ( $N = 58$ ), 65% ( $N = 65$ ), 95% ( $N = 77$ ), 47% ( $N = 71$ ), and 44% ( $N = 109$ ) for Quadra Island, Campbell River, Comox, Denman Island, and Qualicum, respectively. Using these probabilities, we es-

timated movements of over 50 birds to Campbell River from Quadra Island, to Denman Island from Qualicum, and to Qualicum from both Comox and Denman Island. We estimated that 10 winter residents from Hornby Island moved to Denman Island and Comox during spawning, and 24 birds from Hornby Island moved back and forth between Hornby Island and Qualicum, Comox, or Denman Island.

The accuracy of our calculations of the number of birds that moved from each wintering location during spawning depends on the assumption that banded and unbanded birds were equally likely to move. Combined data from 1998–2001 indicate that proportions which were banded did not vary among winter, spawning, and spring at locations other than Hornby Island, and averaged 12.9% at Quadra Island ( $\chi^2_2 = 2.5$ ,  $P = 0.3$ ,  $N = 263$ ), 19.9% at Campbell River ( $\chi^2_2 = 0.6$ ,  $P = 0.7$ ,  $N = 533$ ), 19.0% at Comox ( $\chi^2_1$

	No. in winter (mean $\pm$ SD) <sup>a</sup>	Maximum number during March and April <sup>b</sup>				
		1998	1999	2000	2001	2002
Northeast side						
Grassy	48 $\pm$ 27 (9)	97 (11)*	196 (5)*	117 (19)*	14 (10)*	97 (23)
Squeaker	44 $\pm$ 15 (9)	<b>1650</b> (11)*	<b>3172</b> (23)*	62 (8)	<b>1140</b> (15)*	98 (23)

with bands for those 2 years (21.2%; Table 3) was significantly higher ( $\chi^2_1 = 57.6$ ,  $P < 0.001$ ). Balancing this discrepancy would require that 19.2% of the birds that came to Hornby Island from areas other than those accounted for in Table 4 were banded. Our data indicate that only 3.2% of birds were banded in other parts of the northern Strait of Georgia.

The above results suggest that banded and unbanded birds were equally likely to come to Hornby Island for spawn from study locations where birds have been captured and banded during their postbreeding moult, but that banded birds were more likely than unbanded birds to come to Hornby Island for spawn from other locations where we have not banded birds. Because banded birds wintering at those other areas must have been banded at one of our study sites, it is possible that birds that disperse from the banding sites where they moulted are more likely to return for spawning than those that moult elsewhere. We could not test this idea for birds from these distant areas, but we did have sufficient data to test it for birds that wintered at Bh



of Hornby Island during herring spawning. Aggregations occurred in only a small portion of the total spawning area. The northeast side of Hornby Island was not included in Haegele's (1993) study area, which explains why he failed to detect an increase in Harlequin Duck numbers during spawning. Our results indicate that 49–81% of the midwinter

and pairing behaviour of Harlequin Ducks are currently under study (M.S. Rodway, unpublished data). Benefits to survival and reproductive success seem likely and warrant investigation for all waterbird species that feed on herring spawn.

Our knowledge of the winter ecology and habitat needs of Harlequin Ducks would be enhanced if we understood why they are particularly attracted to northeast Hornby Island during herring spawning. Reasons may relate to the history of spawning in that area in recent years, accessibility of spawn in relation to depth and substrate type, roosting habitat, disturbance, or competition with other marine bird species. Birds may traditionally gather at locations where spawn has been most abundant and most consistently deposited over recent years. The accessibility of spawn to Harlequin Ducks may vary among areas because of differences in substrate type or depth of spawning. The littoral substrate along northeast Hornby Island is mainly a mix of cobble and bedrock, whereas there is more sand and gravel along much of the Vancouver Island and Denman Island shorelines, where herring also spawn. Our observations in intertidal habitat suggest that spawn may weather differently on these different substrates, tending to mix in with a gravel substrate when impacted by wave action. This may reduce the accessibility of spawn to Harlequin Ducks, which feed mainly in shallow intertidal and subtidal habitat. Other sea duck species that were seen in large flocks in other areas fed in slightly deeper waters, where spawn may be less likely to be weathered by wave action. The northeast shore of Hornby Island provides some shelter from prevailing winds and wave action, but not more than other nearby areas where spawn is deposited. In fact, we have seen rafts of several thousand Harlequin Ducks riding out waves in gale-force winds along the northeast shore of Hornby Island when just

