Sex and age differences in distribution, abundance, and habitat preferences of wintering Harlequin Ducks: implications for conservation and estimating recruitment rates

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Abstract: We determined the sex- and age-specific distribution, abundance, and habitat preferences of wintering Harlequin Ducks (*Histrionicus histrionicus*) and evaluated potential biases in measuring ratios of immature males to adult males to estimate recruitment rates. A comparison of the occurrence of birds with habitat availability at the 1-km scale indicated a preference for wide intertidal habitat with cobble–gravel or bedrock–boulder substrate, small offshore islets and shoreline with attached or nearby reefs and islets, areas without streams, and areas with a greater historical abundance of herring spawn. Where the substrate was bedrock–boulder, birds preferred areas with tidal rapids. Densities of birds were highest along linear and complex shorelines with reefs or islets where intertidal habitat was >100 m wide and substrate was cobble–gravel or bedrock–boulder. Patterns of habitat use among sex and age classes were the same at the 1-km scale but differed at smaller scales, with adult and immature males occurring farther offshore than females. Age ratios varied among areas and were biased by survey method and misidentification of distant birds. Correcting for detected biases gave an estimated male age ratio of 9.8%. Calculated estimates of female recruitment suggest a declining population, but it is necessary to incorporate emigration in estimates of adult survival before demographic trends can be confidently inferred.

Résumé : Nous avons étudié la répartition, l'abondance et les préférences d'habitat spécifiques au sexe et à l'âge chez des canards arlequin (*Histrionicus histrionicus*) en hiver et évalué les erreurs possibles reliées à la mesure du rapport entre le nombre d'oiseaux immatures et le nombre de mâles adultes qui sert à évaluer le recrutement. L'évaluation de la présence des oiseaux en fonction de la disponibilité des habitats a mis en lumière les préférences des oiseaux, à l'échelle de 1 km, pour la zone intertidale large, à substrats de gros cailloux et de gravier ou de blocs et de rocher, pour les petits îlots au large de la côte et pour les rives rattachées à des récifs ou des îlots avoisinants, pour les zones sans ruisseaux et pour celles où les frayes de harengs ont été plus fréquentes dans le passé. Sur les substrats de blocs et de rocher, les canards préfèrent les zones de rapides de marée. C'est le long des côtes linéaires et complexes avec des îlots et des récifs, où la zone intertidale a plus de 100 m de largeur et le substrat est constitué de cailloux et gravier ou de blocs et de rocher, que les oiseaux se sont avérés le plus nombreux. Les patterns d'utilisation de l'habitat selon l'âge et le sexe étaient les mêmes à l'échelle de 1 km, mais ces patterns différaient à une échelle plus petite et les mâles adultes et les oiseaux immatures se tenaient plus loin des rives que les femelles. Le rapport entre les âges des oiseaux différaient d'un site à l'autre et son calcul comportait des erreurs dues aux méthodes d'échantillonnage et à l'identification erronée d'oiseaux lointains. La correction des erreurs connues a permis d'estimer à 9,8 % le rapport entre les âges des mâles. Les estimations du recrutement des femelles indiquent que la population est en déclin, mais il faut intégrer les données sur l'émigration des mâles dans les estimations de survie des adultes avant de conclure à une tendance bien définie.

[Traduit par la Rédaction]

Introduction

Information on distribution, demographics, and habitat use is vital for the conservation and management of any species. Many species show sex and age differences in habitat use that are related to differences in body size or dominance status (Fretwell 1972; Calder 1974; Gauthreaux 1978). In northern migratory waterfowl, females and immatures often winter farther south than males (Nilsson 1970; Nichols and Haramis 1980; Alexander 1983), or are relegated to lower quality patches at the local scale (Hepp and Hair 1984; Alexander 1987). Dominance behaviour of paired birds may exclude unpaired birds from preferred habitats (Boyd 1953; Paulus 1983). Habitat segregation can bias estimates of sex

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and age ratios used in demographic studies to determine effective population size and recruitment (Cowardin and Blohm 1992). Information on sex and age differences in habitat use allows the correction of biased estimates and the generation of unbiased sampling designs.

The sheltered marine waters, shorelines, and estuaries of the Strait of Georgia, British Columbia, provide winter refuge for regionally and globally significant populations of numerous waterbird and shorebird species (Butler and Vermeer 1989; Campbell et al. 1990a, 1990b). Since the area is also attractive to people, it has a burgeoning human population whose habitat use often directly conflicts with that of other species (Vermeer and Butler 1994). Management of these conflicts to ensure co-existence requires good information on the population size, habitat use, and demographics of sensitive species (Savard 1989). Our goal in this study was to provide some of this information for Harlequin Ducks (*Histrionicus histrionicus*) because their nearshore habits and low reproductive rate make them particularly vulnerable to the adverse effects of increasing human activity (Goudie et al. 1994).

Our specific objectives were to (*i*) determine the distribution and abundance of Harlequin Ducks wintering in the northern Strait of Georgia and identify areas of concentration; (*ii*) measure habitat preferences by relating the occurrence and abundance of birds to habitat availability; (*iii*) compare distributions and habitat use between the sexes and between immature males and adult males; (*iv*) assess the potential for misidentification of immature males; (*v*) evaluate the potential bias in estimating age ratios caused by differences in distribution or habitat use and by misidentification; and (*vi*) consider the implications of these factors and make recommendations for protecting habitat and conducting surveys to estimate age ratios.

Methods

Surveys

The study was conducted in the northern Strait of Georgia (Fig. 1) during winter 1999–2000, i.e., from 20 November to the end of February. All shorelines within the boundaries of the study area were surveyed once for Harlequin Ducks. We surveyed areas sequentially so that little time elapsed between surveys of adjacent areas, reducing the likelihood that birds would have moved. Also, our study area was large so that even if a few birds did move, this was unlikely to create directional bias in our population estimates or bird–habitat associations. Surveys were conducted from land whenever possible by one observer walking along the shore and scanning for birds with binoculars or a 20–60× spotting scope. In areas where the shoreline could not be walked, surveys were conducted by two observers (M.S. Rodway and H.M. Regehr) travelling along the shore in a 16-ft inflatable Zodiac. Often, one observer was set ashore to walk short accessible sections of shoreline, or just to obtain a solid platform from which to scan for birds. Surveys were not conducted in rough weather, when wind or rain might have reduced our ability to detect birds. We scanned as far as we could with a 60× spotting scope to be sure that we were not missing birds that were unusually far offshore. We estimated the distance of a bird offshore from the current waterline within four categories: 1

(<10 m), 2 (10–50 m), 3 (50–300 m), and 4 (>300 m). Because the waterline changed with the tide, these distances did not correspond to any particular tide level.
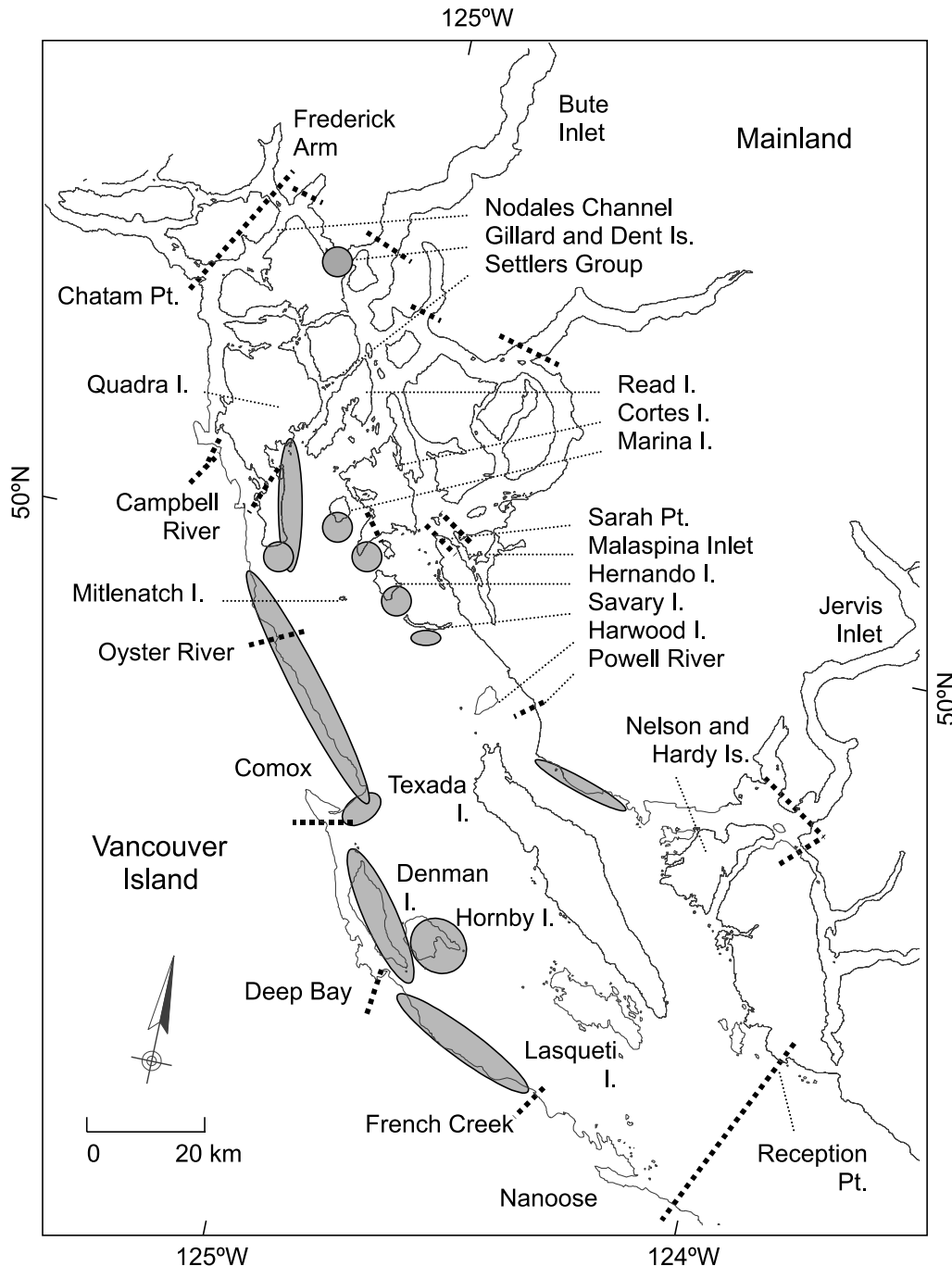
Sex and age ratios

We classified birds as female, adult male, or immature male, based on plumage characteristics (Smith et al. 1998). The sex ratio equalled the ratio of the total number of males to the total number of females. The male age ratio equalled the ratio of immature males (first winter) to adult males (second winter and older) expressed as a percentage. This differs from the age ratios calculated by Smith et al. (2001), who used the ratio of immature males to the total number of males, but is similar to fall age ratios commonly calculated for waterfowl species as the ratio of fledgling females to adult females (Cowardin and Blohm 1992). The alternate I plumage of immature males varies among individuals from female-like to male-like, and for a particular individual appears to remain similar throughout the winter (Smith et al. 2001; M.S. Rodway and H.M. Regehr, unpublished data). We described immature-male plumage using a subjective 5-point scale where 1 was female-like and 5 was adult-male-like. Immature males received a score of 1 if they were indistinguishable from females except for crescent-shaped loral patches and faint traces of white neck or chest stripes. Birds given a score of 5 differed little from adult males except that they had a whitish belly and their neck collar was incomplete. We calculated overall sex and age ratios and compared ratios among areas to assess their geographic variability. Male age ratios and the relative frequencies of the different plumage codes for immature males were compared between surveys conducted by boat and from shore. We also compared these proportions among the four categories used for the distance birds were observed from the waterline to determine whether young males were more frequently misidentified when they were farther away. Proportions of birds in different-sized groups were determined to assess whether immature males tend to be isolated and thus more easily missed. Birds were considered to be in separate groups if they were separated by ≥10 m.

Habitat associations

We estimated distances between all groups of birds to the nearest 10 m and noted prominent landmarks in order to map the number of birds occurring within each kilometre of shoreline. Kilometre divisions were marked on the largest scale (ranging from 1 : 10 000 to 1 : 80 000) marine charts available from the Canadian Hydrographic Service. The following habitat characteristics were described for each kilometre-section (km-section): (*i*) the width of intertidal habitat over most of the km-section, measured from the marine chart and coded 1 (<10 m), 2 (10–100 m), 3 (100–500 m), or 4 (>500 m); (*ii*) the substrate over most of the km-section as indicated on marine charts or based on our observations, coded 1 (bedrock or large boulder), 2 (cobble or gravel), or 3 (sand or mud); (*iii*) shoreline complexity, coded 1 (linear at the 1-km scale), 2 (convoluted with bays or points at the 1-km scale), 3 (reefs or islets <1 km long either connected to or within 1 km of shore), or 4 (islet or islet clusters >1 km offshore, the largest <1 km long); (*iv*) the presence of a stream, coded 1 (present within the km-section) or 2 (absent);

Fig. 1. Location of area surveyed for Harlequin Ducks (*Histrionicus histrionicus*) in the northern Strait of Georgia during the winter of 1999–2000. Thick dotted lines indicate the limits of the survey area and divisions between locations listed in Table 1. Shaded areas show locations of major concentrations of ducks.

(*v*) the presence of tidal rapids, coded 1 (present within the km-section) or 2 (absent); and (*vi*) a measure of the historical (1928–2000) abundance of herring (*Clupea pallasi*) spawn, using the cumulative herring spawn habitat index for each kilometre of shoreline taken from Fisheries and Oceans Canada (DFO 2001). We included abundance of herring spawn because we hypothesized that intertidal productivity may be higher in areas where spawning occurs (Hay and Fulton 1983). Although exposure to wind and waves was related to Harlequin Duck densities in other studies (Esler et al. 2000; Mittelhauser 2000), we did not consider exposure

because the entire Strait of Georgia is semi-protected and there was high redundancy in measures of exposure, intertidal width, and substrate.

Statistical analyses

We used *G* tests to analyse differences in sex and age ratios between land and boat surveys and among habitat categories. Because we surveyed the entire study area rather than sampling it, our age-ratio estimate for the Harlequin Duck population in the northern Strait of Georgia has no sampling error associated with it. It was biased as a result of errors

such as misidentification. We made adjustments based on our results in an attempt to correct some of these biases. To help with future study design, we used a randomization procedure to generate confidence limits for estimates of age ratios based on different sampling regimes. Random samples were drawn from the km-sections of shoreline that contained Harlequin Ducks. The estimated age ratio was the ratio of the total number of immature males to the total number of adult males occurring in each random sample. Simulations were repeated 1000 times for each sample size. The 95% confidence limits were taken as the 2.5 and 97.5 percentiles of the randomly generated age-ratio estimates.

To relate habitat use to habitat availability at the 1-km scale, we entered all habitat variables into a logistic regression model in SPSS 8.0 with the presence or absence of Harlequin Ducks as the dependent variable. We set the reference categories with which others were compared in the logistic model to be <10 m for intertidal width, sand–mud for substrate, linear for shoreline complexity, absent for rapids, and absent for streams. To determine which habitat variables were related to Harlequin Duck abundance, we considered only km-sections where birds were encountered, and entered all habitat variables into a hierarchical analysis of covariance (ANCOVA) model. Duck numbers were natural log transformed to satisfy assumptions of normality and homoscedasticity. Interactions were tested in initial models and were dropped from final models if they were not significant.

We used a hierarchical model with Type I sums of squares because we formulated a priori hypotheses that width and substrate of intertidal habitat were the variables most related to bird density, and because we were concerned that relationships between duck numbers and historical abundance of herring spawn may have been spurious, being simply the result of similar use of habitat rather than an effect of herring spawn on intertidal productivity. The spawn index was entered last into this model, which allowed us to determine whether Harlequin Duck numbers were positively related to spawn abundance after all other habitat effects had been accounted for. Tolerance for Type I error was set at 5% for all tests.

Results

Surveys

We surveyed 2289 km of shoreline (Fig. 1) and counted 6825 Harlequin Ducks in the northern Strait of Georgia (Table 1). Birds were present in 18% of the km-sections surveyed: 75% of the 191 km-sections surveyed from land and 13% of the 2098 km-sections surveyed by boat. Concentrations occurred along the Vancouver Island shoreline, around Denman and Hornby islands, on the southern ends of Quadra, Marina, Cortes, Hernando, and Savary islands, among the Gillard and Dent islands, and along a short stretch of the mainland coast south of Powell River (Fig. 1).

Sex and age ratios

The overall sex ratio was 1.51 males per female, and the age ratio of immature males to adult males was 8.4% (Table 1). Sex ratios did not vary significantly among locations (only locations with ≥100 birds: $G_{[13]} = 13.4$, $P = 0.4$) but male age ratios did ($G_{[13]} = 31.1$, $P = 0.003$).

Age ratios differed between boat surveys (7.0%, immature males : adult males = 99:1409) and land surveys (9.2%, immature males : adult males = 218:2376) ($G_{[1]} = 4.62$, $P = 0.032$). This suggested that we were misidentifying immature males during boat surveys. Misidentification seemed to be more likely around wide intertidal habitats, where we could not boat close to shore. Age ratios did not vary among intertidal-width categories for land surveys ($G_{[2]} = 1.30$, $P = 0.5$; there were no land surveys of intertidal habitat <10 m wide), but did vary for boat surveys ($G_{[3]} = 13.9$, $P = 0.003$), declining with increasing intertidal width (14.3%, immature males : adult males = 4:28 for <10 m; 9.2%, immature males : adult males = 61:666 for 10–100 m; 5.2%, immature males : adult males = 33:634 for 100–500 m; and 1.2%, immature males : adult males = 1:81 for >500 m). Age ratios determined from all land surveys, including all intertidal-width categories, did not differ from those determined on boat surveys of intertidal habitats <10 m wide ($G_{[1]} = 0.61$, $P = 0.4$) or 10–100 m ($G_{[1]} = 0.00$, $P = 1.0$), but were significantly greater than those from boat surveys of intertidal habitats 100–500 m ($G_{[1]} = 9.83$, $P = 0.002$) and >500 m wide ($G_{[1]} = 8.20$, $P = 0.004$). This indicated that we were underestimating age ratios during boat surveys only in wider intertidal habitats. If we considered only data from boat surveys of intertidal habitats ≤100 m wide, the male age ratio was 9.3% (immature males : adult males = 65:696), very similar to that calculated from land surveys only.

We considered that the bias in data from boat surveys might have been due to our missing birds with less conspicuous female-like plumage. However, the ratio of females to adult males did not differ between boat (0.70, females : adult males = 992:1409) and land (0.73, females : adult males = 1731:2376) surveys ($G_{[1]} = 0.43$, $P = 0.5$). It is thus most likely that we simply misidentified some immature males as either females or adult males, and were not missing female-like birds during boat surveys.

Proportions of immature males assigned to each plumage category did not differ between boat and land surveys ($G_{[4]} = 3.73$, $P = 0.4$), and overall were 6.4, 43.4, 33.1, 16.4, and 0.7%, for plumage scores 1 through 5, respectively ($N = 281$). Proportions did differ by distance offshore, and immatures with female-like or adult-male-like plumage (scores 1 and 5) were proportionately less frequent at distances >50 m (3.5%, $N = 115$) than at distances <50 m (9.6%, $N = 166$) offshore ($G_{[1]} = 4.25$, $P = 0.039$).

Proportions of birds <10, 10–50, 50–300, and >300 m offshore from the waterline were 27, 45, 20, and 8%, respectively ($N = 6210$), and differed between females, adult males, and immature males ($G_{[6]} = 44.5$, $P < 0.001$). Proportions at those distances were 29, 46, 18, and 7%, respectively ($N = 2485$), for females, 26, 45, 21, and 9%, respectively ($N = 3433$), for adult males, and 24, 34, 29, and 13%, respectively ($N = 292$), for immature males. Proportions of birds occurring farther from the waterline were higher for immature males than for adult males ($G_{[3]} = 21.0$, $P = 0.001$), and for immature males ($G_{[3]} = 36.5$, $P < 0.001$) and adult males ($G_{[3]} = 16.5$, $P = 0.001$) than for females. Differences in sex and age distributions resulted in higher sex ratios at greater distances offshore (1.33, 1.43, 1.74, and 2.02, respectively; $G_{[3]} = 23.6$, $P < 0.001$) and higher age ratios at greater distances offshore (7.9, 6.5, 12.0, and 12.6%,

Table 1. Midwinter populations of Harlequin Ducks (*Histrionicus histrionicus*) in the northern Strait of Georgia, British Columbia, 1999–2000.

Location[a]	Length of shoreline (km)	Total no. of ducks	Density of ducks (no./km)	No. of females	No. of adult males	No. of immature males	Sex ratio[b]	Male age ratio[c]
Vancouver Island								
Nanoose to French Creek	68	149	2.2	56	84	9	1.66	10.7
French Creek to Deep Bay	34	751	22.1	300	409	42	1.50	10.3
Deep Bay to Comox	44	105	2.4	36	66	3	1.92	4.5
Comox to Oyster R.	41	944	23.0	385	500	59	1.45	11.8
Oyster R. to Campbell R.	30	524	17.5	207	294	23	1.53	7.8
Campbell R. to Chatham Pt.	54	15	0.3	5	6	4	—	—
Strait islands								
Denman I.	49	685	14.0	281	383	21	1.44	5.5
Hornby I.	33	716	21.7	287	399	30	1.49	7.5
Lasqueti I.	118	5	0.0	1	3	1	—	—
Texada I.	127	0	0	0	0	0	—	—
Harwood I.	14	14	1.0	4	8	2	—	—
Savary I.	18	211	11.7	68	127	16	2.10	12.6
Hernando I.	16	234	14.6	101	129	4	1.32	3.1
Mitlenatch I.	3	10	3.3	6	3	1	—	—
Discovery islands								
Quadra I., south end	21	638	30.4	263	355	20	1.43	5.6
Quadra I., north	229	207	0.9	83	113	11	1.49	9.7
Marina I.	13	355	27.3	155	192	8	1.29	4.2
Cortes I., south end	12	262	21.8	90	151	21	1.91	13.9
Cortes I., north	172	253	1.5	106	135	12	1.39	8.9
Read I.	114	175	1.5	69	100	6	1.54	6.0
Settlers Group	19	56	2.9	25	30	1	1.24	3.3
Gillard and Dent Is.	37	94	2.5	36	51	7	1.61	13.7
Nodales Channel	67	31	0.5	16	15	0	—	—
Mainland coast								
Bute to Malaspina Inlets	464	26	0.0	9	15	2	—	—
Malaspina Inlets	91	10	0.1	4	6	0	—	—
Sarah Pt. to Powell R.	54	65	1.2	26	37	2	1.50	5.4
Powell R. to Jervis Inlet	41	201	4.9	72	121	8	1.79	6.6
Nelson and Hardy Is.	169	48	0.3	19	28	1	1.53	3.6
Jervis Inlet to Reception Pt.	137	41	0.3	13	25	3	2.15	12.0
Total	2289	6825	3.0	2723	3785	317	1.51	8.4

[a]See Fig. 1.
[b]Total number of males to total number of females (calculated only for locations with >40 birds).
[c]Immature males to adult males as a percentage (calculated only for locations with >40 birds).

respectively; $G_{[3]} = 21.0$, $P < 0.001$). Trends in age ratios occurred despite the fact that immatures with female-like or adult-male-like plumage were less frequently identified at greater distances from shore, and thus the trends are conservative.

There were no trends in the relationship between sex ratio ($G_{[3]} = 0.4$, $P = 0.9$) or age ratio ($G_{[3]} = 0.5$, $P = 0.9$) and number of birds per kilometre. Most females (67%, $N = 1715$), adult males (72%, $N = 2356$), and immature males (69%, $N = 218$) recorded during land surveys occurred in groups of >2 birds. However, the proportion of birds that were alone rather than in groups of 2 was higher for immature males (17 vs. 14%) than for females (4 vs. 29%) or adult males (7 vs. 22%) ($G_{[2]} = 69.5$, $P < 0.001$).

We adjusted our estimate of the male age ratio (R_{adj}) by considering the biases that we found. First, we considered only data from land surveys because of the lower ratios found from boat surveys. Second, we assumed that the proportion of immature males assigned to each plumage category was correct for distances <50 m offshore, and we used these proportions to adjust the numbers of immature males with plumage score 1 or 5 that might have been misidentified at distances >50 m.

$$R_{adj} = 100 \times \left[\frac{J_L + J_L J_{adj}}{M_L - P_{J5}(J_L J_{adj})} \right]$$

where J_L is the total number of immature males identified on land surveys, J_{adj} is an adjustment for the proportion of immatures with plumage score 1 or 5 missed at distances >50 m offshore, M_L is the total number of adult males identified on land surveys, and P_{J5} is the proportion of birds with plumage scores 1 and 5 that were in fact 5, and thus were likely to be mistakenly called adult males.

$$J_{adj} = \frac{\left[\left(\dfrac{J_{1,5}}{J_{2-4}} \right)_{<50} (J_{2-4})_{>50} \right] - (J_{1,5})_{>50}}{(J_{1-5})_{total}}$$

where $(J_{1,5})_{<50}$ is the number of immature males with plumage score 1 or 5 identified <50 m offshore, $(J_{2-4})_{<50}$ is the number of immature males with plumage score 2, 3, or 4 identified <50 m offshore, $(J_{2-4})_{>50}$ is the number of immature males with plumage score 2, 3, or 4 identified >50 m offshore, $(J_{1-5})_{>50}$ is the number of immature males with plumage score 1 or 5 identified >50 m offshore, and $(J_{1-5})_{total}$ is the total number of immature males scored for plumage. Thus,

$$J_{adj} = \frac{\left(\dfrac{14}{77} \times 99 \right) - 4}{194} = 0.072$$

and

$$R_{adj} = 100 \times \left\{ \frac{205 + 205(0.072)}{2258 - 0.14[205(0.072)]} \right\} = 9.8\%$$

This estimate is likely still somewhat conservative because we only corrected for misidentification of birds with plum-

age score 1 or 5 at distances >50 m offshore, and assumed that all others were correctly identified.
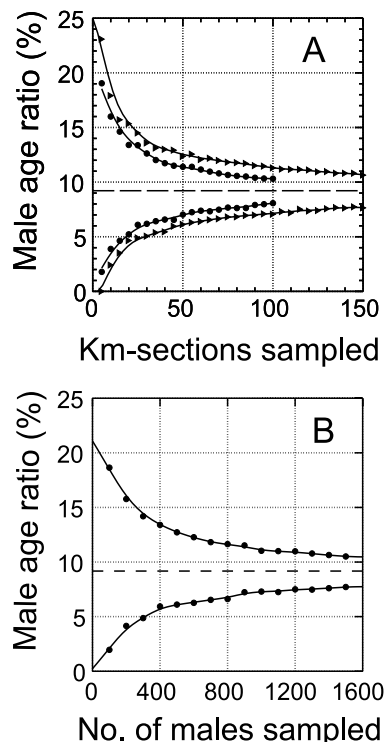
We randomly subsampled our data to simulate 95% confidence limits for age-ratio estimates determined from samples of various sizes. Because of the bias in identifying immature males during boat surveys of areas with wide intertidal habitat, in this simulation we excluded data from boat surveys of intertidal habitats >100 m wide. Results indicate that surveys of 105 random km-sections of shoreline with Harlequin Ducks are required in order to obtain confidence intervals less than ±2% (Fig. 2A). If we considered only km-sections that were surveyed from land, confidence intervals less than ±2% could be obtained with a random sample of 60 km-sections. This difference between including or excluding areas surveyed by boat is likely due to the fact that where Harlequin Ducks were present in our study area, densities were higher in areas surveyed from land (30.0 ± 27.9 birds/km) than by boat (9.3 ± 10.3 birds/km; $F_{[1,411]} = 118.5$, $P < 0.001$). Thus, total numbers of males (including immatures) sampled were similar in 105 random km-sections surveyed from land or boat (range in 1000 simulations = 726–1444; mean = 1057) and in 60 random km-sections surveyed only from land (range in 1000 simulations = 745–1452; mean = 1078). Simulations indicate that samples of random km-sections of shoreline containing 1000 males in total will serve to provide age-ratio estimates with confidence intervals less than ±2% (Fig. 2B).

Habitat associations

There was a high correlation between abundances of females and males ($r = 0.95$, $P < 0.001$) and between abundances of immature males and adult males ($r = 0.65$, $P < 0.001$) within km-sections, and trends in relation to habitat variables were the same for females, adult males, and immature males. We therefore present statistical results for all males and females combined.

Logistic regression analyses indicated that intertidal-habitat width and substrate, shoreline complexity, the presence of streams, and the historical abundance of herring spawn were significant predictors of the occurrence of Harlequin Ducks (Table 2). The presence of ducks was positively related to the width of intertidal habitat: ducks were present in 2, 18, 54, and 33% of km-sections with <10 m ($N = 880$), 10–100 m ($N = 977$), 100–500 m ($N = 369$), and >500 m ($N = 63$) of intertidal habitat, respectively. Ducks were more likely to be present when the substrate was cobble–gravel (42%, $N = 584$) than when it was bedrock–boulder (10%, $N = 1490$) or sand–mud (8%, $N = 215$), and more likely to be present when it was bedrock–boulder than sand–mud. Differences between bedrock–boulder and sand–mud were most pronounced in wider intertidal habitats (Table 3). For example, along linear shorelines where the intertidal habitat was >100 m wide, birds were present in 100% of km-sections with bedrock-boulder substrate but in only 14% of km-sections with sand–mud substrates. The presence of birds was positively related to the historical abundance of herring spawn and negatively related to the occurrence of streams: birds were present in 10% ($N = 249$) of km-sections with streams compared with 19% ($N = 2040$) of km-sections without streams. Birds were more likely to be present on offshore islet clusters (41% of km-sections, $N = 167$) and along shore-

Fig. 2. Upper and lower 95% confidence limits of estimates of male age ratios of Harlequin Ducks from different-sized random samples of km-sections of shoreline that contained birds (A) and in relation to the total number of males sampled in those shoreline sections (B) in the northern Strait of Georgia during winter 1999–2000. Confidence limits were derived through simulation by drawing random samples from 144 km-sections of shoreline surveyed from land (●) and 313 km-sections of shoreline surveyed from land or boat (▶). Data from boat surveys of intertidal habitats >100 m wide were excluded from the latter simulation because of the bias in identifying immature males during boat surveys of areas with wide intertidal habitat (see the text). Simulations were repeated 1000 times for each sample size. The central broken line indicates the population age ratio from all km-sections sampled.

lines with nearby reefs or islets (21%, $N = 309$) than on linear (19%, $N = 1222$) and convoluted (7%, $N = 591$) shorelines. The differences between linear shorelines and shorelines with nearby reefs or islets were not large and were most apparent where intertidal habitat was narrower (Table 3).

The presence of birds was not significantly related to the presence of tidal rapids. However, tidal rapids were present in only 3.3% ($N = 2289$) of km-sections, and occurred only in the channels among the northern Discovery Islands, mainly in the Settlers Group and Gillard and Dent islands (Table 1, Fig. 1). Shoreline in these areas was mostly steep rock with narrow intertidal habitat. Few Harlequin Ducks were encountered in these areas except in those with tidal rapids. If we considered only shoreline with bedrock–boulder substrate, Harlequin Ducks were more likely to be present in areas where tidal rapids occurred (23% of km-sections, $N = 64$) than where they did not (9%, $N = 1426$; $G_{[1]} = 10.3$, $P = 0.001$).

When we considered only km-sections where Harlequin Ducks occurred, a hierarchical ANCOVA model indicated that numbers of Harlequin Ducks per km-section were related to the width ($F_{[3,399]} = 88.2$, $P < 0.001$) and substrate ($F_{[2,399]} = 14.8$, $P < 0.001$) of intertidal habitat, shoreline complexity ($F_{[3,399]} = 3.8$, $P = 0.01$), the intertidal width × presence of streams interaction ($F_{[2,399]} = 6.2$, $P = 0.002$), and the historical abundance of herring spawn ($F_{[1,399]} = 11.8$, $P = 0.001$). Numbers were not significantly related to the presence of streams ($F_{[1,399]} = 0.0$, $P = 0.9$) or tidal rapids ($F_{[1,399]} = 0.7$, $P = 0.4$). For the overall model, $r^2 = 0.44$. Tukey's post-hoc tests showed that ducks were more abundant in wider intertidal habitats (unadjusted means ± SD were 4 ± 3, 7 ± 6, 21 ± 16, and 60 ± 54 birds per km-section for intertidal-width categories 1, 2, 3, and 4, respectively) for every pairwise comparison between width categories (all $P < 0.001$). Numbers of ducks were higher over cobble–gravel (21 ± 24 birds per km-section) than over bedrock–boulder (9 ± 11 birds per km-section; $P < 0.001$) and sand–mud (11 ± 12 birds per km-section; $P = 0.001$) substrates. Numbers were higher along linear shorelines (21 ± 21 birds per km-section) than for all other complexity categories (all $P < 0.001$), and were higher where there were reefs or islets nearby (15 ± 30 birds per km-section) than along convoluted shorelines (6 ± 5 birds per km-section; $P = 0.012$). The intertidal width × presence of streams interaction was significant because duck numbers were higher at wider intertidal habitats where streams were absent but were lower at habitat widths >500 m than at widths 100–500 m where streams were present.

Densities of birds were highest along linear and complex shorelines with reefs or islets where intertidal habitat was >100 m wide and the substrate was cobble–gravel or bedrock–boulder (Table 3). Densities in occupied km-sections ranged from 2 to 108 birds/km and averaged 17 birds/km. Over 60% of Harlequin Ducks occurred along linear shorelines where the intertidal habitat was >100 m wide with cobble–gravel substrate. Offshore islets with wide intertidal habitat were uncommon but were used by Harlequin Ducks wherever they occurred (Table 3).

Discussion

Habitat and population management is often crippled by a lack of adequate information on basic aspects of species' ecology and demography (Doak and Mills 1994). This may be because species are difficult to study, funds for studies have not been committed, or inappropriate methodologies were used. Dedicated methodologies are required for a census of Harlequin Ducks because conventional aerial or boat surveys of waterfowl do not adequately detect Harlequin Ducks (Savard 1989; Breault and Savard 1991). In our study area, some important wintering areas along the east coast of Vancouver Island were previously recognised (Mitchell 1952; Campbell et al. 1990a), but many areas of concentration had not been identified prior to our study. The large reef systems at the south ends of Quadra, Marina, Cortes, Hernando, and Savary islands support high densities of Harlequin Ducks. In these areas of extensive intertidal habitat, Harlequin Ducks were foraging as far as 2 km offshore. This contrasts with

Table 2. Logistic regression model relating presence or absence of Harlequin Ducks to shoreline habitat characteristics in the northern Strait of Georgia, winter 1999–2000.

Variable	Regression coefficient	SE	Wald's χ^2	df	P	R
Intertidal-habitat width (m)			166.2	3	0.0000	0.27
<10	0.00					
10–100	2.26	0.29	59.8	1	0.0000	0.16
100–500	4.23	0.35	149.4	1	0.0000	0.26
>500	4.51	0.55	67.3	1	0.0000	0.17
Substrate			99.0	2	0.0000	0.21
Bedrock–boulder	2.92	0.41	50.4	1	0.0000	0.15
Cobble–gravel	3.60	0.38	91.2	1	0.0000	0.20
Sand–mud	0.00					
Complexity			100.3	3	0.0000	0.21
Linear	0.00					
Convoluted	–0.22	0.21	1.1	1	0.3015	0.00
Nearby reefs/islets	0.55	0.21	6.8	1	0.0091	0.05
Offshore islets	2.20	0.25	79.9	1	0.0000	0.19
Rapids present	0.45	0.34	1.7	1	0.1883	0.00
Stream present	–0.73	0.29	6.4	1	0.0117	–0.04
Herring spawn index	1.03×10^{-6}	1.35×10^{-7}	58.2	1	0.0000	0.16

the previous perception that they forage very close to shore (Vermeer 1983; Robertson and Goudie 1999; Esler et al. 2000). Harlequin Ducks are best surveyed from land or a small boat that can closely approach shallow intertidal habitat.

We counted almost 7000 Harlequin Ducks in the northern Strait of Georgia. Based on numbers of birds wintering in other parts of British Columbia (Savard 1989; Campbell et al. 1990*a*; Breault and Savard 1991; Smith et al. 2001; K.G. Wright unpublished data; M.S. Rodway and H.M. Regehr, unpublished data), the total known wintering population is 8000 – 10 000 in the Strait of Georgia and 12 000 – 15 000 in British Columbia. Overall numbers are probably higher because many coastal areas remain unsurveyed.

We found no evidence of habitat segregation between the sexes or ages at the 1-km scale. Numbers of males and females and immature males and adult males were highly correlated and their patterns of habitat use were similar. However, variation among locations found in this study and other studies (Smith et al. 2001) indicates that estimates of population sex and age ratios may be biased if only a few areas are surveyed.

Sex ratios found in this study were similar to those previously reported during winter from large samples of birds in British Columbia (Savard 1989; Campbell et al. 1990*a*; Robertson and Goudie 1999; Smith et al. 2001) and Alaska (Rosenberg and Petrula 1998). Similar sex ratios across broad geographic areas suggest that latitudinal segregation between the sexes does not occur in Pacific Harlequin Ducks. There may be little energetic advantage for Harlequin Ducks in latitudinal segregation related to body size (Nichols and Haramis 1980) because coastal wintering habitats have moderated climates and dependable food resources that are difficult to defend. However, Harlequin Ducks spend a majority of daylight hours feeding during winter, females more than males (Goudie and Ankney 1986; Fischer and

Griffin 2000), and time constraints may be more important than food availability (Esler et al. 2000). If so, this would imply an advantage to birds, especially females, in wintering farther south, where winter daylight hours are longer. Birds could compensate for a shorter day length by feeding nocturnally, but there is as yet no evidence that they do so (Rodway and Cooke 2001). High winter philopatry (Breault and Savard 1999; Robertson et al. 2000), early pairing (Gowans et al. 1997; Robertson et al. 1998), and small winter ranges (Robertson et al. 1999) suggest that there are benefits to both sexes, especially for paired birds, in remaining together in familiar, local habitats.

We did find evidence of small-scale differences in habitat use, with immature and adult males tending to occur farther offshore than females. Robertson et al. (1999) reported that some radio-marked males occasionally move offshore to roost and feed. Birds foraging at greater distances from shore likely incur greater energetic costs from diving in deeper water (Guillemette et al. 1993). Males may be more capable of bearing these costs because of their larger body size, and may gain some benefit from foraging where there are fewer competitors. However, if this were the sole explanation, we would not expect a higher proportion of immature males than adult males to occur farther offshore because young birds often have poorer foraging skills than adults (Burger 1988). Alternatively, segregation by distance offshore may occur because paired birds are dominant to unpaired birds. Greater access to preferred habitat is thought to be one of the benefits of early pairing in Harlequin and other ducks (Rohwer and Anderson 1988; Robertson et al. 1998). Although Harlequin Ducks do not defend feeding areas, paired birds are aggressive towards unpaired birds, particularly males (Robertson and Goudie 1999; M.S. Rodway, unpublished data). Such interference may increase costs in nearshore areas and make foraging offshore more cost-effective for unpaired birds (Sutherland and Parker 1985; Ranta et al. 1993). This could

Table 3. Habitat use by wintering Harlequin Ducks in relation to shoreline complexity, substrate, and width of intertidal habitat in the northern Strait of Georgia, British Columbia, 1999–2000.

Shoreline complexity and substrate	Intertidal-habitat width (m)	No. of km-sections	No. of kilometres with ducks[a]	No. of ducks[a]	Density of ducks[b]
Linear shoreline					
Bedrock–boulder	<10	549	1 (0.2)	2 (0.0)	2.0
	10–100	157	16 (10.2)	121 (1.8)	7.6
	100–500	11	11 (100)	294 (4.3)	26.7
	>500	2	2 (100)	62 (0.9)	31.0
Cobble–gravel	<10	4	0 (0)	0 (0)	0
	10–100	171	34 (19.9)	269 (3.9)	7.9
	100–500	200	149 (74.5)	3406 (49.9)	22.9
	>500	12	12 (100)	785 (11.5)	65.4
Sand/mud	10–100	32	0 (0)	0 (0)	0
	100–500	56	9 (16.1)	112 (1.6)	12.4
	>500	28	3 (10.7)	37 (0.5)	12.3
Convoluted shoreline					
Bedrock–boulder	<10	212	5 (2.4)	17 (0.2)	3.4
	10–100	190	21 (11.1)	101 (1.5)	4.8
	100–500	3	2 (66.7)	36 (0.5)	18.0
Cobble–gravel	<10	1	0 (0)	0 (0)	0
	10–100	89	8 (9.0)	43 (0.6)	5.4
	100–500	16	5 (31.3)	37 (0.5)	7.4
Sand–mud	10–100	26	1 (3.8)	4 (0.1)	4.0
	100–500	38	1 (2.6)	2 (0.0)	2.0
	>500	16	0 (0)	0 (0)	0
With reefs or islets within 1 km					
Bedrock–boulder	<10	59	4 (6.8)	15 (0.2)	3.8
	10–100	146	25 (17.1)	165 (2.4)	6.6
	100–500	4	3 (75.0)	101 (1.5)	33.7
	>500	1	1 (100)	42 (0.6)	42.0
Cobble–gravel	<10	1	0 (0)	0 (0)	0
	10–100	54	16 (29.6)	120 (1.7)	7.5
	100–500	21	10 (47.6)	163 (2.3)	16.3
	>500	4	3 (75.5)	324 (4.7)	108.0
Sand–mud	10–100	6	0 (0)	0 (0)	0
	100–500	13	3 (23.1)	32 (0.5)	10.7
Offshore islets					
Bedrock–boulder	<10	53	5 (9.4)	20 (0.3)	4.0
	10–100	97	47 (48.5)	297 (4.4)	6.3
	100–500	6	6 (100)	92 (1.3)	15.3
Cobble–gravel	<10	1	0 (0)	0 (0)	0
	10–100	10	10 (100)	126 (1.8)	12.6

[a]Values in parentheses are percentages.
[b]Calculated as the number of ducks per kilometre of occupied shoreline.

explain the higher proportion of immature males than adult males offshore because all immatures are unpaired, while a large proportion of adult males are paired.

This is the first study of Harlequin Ducks to investigate habitat use in relation to habitat availability. Occurrence of birds indicated a preference for wide intertidal habitat with cobble–gravel or bedrock–boulder substrate, for clusters of small offshore islets and shoreline with attached or nearby reefs and islets, and for areas with a greater historical abundance of herring spawn. Birds avoided streams and were least likely to occur where there was minimal intertidal habitat, where the substrate was sand–mud, or where the shoreline was convoluted, with small bays and points. Where little intertidal habitat was available, birds exhibited a preference

for areas with tidal rapids. Although birds showed a stronger preference for shorelines with small islets and reefs than for linear shorelines, differences in habitat availability resulted in most of the population using linear shorelines with wide cobble–gravel intertidal habitat.

Preferred habitats are generally assumed to be those where resource availability confers the greatest individual fitness (Rosenzweig 1991), but habitat use may reflect trade-offs between feeding, predation risk, and the availability of other resources such as roost sites or mates (Stephens and Krebs 1986; Lima and Dill 1990). Wide cobble or rock intertidal habitat likely provides the greatest availability of benthic invertebrates preyed upon by Harlequin Ducks (Vermeer 1983; Rodway and Cooke 2002). Small islets and

reefs may be most attractive because they provide roost sites and offer protection from terrestrial predators and human disturbance. Previous studies also have reported that reefs are important (Goudie and Ankney 1988; Esler et al. 2000). Our finding that the presence of streams was negatively related to occurrence and not related to abundance of Harlequin Ducks contrasts with that of Esler et al. (2000). Many streams in our study area occurred along steep, rocky shoreline with little intertidal habitat, or, in areas with gentler topography, in small bays along convoluted shorelines with intertidal substrates of sand or mud, habitats that were generally unattractive to Harlequin Ducks. Tidal rapids provide productive upwelling environments that are used by a variety of waterbirds (Edwards 1965; Campbell et al. 1990*a*), and likely provide richer foraging habitat for Harlequin Ducks in fjord-like channels generally devoid of extensive intertidal habitat.

The positive association between Harlequin Duck abundance and the historical abundance of herring spawn provides circumstantial evidence to support the hypothesis that spring spawning by herring increases the productivity of inter- and sub-tidal habitats during other times of the year. We think it unlikely that this relationship merely reflects similar habitat use by these species because it was significant after all other habitat effects had been considered. However, an alternative explanation for the association could be that Harlequin Ducks benefit from wintering in proximity to spawning sites so as to access them more easily in spring (Rodway et al. 2003). The effect of spawn deposition on benthic productivity warrants investigation (Hay and Fulton 1983). Intertidal invertebrates that are the main winter prey of Harlequin Ducks (Rodway and Cooke 2002) are major consumers of herring spawn (Haegele 1993), therefore it is plausible that the massive spring influx of nutrients from herring spawn into the intertidal community (Hay and Fulton 1983) increases prey abundance for Harlequin Ducks during other times of the year. The recent spatial and temporal contraction of spawning in the Strait of Georgia (Hay and McCarter 1999) may be a conservation concern for wintering birds like Harlequin Ducks if the input of spawn is a determinant of benthic productivity.

Variation in male age ratios at large and small spatial scales and biases in age-ratio estimates due to survey method and misidentification have important implications for survey design. Differences among geographic areas indicate that larger scale sampling is required to accurately estimate population age ratios. Where density variation is similar to that which we found in the northern Strait of Georgia, random samples of about 100 km-sections of shoreline with Harlequin Ducks will provide age-ratio estimates with 95% confidence limits of ±2%. In our study area, similar precision could be obtained with smaller samples (60 km-sections) surveyed from land, and we recommend using only land surveys for monitoring age ratios in that area. Land surveys were more efficient in that area because densities of Harlequin Ducks were higher along accessible shoreline and more birds were contained in fewer km-sections. Systematic sampling of shoreline habitat where birds are present could provide accurate estimates with similar precision as long as sampling is done over a large portion of the study area. Overall, our simulations indicate that surveys of

samples of shoreline habitat need to enumerate about 1000 male Harlequin Ducks, or, in our study area with a sex ratio of 1.51, about 1700 Harlequin Ducks in total, to obtain male age ratio estimates with 95% confidence limits of ±2%.

All birds within sample sections should be identified and included regardless of distance offshore and group composition because age ratios are higher at greater distances offshore and a substantial proportion of immature males occur singly. The greater chances of misidentifying immature males with female- or adult-male-like plumage at greater distances offshore need to be considered and correction factors similar to those used in this study employed. The need to identify more distant birds makes it important to conduct surveys when visibility is good. Boat surveys of wide intertidal areas underestimate age ratios and their use for that purpose should be avoided; however, they can be useful for enumerating all birds using those areas and thus determining habitat-use patterns. We found no relationship between age ratios and habitat type or total Harlequin Duck density, and excluding wide intertidal areas where density was often high did not bias age-ratio estimates.

Demographic rates of recruitment of young birds into the breeding population and mortality of breeding adults must balance in order to maintain a stable population. Local survival rates have been estimated as 0.76 for paired females and 0.91 for paired males (Cooke et al. 2000). Our unadjusted estimate of the male age ratio, 8.4%, was similar to that reported from Alaska (8.8%; Rosenberg and Petrula 1998) and to previous estimates determined during boat surveys of a wide geographic area in the Strait of Georgia (8.9%; Smith et al. 2001). Estimates by Smith et al. (2001) that were based on land surveys of a small number of areas were lower and highly variable. After adjusting for biases, we estimated the male age ratio to be 9.8%. Because females are the limiting sex, we calculated a female age ratio of 15.6% by assuming an equal sex ratio for immature birds and using the overall male-to-female sex ratio of 1.51. Almost all females pair in their second year (Robertson et al. 1998; M.S. Rodway, unpublished data). If we make the assumption that they also start breeding in their second year, which is not always the case (Robertson and Goudie 1999), the actual rate of recruitment of females into the breeding population would be 15.6% times an annual survival rate of 76% (Cooke et al. 2000), or 11.9%. Even if the annual rate of survival of nonbreeding females is higher than 76% and the actual recruitment rate is higher, it is still clearly insufficient to balance estimated mortality.

Although conservation concern for west-coast Harlequin Ducks seems warranted, there is still uncertainty about current estimates of recruitment and survival rates. Our adjusted male age ratio of 9.8% is likely still conservative. While juvenile males may be misidentified as adult males, adults are unlikely to be misidentified as juveniles. We assumed that juveniles with plumage scores 2–4 were always identified correctly regardless of their distance offshore, which is unlikely to be so. However, we do not think that further biases in identifying immature males would greatly increase recruitment-rate estimates. A second consideration is that our recruitment-rate estimate is based on only 1 year of data. Inter-annual variation in male age ratios have been reported (Smith et al. 2001), although our results indicate that such

variation would be expected when only a few sites are sampled. Determining inter-annual changes in age ratios is difficult without random large-scale sampling because variation by location and year may be confounded. Further study with adequate sampling is required to determine annual variation.

Estimates of adult survival rates are also likely to be conservative. Although we have considered local survival rates of paired birds, and paired birds are highly philopatric (Robertson et al. 2000), estimates of true adult survival rates are lacking. Emigration needs to be incorporated into demographic models before true survival estimates can be derived.

Industrial, residential, and recreational development by humans is often concentrated along coastlines and competes directly with other species' habitat use. Harlequin Ducks depend on a productive littoral environment that is readily impacted by human activities. Their small body size and high feeding rates suggest that they are living near an energetic threshold during winter and have little flexibility to accommodate increased stress (Goudie and Ankney 1986; Mittelhauser 2000). The rapid expansion of the aquaculture industry in British Columbia is a major concern because of its direct and indirect habitat impacts and the risk of entanglement for marine birds (Vermeer and Morgan 1989). Extensive intertidal and shallow subtidal habitats are attractive for both shellfish tenures and Harlequin Ducks. A further concern comes from our finding that Harlequin Ducks prefer small islet and reef clusters. Both shellfish and finfish operations may usurp small islets for gear storage or residences. The recent lifting of the moratorium on new finfish farms in British Columbia is likely premature. Meeting our responsibilities in ensuring the health of marine bird populations in coastal habitats requires management that is cautious, acknowledges the limitations of our ecological understanding, and has the resources and will to pursue informed decisions.

Acknowledgments

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