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

**Michael S. Rodway, Heidi M. Regehr, John Ashley, Peter V. Clarkson, R. Ian Goudie, Douglas E. Hay, Cyndi M. Smith, and Kenneth G. Wright**

**Abstract:** We determined the scale of aggregative response of Harlequin Ducks (*Histrionicus histrionicus*) to seasonally and locally superabundant prey at Pacific herring (*Clupea pallasi*) spawning sites in the northern Strait of Georgia, British Columbia, in 1995–2002. Aggregations of 3400–5500 birds gathered at a small number of sites along the same 8-km stretch of shoreline each year that spawn was available there. Aggregations occurred in only a small fraction of the habitat area where spawn was available. Duration of stay at spawning sites averaged 2–3 weeks and many birds returned to their wintering grounds afterwards. Birds moving to spawning sites represented 55–87% of the total wintering population. The proportion of local wintering populations that moved to spawning sites was negatively related to the distance they had to travel, and few birds travelled farther than 80 km. The decline in proportions moving with increasing distance suggests that more distant individuals may be constrained by a lack of information or that there are trade-offs between the benefits of exploiting spawn and the costs of movement. This raises a conservation concern because the temporal and geographic range of herring spawning in British Columbia is contracting and some wintering waterbird populations may be losing access to this important late-winter food.

**Résumé :** Nous avons déterminé l'échelle de la réaction de regroupement de canards arlequin (*Histrionicus histrionicus*) à une surabondance saisonnière et locale de proies sur les frayères de harengs (*Clupea pallasi*) dans la partie nord du détroit de Géorgie en Colombie-Britannique de 1995 à 2002. Des rassemblements de 3400–5500 oiseaux se forment à un petit nombre de sites le long de 8 km de rive chaque année que la fraye s'y produit. Les rassemblements ont lieu dans seulement une petite fraction de l'habitat où se fait la fraye. La durée de séjour aux sites de fraye est en moyenne de 2–3 semaines et plusieurs des oiseaux retournent ensuite à leurs quartiers d'hiver. Les oiseaux qui se rassemblent aux sites de fraye représentent 55–87 % de la population totale d'hiver. Le pourcentage de la population locale d'hiver qui se déplace vers les sites de fraye est en corrélation négative avec la distance à parcourir et peu d'oiseaux se déplacent de plus de 80 km. Le pourcentage qui diminue avec l'accroissement de la distance indique que les oiseaux plus éloignés peuvent être limités par un manque d'information ou alors qu'il y a des compromis entre les bénéfices reliés à l'utilisation de la fraye et les coûts du déplacement. Il y a donc ici un problème de conservation parce que les étendues temporelle et spatiale de la fraye du hareng en Colombie-Britannique se réduisent et certains populations d'hiver d'oiseaux aquatiques peuvent donc perdre leur accès à cette importante nourriture de fin d'hiver.

[Traduit par la Rédaction]

## Introduction

Many animals exhibit an aggregative response to the abundance of an ephemeral resource and may depend on seasonally superabundant prey for fueling migration or reproduction or for survival (Botton et al. 1994; Hilderbrand et al. 1999; Restani et al. 2000). Determining or predicting the conse-quences for predator populations of changes in abundance or distribution of such prey requires an understanding of the scale of the aggregative response in terms of the proportion of the population involved and the distances over which they move to exploit the prey. "Ideal-free" models of habitat selection assume that individuals are free to aggregate at a highly profitable resource (Fretwell and Lucas 1970), but

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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 pallasi*) 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$^2$ or more — the equivalent of 2–3 kg/m$^2$ 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).
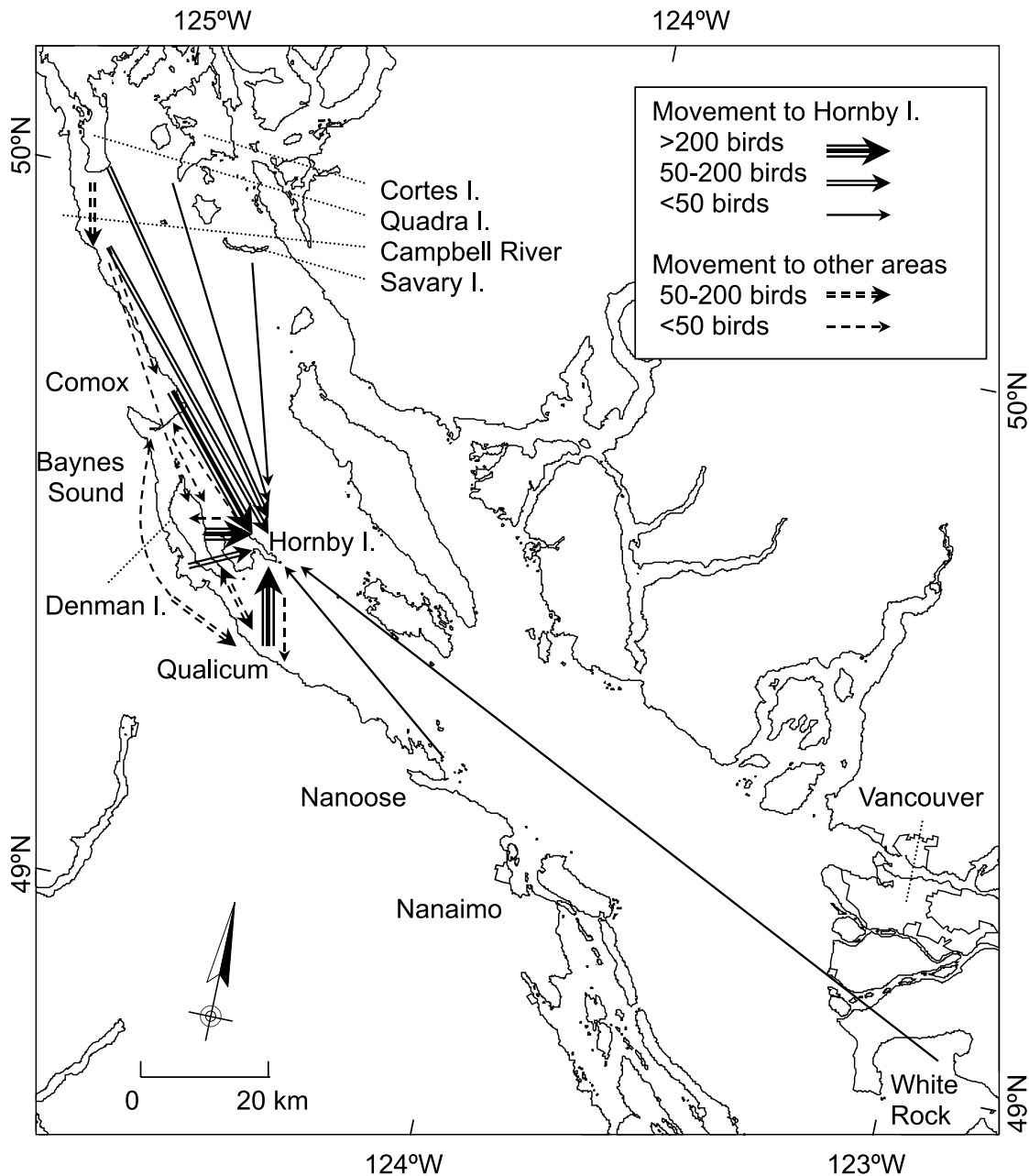
Maximum counts at Hornby Island during spawning did not indicate the total numbers of birds moving there for herring spawn because there was a turnover of birds due to variation in when individuals arrived and how long they stayed. We followed Jolly (1965) to estimate this total population ($\hat{N}_t$) during each annual spawning period, $t$, using the relationship

$$\hat{N}_t = \frac{\hat{M}_t}{\hat{\alpha}_t}$$

where $\hat{M}_t$ is the size of the marked population and $\hat{\alpha}_t$ is the proportion of birds marked.

$$\hat{M}_t = m_t + u_t$$

**Fig. 1.** Locations of study areas and movement of Harlequin Ducks (*Histrionicus histrionicus*) from their wintering areas to Pacific herring (*Clupea pallasi*) spawning grounds in the Strait of Georgia, British Columbia, in March of 1999 and 2000.



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 $t$ either between years or within years. To obtain an estimate of $u_t$ we fit the regression
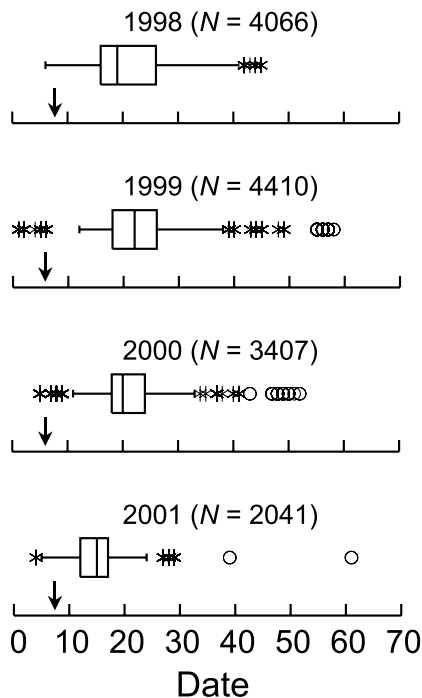
$$\ln Y = b_0 + b_1(X)$$

where $X$ is the number of sightings per bird and $Y$ is the frequency of birds with that number of sightings. The estimate of $u_t$, the frequency of birds with zero sightings (i.e., when $X = 0$), is then given by $\exp(b_0)$. Linear regression lines were fit to the log-transformed $Y$ values in SPSS 8.0. We determined $\hat{\alpha}_t$ by scanning groups of birds whose legs were visible. We only included in the sample those birds for which the tarsi of both legs were entirely visible because it is easier to see that a bird is banded than to confirm that it has no band when only part of the tarsi are seen. Scans were conducted throughout the spawning period.

We tested our assumption that most birds with identifiable bands present at Hornby Island during spawning were actually identified. We first determined the proportion of colour bands that were unreadable ($B_w$) in 2000 and 2001 by telescopic inspection of samples of birds whose bands were vis-

**Fig. 2.** Box plots showing band-reading effort over the herring spawning period on Hornby Island, British Columbia, in 1998–2001 (1 = 1 March). The arrow on the *x* axis shows the date of first spawning. *N* is the total number of resightings of marked Harlequin Ducks.



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 $u_t$. 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:

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

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, $m_{C \to A}$ 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

**Table 1.** Comparison of counts of Harlequin Ducks (*Histrionicus histrionicus*) during winter (January–February), spawning (March), and spring (April) in sampling areas in the Strait of Georgia, British Columbia, in 1998–2001.

|  | Winter | Spawning | Spring |
|---|---|---|---|
| Quadra Island | 590 (1) | 470 (1) | 479 (1) |
| Campbell River | 373 ± 73 (5) | 265 ± 52 (4) | 358 (1) |
| Comox | 378 ± 101 (7) | 298 ± 86 (5) | 418 (1) |
| Denman Island | 148 ± 52 (2) | 108 (1) | 222 (1) |
| Hornby Island | 612 ± 89 (7) | 2972 ± 958 (52) | 927 ± 442 (6) |
| Qualicum | 751 (1) | 505 ± 88 (2) | — |
| White Rock | 61 ± 10 (6) | 94 ± 14 (5) | 67 ± 24 (5) |

**Note:** The sampling areas where Harlequin Ducks were counted repeatedly were often a subset of the total areas whose winter populations are presented in Table 4. Values are given as the mean ± SD, with the sample size in parentheses.

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 ± SD.

### Consumption of spawn

Daily consumption of herring spawn was estimated using the equation

$$F = 0.51W^{0.85}$$

where $F$ is daily food consumption (g) and $W$ is bird mass (g) (Nilsson and Nilsson 1976; Haegele 1993). Weighting by a male:female ratio of 1.51 (Rodway et al. 2003), we calculated the mean mass of adult Harlequin Ducks to be 611 g from a sample of 586 females (569 ± 31 g) and 1204 males (638 ± 37 g) captured during their postbreeding moult in the Strait of Georgia. Total spawn consumed was given by $F$ times the number of days that birds fed on spawn times the total number of birds present.

## Results

### Locations and timing of spawning aggregations

Harlequin Ducks in the northern Strait of Georgia aggregated in only a small portion of the area where herring spawn was available. In the years 1998–2001, increases in numbers of Harlequin Ducks during herring spawning occurred mainly at Hornby Island (Table 1). Numbers at other Harlequin Duck wintering sites in the northern Strait of Georgia declined, even at Comox, Denman Island, Baynes Sound, and Qualicum, where herring also spawned. There were brief increases at other spawning locations if spawning occurred there earlier than at Hornby Island. For example, herring spawned near Comox on 6 March and at Hornby Island on 7 March in 2001. Numbers of Harlequin Ducks in the Comox area increased from 433 to 578 on 6 March, then declined to 347 on 7 March coincident with an increase in numbers at Hornby Island. In 2002, herring did not spawn at Hornby Island and spawned mainly along the Vancouver Island shore (DFO 2002). Compared with wintering populations, there was no increase in Harlequin Duck numbers at

Hornby Island or elsewhere that year, and the largest aggregation of Harlequin Ducks we found at other sites where herring did spawn was 156 near Qualicum on 30 March.
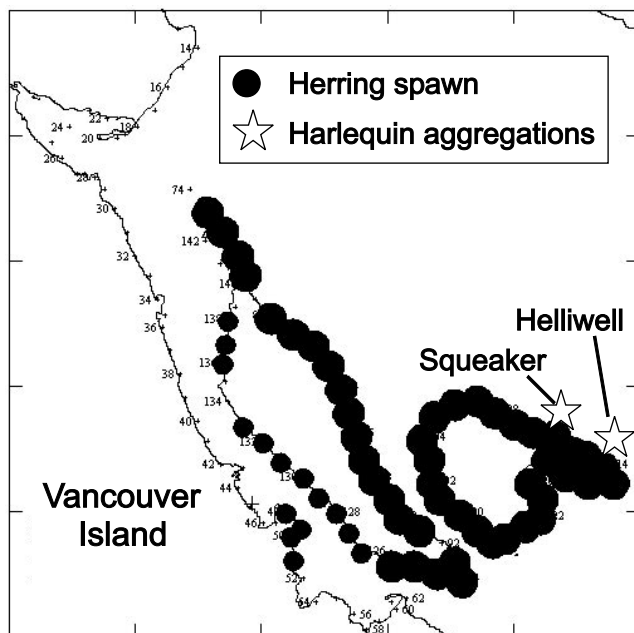
At a smaller scale at Hornby Island, birds also aggregated in only a portion of the habitat where spawn was available (Fig. 3). Most birds present during spawning aggregated into one or two large flocks (Table 2). The location of those aggregations varied among years and was related to the location and timing of spawning. Aggregations occurred only at sites where spawn was available. Again, similar to events at the larger geographic scale, there were brief increases at some sites where spawning occurred first. For example, numbers increased at Grassy and Phipps when spawning occurred there on 5 March 1999, but decreased again after herring spawned nearby at Squeaker on 6 March (Table 2). The largest persistent aggregations were seen at Squeaker, Anderson, or Helliwell in all years, but did not necessarily occur at all those sites in any one year, even if spawn was available at all of them. Among those sites, numbers first increased where herring first spawned. In 1998, herring spawned at Squeaker on 7 March and at Anderson and Helliwell on 11 March. Numbers initially increased at Squeaker to a maximum of 1650, then gradually declined at Squeaker and increased at Helliwell during the 2 weeks after 11 March (Fig. 4). Smaller aggregations on the south and west sides of the island generally occurred later, often in April, after most herring eggs would have hatched, except in 2000, when spawning was less extensive along the northeast side (Table 2).

The aggregative response by Harlequin Ducks was immediate, numbers often increasing at a particular location on the same day spawning occurred, but maximum flock sizes were not reached until several days after spawning (Fig. 4). In no cases did we witness birds aggregating prior to herring spawning.

### Size of spawning aggregations

Direct counts gave maximum estimates of between 2114 and 5000 birds at Hornby Island during spawning over the years 1995–2001 (Table 3). Fitting the regression $\ln Y = b_0 + b_1(X)$ to estimate the number of banded birds missed ($u_t$) gave $r^2$ values of 0.88, 0.95, 0.96, 0.86, 0.96, and 0.95 for the consecutive years 1996–2001, respectively. Estimates of the total number of birds that used Hornby Island during spawning in 1996–2001 ranged from 3400 to 5500 (Table 3).

**Fig. 3.** Location of herring spawning and Harlequin Duck aggregations in the Hornby Island and Denman Island area, British Columbia, in March 1998. Herring spawning data are from DFO (2002).
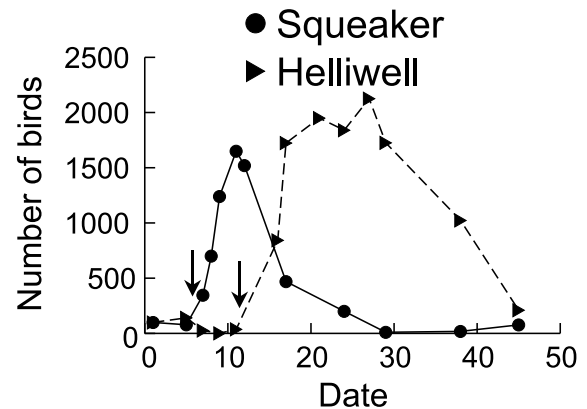


**Fig. 4.** Timing of Harlequin Duck aggregations relative to herring spawning at sites on Hornby Island, British Columbia, in March 1998 (1 = 1 March). The arrows indicate the dates when herring spawned at the two locations.



The proportion of bands that were unreadable ($B_w$) 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 ($u_t$) 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%, $N = 82$; $\chi_1^2 = 32.6$, $P < 0.001$).

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 ($\chi_1^2 = 1.4$, $P = 0.5$, $N = 1028$), 20.3% at Denman Island ($\chi_2^2 = 0.8$, $P = 0.7$, $N = 128$), 15.5% at Qualicum ($\chi_1^2 = 3.4$, $P = 0.07$, $N = 142$; no spring samples were obtained), and 3.2% ($N = 248$; numbers of banded birds were too small for $\chi^2$ tests) at all other areas in the northern Strait of Georgia. The overall average proportion of birds with bands at Quadra Island, Campbell River, Comox, Denman Island, and Qualicum was 19.6% ($N = 832$) in winter and 18.3% ($N = 847$) during spawning ($\chi_1^2 = 0.5$, $P = 0.5$). These similar proportions in winter and spawning indicate that banded and unbanded birds were equally likely to move from these locations.

In contrast, seasonal changes in proportions of birds with bands on Hornby Island suggest that banded birds were more likely to move there during spawning than unbanded birds. On Hornby Island, proportions with bands differed among seasons and were 30.7% ($N = 758$), 21.7% ($N = 5045$), and 24.8% ($N = 290$) in winter, spawning, and spring, respectively ($\chi_2^2 = 16.3$, $P < 0.001$). Considering that 30.7% of the 706 wintering birds that stayed at Hornby Island for spawn, and 19.6% of the 2291 birds wintering at other study locations that came to Hornby Island for spawn in 1999–2000 (Table 4) were banded, the number of banded birds from those locations that came to Hornby Island for spawn would have been 666. This would equal 15.0% of the average number of birds (4429) estimated to come for spawn in 1999 and 2000 (Table 3). The observed proportion of birds

**Table 2.** Mean wintering numbers and maximum aggregations of Harlequin Ducks during herring spawning at four sites on the northeast side and four sites on the south and west sides of Hornby Island, British Columbia, in 1998–2002.

| | No. in winter (mean ± SD)[a] | Maximum number during March and April[b] | | | | |
|---|---|---|---|---|---|---|
| | | 1998 | 1999 | 2000 | 2001 | 2002 |
| **Northeast side** | | | | | | |
| Grassy | 48 ± 27 (9) | 97 (11)* | 196 (5)* | 117 (19)* | 14 (10)* | 97 (23) |
| Squeaker | 44 ± 15 (9) | **1650** (11)* | **3172** (23)* | 62 (8) | **1140** (15)* | 98 (23) |
| Anderson | 25 ± 13 (10) | 548 (13)* | **834** (23)* | **1110** (19)* | **1150** (15)* | 74 (24) |
| Helliwell | 96 ± 53 (10) | **2126** (27)* | **514** (28)* | 67 (8)* | 45 (10) | 89 (23) |
| **South and west sides** | | | | | | |
| Sandpiper | 129 ± 44 (6) | 281 (45)* | 98 (39)* | **523** (29)* | 50 (10) | 82 (28) |
| Heron | 42 ± 27 (6) | 265 (45)* | 249 (39)* | 212 (19)* | 20 (10)* | 142 (28) |
| Ford's | 9 ± 5 (7) | 128 (45)* | 168 (28)* | 178 (19)* | 12 (10)* | 35 (18) |
| Phipps | 36 ± 29 (10) | 160 (8)* | 249 (5)* | 34 (19) | 61 (10)* | 49 (23) |

**Note:** The sites listed from top to bottom are ordered clockwise around the island, beginning at the northeast corner, and encompass similar linear extents of shoreline. Herring first spawned on Hornby Island on 7, 5, 6, and 7 March in 1998–2001, respectively. Numbers in boldface type denote aggregations that persisted at similar sizes for a week or more. Surveys during spawning were conducted through March and the first half of April in 1998–2000 and ended on 15 March in 2001 and 30 March in 2002.
[a]Numbers in parentheses are sample sizes.
[b]Numbers in parentheses show the date of maximum count (1 = 1 March). An asterisk indicates that spawning occurred at that site.

**Table 3.** Numbers of Harlequin Ducks at Hornby Island during herring spawning, estimated by direct counts and by proportions of banded birds, in 1995–2002.

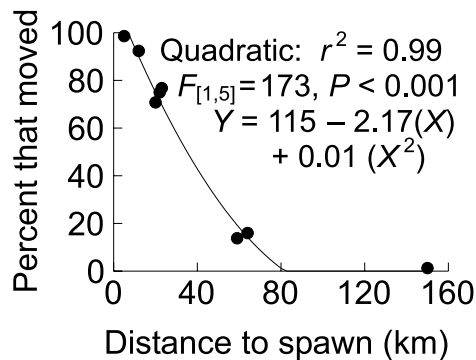| Year | Max. count during spawning (mean ± SD) | No. of banded birds identified ($m_t$) | Estimated no. of banded birds not identified ($u_t$) | Percentage of birds with bands ($\hat{\alpha}_t$) | Calculated total during spawning $((m_t + u_t)/\hat{\alpha}_t)$ |
|---|---|---|---|---|---|
| 1995 | 5000 (1) | 186 | — | — | — |
| 1996 | 2457 (1) | 497 | 474 | 24.2 (1040) | 4007 |
| 1997 | 2375 (1) | 679 | 285 | 17.5 (905) | 5522 |
| 1998 | 2655 ± 218 (13) | 801 | 258 | 26.5 (1226) | 3995 |
| 1999 | 4277 ± 545 (16) | 821 | 128 | 20.5 (2046) | 4623 |
| 2000 | 2114 ± 192 (9) | 711 | 212 | 21.8 (959) | 4235 |
| 2001 | 2325 ± 180 (14) | 467 | 135 | 17.9 (814) | 3356 |
| 2002 | 519 (1) | 110 | — | — | — |

**Note:** Herring spawned on Hornby Island in 1995–2001 but not in 2002. Numbers in parentheses are sample sizes.

**Table 4.** Proportions of marked wintering populations of Harlequin Ducks in the northern Strait of Georgia that moved to Hornby Island during herring spawning in 1999 and 2000.

| | Winter population size | Percentage of banded winter residents sighted on Hornby Island during spawning | Estimated total numbers that moved to Hornby Island | Percentage of total number of birds at Hornby Island for spawn |
|---|---|---|---|---|
| Quadra Island | 845 | 13.6 (22) | 141 | 3.2 |
| Campbell River | 524 | 11.7 (60) | 75 | 1.7 |
| Comox | 944 | 65.1 (129) | 754 | 17.0 |
| Baynes Sound | 105 | 60.0 (5) | 77 | 1.7 |
| Denman Island | 685 | 78.3 (23) | 658 | 14.9 |
| Hornby Island | 716 | 86.1 (238) | 706 | 15.9 |
| Qualicum | 751 | 63.6 (22) | 586 | 13.2 |
| White Rock | 65 | 1.1 (94) | 1 | 0.0 |

**Note:** Winter numbers are from a midwinter survey conducted in 1999–2000 (Rodway et al. 2003). The percentage of birds sighted on Hornby Island during spawning was adjusted by the average estimate (22.7%) of the proportion of marked birds that were present but not identified in 1999 and 2000 (see Table 3) in order to estimate total numbers that moved. The calculated average total number of birds at Hornby Island during spawning in 1999 and 2000 (4429; see Table 3) was used to estimate the percentage of the total number of birds at Hornby Island. Numbers in parentheses are sample sizes.

**Fig. 5.** Percentages of wintering Harlequin Duck populations in the Strait of Georgia, British Columbia, that moved to Hornby Island for herring spawn in 1999–2000 in relation to the distance the birds had to travel.



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 Comox and Campbell River. Birds wintering at Comox and Campbell River that moulted at Hornby Island were more likely to come to Hornby Island for spawn (83%, $N = 24$) than those that moulted at Comox and Campbell River (63%, $N = 78$; one-sided test, $\chi^2_1 = 3.53$, $P = 0.030$).

**Effect of travel distance**

The proportion of different Harlequin Duck wintering populations that moved to Hornby Island during herring spawning was strongly dependent on the distance birds had to travel. The relationship between the proportion of birds moving to Hornby Island and the distance they had to travel was quadratic and indicated that the percentage moving would approach zero at a distance of about 80 km (Fig. 5).

**Duration of stay during spawning**

The estimated number of days that immigrant birds stayed at Hornby Island during spawning ranged from 1 to 55 and was 22 ± 13 ($N = 81$) in 1999 and 11 ± 8 ($N = 106$) in 2000. Birds that spent the winter on Hornby Island were observed to be present for longer periods of time during spawning: 32 ± 15 d ($N = 37$) in 1999 and 18 ± 10 d ($N = 81$) in 2000. A two-way ANOVA indicated that differences were signifi-

cant between years ($F_{[1,301]} = 84.5$, $P < 0.001$) and between resident and immigrant birds ($F_{[1,301]} = 44.5$, $P < 0.001$). The difference between years may be partially attributable to lower resighting effort in 2000 than in 1999 (Fig. 2), but the difference in length of stay was much greater than the difference in effort and we are confident that the difference in the estimated lengths of stay was real. The longer duration of stay detected for resident birds also increases our confidence that the length of stay measured for immigrant birds was accurate.

**Where birds went after spawning**

Repeated counts at sample areas (Table 1) plus resightings of banded birds indicate that many birds return to their main wintering ground after coming to Hornby Island for spawn and prior to departing for breeding streams. Twenty-two birds that came to Hornby Island for spawn were resighted in April: 73% had returned to their winter residence and the rest were still on Hornby Island. Of 63 winter residents of Hornby Island resighted in April, 58 (92%) were still on Hornby Island, 2 were sighted at Comox, and 3 were seen inland.

**Consumption of spawn**

We calculated the amount of spawn consumed by Harlequin Ducks at Hornby Island in 1999 and 2000 and in the total spawning area in that vicinity in 1995–2001. Harlequin Ducks at Hornby Island appear to feed almost exclusively on herring spawn for 20 d and then partially on spawn for another 10 d after it is first deposited (Rodway and Cooke 2002). We thus assumed that birds fed entirely on spawn for an average of 25 d, which is similar to the average length of time Haegele (1993) estimated that spawn was available to marine birds in the area. Though the mean length of stay of immigrant birds at Hornby Island during herring spawning was less than this, we assumed that birds which moved away from Hornby Island went to other spawning locations as long as spawn was available. This assumption was justified because all movements from Hornby Island that we detected during the spawning period were to Denman Island, Qualicum, and Comox, where spawning also occurred. Consumption on Hornby Island was based on the numbers of resident and immigrant birds (Tables 3 and 4) and their respective mean durations of stay, to a maximum of 25 d, during spawning. Consumption in the entire area was based on the total numbers of birds that moved to Hornby Island for spawn (Table 3) plus the numbers at spawning locations on Denman Island, Baynes Sound, Qualicum, and Comox that did not move to Hornby Island (Table 4). Daily food consumption ($F$) per duck was calculated to be 119 g. Extrapolating gave estimates of 12.4 and 6.2 t of herring spawn consumed on Hornby Island in 1999 and 2000, respectively, and 16.2, 13.3, 17.8, 13.2, 15.1, 13.9, and 11.3 t of spawn consumed in the entire area in the years 1995–2001, respectively.

## Discussion

We found large aggregations of several thousand Harlequin Ducks gathering at few locations on the northeast side

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 population in the northern Strait of Georgia (Rodway et al. 2003) spent time at Hornby Island during herring spawning. The presence of Harlequin Ducks at other spawning sites suggests that 55–87% of the midwinter population exploited herring spawn in the northern strait in the years 1995–2001. Clearly, herring spawn is an important late-winter food for Harlequin Ducks in this area and probably throughout their Pacific range.

Birds aggregating at Hornby Island consumed an estimated 12.4 and 6.2 t of herring spawn in 1999 and 2000, respectively. In total, Harlequin Ducks consumed between 11.3 and 17.8 t of spawn annually in the larger spawning area between Comox and Qualicum. Haegele (1993) estimated the annual consumption of spawn by all waterbirds gathering along Denman and Hornby islands to be 198–216 t, representing 3–4% of the spawning biomass of herring in that area. Consumption by Harlequin Ducks is a small proportion of this total, but aggregation of Harlequin Ducks along northeast Hornby Island may have a greater local impact.

Maximum counts of Harlequin Ducks at Hornby Island during spawning underestimated total numbers coming there because there was a turnover of birds throughout the herring spawning period. The length of time that immigrant birds stayed at Hornby Island averaged 2–3 weeks, but varied considerably among individuals and between years. In the Hornby Island area, spawning is typically concentrated over a period of several weeks and eggs hatch within 2–3 weeks, making them available in large numbers to predators for 3–4 weeks (Haegele 1993). The difference between calculated estimates and maximum counts of numbers of birds was greater in 2000 than 1999. This was related to a shorter residence time for birds in 2000. Lower numbers, a shorter stay, and larger flocks on the south side of Hornby Island during spawning in 2000 were associated with less extensive herring spawning along the northeast shore of Hornby Island than in 1999 (DFO 2002). Fewer bands read and lower numbers estimated in 2001 were also associated with less extensive spawning on Hornby Island, but may also have been partially due to lower band-reading effort that year. In 2002, when herring did not spawn on Hornby Island, there were no large aggregations of Harlequin Ducks at Hornby Island or at other sites, even those where herring did spawn. Herring spawned extensively along the Vancouver Island shoreline that year (DFO 2002) and it is likely that Harlequin Duck populations from those areas that aggregated at Hornby Island in previous years remained dispersed in 2002. A number of birds from Hornby Island may have moved elsewhere for spawn in 2002 because the maximum count on Hornby Island during the spawning period was considerably lower than wintering numbers (see Tables 3 and 4).

Sixty-eight percent of birds at Hornby Island during spawning originated from study areas where birds were marked. The remainder probably came from populations wintering in the north and eastern strait and in the area south of Qualicum. Our data indicate that banded and unbanded birds were equally likely to come to Hornby Island for spawn from locations where Harlequin Ducks have been banded, but banded birds were more likely than unbanded birds to come from locations where we did not band. This apparent discrepancy can be explained by our finding that birds which moulted in the Hornby Island area were more likely to return there for spawn than those which moulted elsewhere. This tendency would result in more banded birds coming from more distant areas because the only banded birds present in those areas must have moulted elsewhere, at one of our banding sites. In contrast, marked birds in wintering populations at our banding locations included both birds that moulted there and those that moulted at one or more of the banding sites. Overall proportions of birds with bands did not change at those sites when birds moved to Hornby Island for spawn because the proportions of banded birds were similar in those two groups.

Harlequin Ducks migrate to their inland breeding grounds in late March, April, and May (Robertson and Goudie 1999). Counts at sample areas, and sightings of banded birds revealed that most of the wintering population is still at coastal habitats through much of April. Thus, for many or most Harlequin Ducks, moving to herring spawning grounds is not a way stop en route to the breeding grounds, but is a shift in winter habitat use to exploit a valuable short-term resource. Aggregations of a few hundred birds on the south and west sides of Hornby Island, which generally occurred in April after most herring eggs would have hatched, may have been associated with movements back to wintering grounds to the south of Hornby Island.

Aggregating Harlequin Ducks did not behave as ideal-free predators. The proportion of birds that moved to Hornby Island for spawn from other locations was strongly related to the distance birds had to travel. Few birds travelled more than 80 km. Why only some birds came and how they knew to go to Hornby Island is not known, although our finding that birds which moulted on Hornby Island were more likely to return there during spawning identifies a possible mechanism for some birds. The decline in proportions moving with increasing distance may result from differences in information among local populations. The activity of foraging flocks and the movement of birds to and from their nocturnal roosts several kilometres offshore (Rodway and Cooke 2001) may facilitate information transfer among adjacent populations. The time lag and reduced effectiveness of information transfer with increasing distance may explain why flock sizes increased for several days after spawning occurred and why the proportions of birds moving declined as travel distance increased. Alternatively, the trade-off between the costs of moving and the benefits of being at Hornby Island during spawning may vary among individuals.

Reductions in the number of herring spawning locations in the northern, eastern, and southern Strait of Georgia (DFO 2002) likely impose costs of greater movement distances or loss of access to spawn for Harlequin Ducks and other waterbirds wintering in those areas. Interestingly, White Rock was the only surveyed location other than Hornby Island where numbers of Harlequin Ducks increased during spawning (see Table 1). Herring used to spawn in the White Rock area but have not done so since 1992 (DFO 2002). The potential benefits of feeding on herring spawn to the social

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 around the corner were sheltered waters and abundant herring spawn.

The quality of roosting habitat may affect habitat choices. The shoreline of Hornby Island, with its sandstone shelves and offshore skerries, may offer more attractive roosting habitat for Harlequin Ducks than other spawning areas. This would not be as pertinent for other sea duck species because they do not haul out on shoreline rocks like Harlequin Ducks do. Disturbance of roosting birds by humans and dogs may be less on Hornby Island than on the extensive beaches of Vancouver Island, which are closer to larger human populations and easily accessible. Activity of the fishery, which during the years of this study occurred along Vancouver Island and along the south and west but not the northeast side of Hornby Island, may also disturb feeding and roosting birds, but only for short periods, as the fishery generally lasts only a few days.

Finally, competition with other marine birds may be a factor. We saw up to 300 Harlequin Ducks in mixed-species flocks with several thousand other sea ducks, and small numbers of Harlequin Ducks were frequently observed in multispecies flocks at herring spawn in the Queen Charlotte Islands (Vermeer et al. 1997). However, the large aggregations of Harlequin Ducks along northeast Hornby Island were primarily single-species flocks. Dense flocks of gulls often excluded or displaced Harlequin Ducks from roosting areas, and also foraged in the same intertidal habitat, but this

seemed to be as common on Hornby Island as elsewhere. Competitive exclusion seemed unlikely to be operating because of the extent of unused habitat where herring spawn was available.

Conservation of marine birds in increasingly populated and exploited environments like the Strait of Georgia requires careful management of the resources and habitats essential to their continued survival. Most Harlequin Ducks, and likely the majority of wintering populations of other sea ducks (Vermeer 1981), undertake seasonal movements to feed on herring spawn. It will thus be prudent to integrate the management of sea ducks with that of the herring fishery, as well as the management of any other extraction industry that affects the food supply or foraging habitat of waterbirds. Understanding the importance of herring spawn to wintering birds will help us predict the potential impacts of natural or human-induced climatic changes that may reduce the abundance of herring in these waters (Schweigert 1995; Alheit and Hagen 1997).

## Acknowledgments

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