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Movement Rates and Distances of Wintering Harlequin Ducks: Implications for Population Structure

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Abstract.—Population structure of Harlequin Ducks (*Histrionicus histrionicus*) wintering in the Strait of Georgia, British Columbia, was evaluated by generating age, sex, paired status and distance-specific movement rates with multi-stratum mark-recapture analyses, and age and sex-specific movement distances through surveys of marked individuals. Annual movement distances and rates did not differ by sex, but only 2-4% of adults (third year and after-third year) compared to 7-11% of subadults (hatch year and second year) moved among locations per year and distance moved decreased with age. Adults were highly site faithful regardless of sex and paired status. The stepping stone gene flow model estimated the among population component of genetic variance (F_{ST}) at 0.005, suggesting that winter movement by subadults was sufficient to explain results of previous genetic analyses that detected no fine scale genetic structuring. Seasonal movement rates indicated that at least 95% of individuals molt and winter in the same location, and that annual aggregation at Pacific Herring (*Clupea pallasi*) spawning sites facilitates demographic mixing and gene flow. Low annual movement rates (0.001) between the northern and southern Strait of Georgia and dispersal by both sexes suggest that a metapopulation distribution may function within the Pacific Coast range, which is relevant to the geographic scale of management. Movement rates and distances suggest that subadult survival rates are particularly vulnerable to underestimation. *Received 28 February 2010, accepted 3 June 2010.*

Key words.—age, dispersal distances, Harlequin Ducks, *Histrionicus histrionicus*, movement rates, paired status, population structure.

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The relationship between spatial distribution and population structure can be complex for species that have separate breeding and wintering distributions, especially when mates are chosen at wintering areas (Cooke *et al.* 1995; Scribner *et al.* 2001). Many waterfowl species migrate between breeding and wintering areas, and many form pair bonds during winter (Rohwer and Anderson 1988; Rodway 2007a). For species with a dispersed winter distribution and winter pairing, genetic differentiation could potentially develop among wintering populations regardless of whether or not they contain individuals from multiple breeding areas. If individuals pair at wintering areas, and if no genetic exchange outside of the pair bond occurs at breeding areas, then the distribution, movement and pairing choices of individuals at wintering areas would be important to genetic population structure (Robertson and Cooke 1999), whereas the location of breeding areas and geographical mixing of conspecifics there would be unimportant. Demographic population structure, on the other hand, needs to be defined for breeding and wintering areas separately (Esler 2000). Knowledge of genetic and demographic connections between groups of wintering birds is important for informed conservation decisions (Moritz 1994; Esler *et al.* 2006).

For Harlequin Ducks (*Histrionicus histrionicus*), genetic studies of wintering populations in western North America have detected no fine scale genetic structuring (Lanctot *et al.* 1999). However, family migration from inland breeding to coastal wintering areas (Regehr *et al.* 2001), high levels of philopatry to wintering areas (Breault and Savard 1999; Robertson *et al.* 2000; Iverson *et al.* 2004), and winter pairing (Rodway 2007a), implicate potential for genetic divergence. If mothers bring their offspring to the same wintering sites each year, these juveniles could later choose mates with a high probability of relatedness. Contrasting results from genetic and behavioral studies thus suggest that either more dispersal exists than that implied by reported high levels of winter philopatry, or that the genome is largely reflecting historical population processes (Lanctot *et al.* 1999; Pearce and Talbot 2006). Some winter dispersal has been reported (e.g. Cooke *et al.* 2000; Regehr 2003; Iverson *et al.* 2004; Iverson and Esler 2006; Mittlehauser 2008; Thomas and Robertson 2008), however, sample sizes of young birds have been small, movement and mortality have frequently been confounded, and movement has not been evaluated in a manner allowing comparison to genetic results.

Harlequin Ducks form long-term pair bonds, thus movement of individuals that have not yet paired is most likely to contribute to gene flow. Paired status is closely linked to sex and age in Harlequin Ducks: females are unpaired at least until their second winter, males generally remain unpaired even longer, and almost all adult females are paired but many adult males are unpaired (Rodway 2007b). Thus, determining if there are differences in movement probability and movement distances among classes of individuals is important. In many species, young individuals have greatest dispersal tendencies (Dobson 1982; Greenwood and Harvey 1982) and dispersal is typically male-biased in ducks, likely related to predominantly female parental care (Greenwood 1980; Rohwer and Anderson 1988; Anderson *et al.* 1992). In Harlequin Ducks, male-biased sex ratio would also be expected to contribute to male-biased dispersal because unpaired males are not constrained to be site faithful in order to reunite with a mate and they are known to spend more time moving than other individuals (Rodway 2007b), presumably in the search for mates.

The objective of this study was to quantify annual and seasonal movement rates and distances for Harlequin Ducks on a large geographic scale in an important wintering area in western North America in order to contribute to our understanding of their genetic and demographic population structure and their dispersal behavior. Multi-stratum mark-recapture analyses were used to estimate movement rates not confounded with mortality, and winter surveys of marked individuals were used to estimate movement distances. The use of a gene flow model, which converts movement statistics into estimates of gene flow and partitions the total genetic variation into within and among population components (Kimura and Weiss 1964; Rockwell and Barrowclough 1987), allowed evaluation between the following two alternative explanations for the lack of observed genetic structuring: 1) there is little current gene flow and the genome is largely reflecting historical population processes, and 2) dispersal is sufficient to homogenize groups of birds genetically in spite of the isolating effects of family migration and high rates of philopatry. Movements within wintering seasons may be particularly relevant for demographic population structure of Harlequin Ducks in the Strait of Georgia, where aggregations of thousands of birds feed at Pacific Herring (*Clupea pallasi*) spawning sites each spring (Rodway *et al.* 2003a).

METHODS

Study Area and Field Methods

The study took place in the Strait of Georgia (SOG), an important wintering area for western Harlequin Ducks (Robertson and Goudie 1999). Over 2,500 Harlequin Ducks were captured from July to September during their wing molt using drive traps at five locations in the SOG in 1994-2000 (Fig. 1). All individuals were marked with a metal leg band and a plastic alphanumerically-encoded color leg band. Individuals were sexed by plumage and aged as after-third year (ATY), third year (TY), or second year (SY) by absence or length of the Bursa of Fabricius, considered a reliable aging technique (Kortright 1942; Mather and Esler 1999), or as hatch year (HY) by plumage (Regehr *et al.* 2001) (Table 1). During August and September 1999, 208 Harlequin Ducks captured in the northern SOG also were marked with nasal discs to improve identification during mid-winter when birds rarely haul out. In September 2000, 15 HY birds, captured with mist nets and decoys, were marked with leg bands, nasal discs and external radio transmitters (three transmitters detached shortly after marking). Banding was conducted under permits 10201 and 10759 and animal care approvals 540B and 462B were issued by the Simon Fraser University Animal Care Committee.

Leg bands of marked individuals were identified with 15-60 X spotting scopes from fall through spring, 1994 to 2001. A mid-winter shoreline survey of the entire northern SOG (survey boundaries shown in Fig. 1) was conducted from November 1999 to February 2000 to locate ducks marked with nasal discs in fall 1999. Shorelines were surveyed by walking beaches where Harlequin Duck densities were high, and from an inflatable boat where densities were low. Radio telemetry was

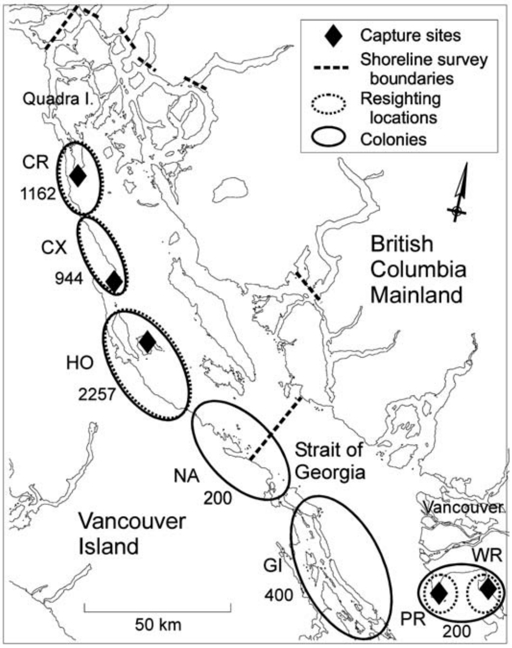

Figure 1. Harlequin Duck capture sites in the Strait of Georgia, the five resighting locations (Campbell River [CR], Comox [CX], Hornby [HO], Point Roberts [PR] and White Rock [WR]) between which movement rates were estimated, boundaries of the northern Strait of Georgia mid-winter shoreline survey, and subdivision of the entire wintering area into six colonies for use of the stepping stone gene flow model. The mid-winter shoreline survey included all shorelines south and west of the six thick dashed lines north and east in the study area, and all shorelines north of the single thick dashed line through the central Strait of Georgia. The six colonies include replicates of the CR, CX, and HO locations each as single colonies, two added colonies, Nanaimo (NA) and Gulf Islands (GI), and a single colony containing the PR and WR locations combined. Census population sizes are shown for each colony.

used to locate HY individuals marked in fall 2000. In addition to land-based telemetry surveys, three telemetry flights were conducted in October and November 2000 in which the entire area that had been surveyed during mid-winter the previous year was covered at least once and most parts were covered at least twice. Paired status was recorded for marked individuals when possible; birds were considered paired if they remained in close proximity, behaved synchronously, and exhibited defense behaviors such as mate guarding (Gowans *et al.* 1997).

Movement Distances

Sightings of individuals marked with nasal discs in 1999 and transmitters in 2000 were used to compare movement distances (i.e. the maximum distance observed from the marking location) by sex and age. Maximum movement distances from capture locations were recorded to the nearest km using a handheld GPS unit or were measured from 1:80,000 scale marine charts. Movements during mid-winter (November to February) were reported separately from those during the full wintering season (November to April), which includes movements to herring spawning sites in spring.

Annual and Seasonal Movement Rates

Locations—Five locations were defined based on capture sites between which movement rates were estimated with capture-mark-recapture (CMR) analysis: White Rock (WR), Point Roberts (PR), Hornby Island (HO), Comox (CX), and Campbell River/Quadra Island (CR) (Fig. 1). All five locations were used to evaluate effects of distance between locations and sex on annual movement rates. Due to data limitations in the southern SOG (WR and PR), the three locations in the northern SOG (HO, CX, and CR) were used to evaluate effects of age and paired status on annual movement rates, and to estimate seasonal movement rates.

Seasons—Three time periods ("seasons") were defined for the estimation of annual and seasonal movement rates: molt (July-October), winter (November-February), and spawn (March, when herring spawn is available; Rodway *et al.* 2003a). Annual movement rates were estimated from the molt season and thus represent movement probabilities between locations from one molt season to the next. Although pair formation occurs throughout the winter months in Harlequin Ducks, annual movement rates were estimated from the molt season because 1) most individuals molt and winter in the same location, given the geographic scale considered in this study (Breault and Savard 1999; Iverson and Esler 2006), 2) marking occurred during the molt season, thus dispersal before the winter season would be missed if winter sightings were used, and 3) birds are more visible during the molt season. Seasonal movement rates between locations were estimated from the molt to the winter season and from the winter to the spawn season. Individuals were rarely seen in more than one location in a single season (observed for 2% of individuals), but when this occurred one of the two locations was chosen randomly, weighted by the number of sightings in each location.

Age Categories—Two age categories were defined: "subadult" (HY and SY), and "adult" (TY and ATY). Thus individuals aged HY and SY at capture (N = 343, Table 1) spent either the first two years or the first year in the "subadult" category, respectively.

Paired Status—Three paired status groups were compared: paired males, unpaired males, and paired females (unpaired females were excluded due to sample size). Only individuals in CMR analysis that had been assigned a consistent paired status for the majority of years in which they had been sighted (33 paired males, 44 unpaired males, 157 paired females) were included. Due to the potential bias in selecting a sample of individuals for which paired status was known for more than one year, a second sample was added that allowed comparison of movement between paired and unpaired birds if paired status was known for only one year. Proportions of individuals were compared within the entire SOG that were detected at different locations during two consecutive molt seasons when paired status was known for the first of the two years. For this analysis that compared proportions, paired status was considered acceptable for a year if 1) there were at least two consistent opportunistic records of paired status or if birds were

Table 1. Numbers of male and female after-third year (ATY), third year (TY), second year (SY), and hatch year (HY) Harlequin Ducks, and those of unknown age (U), captured and marked with alphanumerically encoded color leg bands in the northern (HO, CX, and CR) and southern (WR and PR) Strait of Georgia (see Fig. 1).

	Total Captured		Males					Females				
Year	Males	Females	ATY	TY	SY	HY	U	ATY	TY	SY	HY	U
Northern Strait of Georgia												
1994	643	104	614	20	7	0	2	17	20	67	0	0
1995	262	278	229	18	8	2	5	188	20	62	6	2
1996	197	46	159	26	11	0	1	8	5	32	0	1
1997	116	65	87	18	10	0	1	32	19	10	0	4
1998	117	164	82	13	13	2	7	117	28	15	2	2
1999	79	195	37	24	13	2	3	97	32	62	2	2
2000	10	32	4	0	0	6	0	18	3	2	9	0
Southern Strait of Georgia												
1994	43	29	40	3	0	0	0	17	10	2	0	0
1995	8	40	6	0	2	0	0	26	8	6	0	0
1996	35	14	19	11	4	1	0	6	4	3	1	0
1997	12	19	11	0	1	0	0	6	8	4	1	0
1998	9	19	2	5	0	0	2	13	3	3	0	0
1999	4	11	1	2	1	0	0	5	5	1	0	0

identified as paired or unpaired during behavioral observations conducted for other purposes (Rodway 2007b), and 2) if unpaired records were from 1 March or later.

Multi-stratum Models

Model Notation and Assumptions—Multi-stratum models in the program MARK (White and Burnham 1999) were used to estimate movement rates. Multi-stratum models permit estimation of transition probabilities (ψ) in addition to estimates of survival (S) and sighting rates (p) by separating the joint probability of surviving and making a transition between two states (ϕ_i^{rs}) into a survival component (S_i^r, the probability that an animal survives in location r from time i to time $i + 1$) and a transition component (ψ_i^{rs}, the probability that an animal alive in state r at time i is in state s at time $i + 1$, given that the animal is alive at time $i + 1$). In this study, transitions between states represent movement among geographic locations.

Multi-stratum models assume that survival from time i to $i+1$ depends only on the location in time i, and that marked individuals do not leave the study area, i.e., $\sum \psi_i^{rs} = 1$. Potential for violation of the first assumption was evaluated by including the effect of location in the estimation of survival rates and this was found not to improve model fit. To minimize potential for violation of the second assumption, resighting location boundaries were defined to fully include high density Harlequin Duck areas (Fig. 1). Multi-stratum models also share the general assumptions of CMR analyses: capture and sighting probabilities of individuals are equal, marks are not lost or missed and do not affect behavior, and behavior of marked individuals is independent (Lebreton *et al.* 1992). Due to differences in sighting probability between leg bands and nasal discs (Regehr and Rodway 2003), CMR analyses included only sightings from leg bands. Leg band wear, a form of marker loss, is a concern for the estimation of survival rates, however, movement rates are estimated from survivors and, assuming that band wear does not differ among locations, are not biased. The assumption of independent behavior was likely violated at times, especially during spring when groups of birds congregated at herring spawning sites, and likely resulted in inflated $\hat{c}$ values and some loss of power.

Selection and Evaluation of Models—Sets of candidate models were developed that were based on *a-priori* biological and sampling information (Lebreton *et al.* 1992; Burnham and Anderson 2002). Explanatory variables included in the estimation of survival and sighting rates were considered with the objective of balancing model fit and estimator precision; those included in model parameterizations of movement were included to test hypotheses and generate movement rates of interest. Effects of variables were incorporated into models by modifying parameter index matrices (PIMs). For survival rates, effects of sex and age were believed to potentially improve model fit, and time dependence and effects of location were considered for all but the small paired status data set. For sighting rates, time (with the exception of the paired status data), location, and season (in the estimation of seasonal rates) were believed to potentially improve model fit. The hypothesis that individuals moved with highest probability to adjacent locations was tested by including distance between locations as a covariate in the estimation of movement rates. Sex, age, paired status, and distance effects on movement were tested by comparing models with and without these effects included. Hypotheses that movements were direction-specific were tested by including models with and without direction-specific parameters for movement. Models allowed for fully interactive effects between variables. Sighting rates, which varied by location and time, and survival rates, the estimation of which was biased by band wear, are not reported here.

Competing models were evaluated using Akaike's Information Criterion (AIC) adjusted for overdispersion and small sample size ($QAIC_c$). Randomizations were used to estimate the variance inflation factor, $\hat{c}$, by comparing observed frequencies of encounter histories to 1,000 simulated values generated by model parameters and the binomial distribution (Roff and Bentzen 1989). $QAIC_c$ and the ratio of $QAIC_c$ weights indicated models that were substantially supported by the data (Burnham and Anderson 2002). When two or more models received similar support ($\Delta QAIC_c < 2$) inferences were drawn from this subset of models (Lebreton *et al.* 1992) by model averaging to generate estimates weighted by model support, thus incorporating model selection uncertainty into estimates. An exception was the small data set used for analyses of paired status effect; for this estimates from the most highly parameterized model are presented in a subset of models with similar $QAIC_c$s, because models with few parameters tend to be favored when sample size is very small (Burnham and Anderson 2002). Due to the large number of models included in some analyses, highest ranking models up to $\Delta QAIC_c < 10$ are presented.

Estimating F_{ST}

Isolation by distance and stepping stone gene flow models (Rockwell and Barrowclough 1987) both assume that dispersing individuals move with highest probability to adjacent locations but differ in assumptions regarding the distribution of individuals (continuous vs. colonial, respectively). Evaluation of gene flow models and estimation of the among population component of genetic variance (F_{ST}) thus began by assessing whether movement rates decreased with distance between locations. Based on these results, and because the spatial distribution of Harlequin Ducks is more colonial than it is continuous, with concentrations found along the coastline where habitat is most suitable (Rodway *et al.* 2003b), F_{ST} was estimated using the stepping stone gene flow model (Kimura and Weiss 1964). This model assumes that individuals are distributed in colonies and that migration occurs to adjacent colonies at a certain rate. Thus, the fraction of the total number of recruits in one colony that came from adjacent colonies represents gene flow. It was first determined whether movement differed among classes of Harlequin Ducks (see results), and, because individuals in the subadult age class are largely unpaired, their movement was taken to represent gene flow. Following Kimura and Weiss (1964) and Rockwell and Barrowclough (1987), F_{ST} was estimated as $1/[1 + 2NeC_o]$, where $C_0 = 2[2m_{adj}m_{\infty}]^{0.5}$, Ne is the effective population size of colonies, m_{adj} is the gene flow from adjacent colonies, and m_{∞} is the long-range gene flow, formally equivalent to mutation (10^{-6}; Rockwell and Barrowclough 1987), and defined as the rate at which genes are uniformly spread over the entire species' range. A correction factor used to adjust F_{ST} for a finite number of colonies in a reduced portion of the species range is given in Kimura and Weiss (1964, p. 574).

F_{ST} was estimated for Harlequin Ducks in the SOG by dividing the entire study area into six "colonies" (Fig. 1). Each of the sighting locations used for CMR analysis in the northern SOG represented one colony (CR, CX and HO), and census population sizes for these colonies were taken from Rodway *et al.* (2003b). The colony surrounding Nanaimo (NA) and the Gulf Islands colony (GI) were estimated to contain 200 and 400 birds, respectively, based on partial surveys (Rodway *et al.* 2003b). White Rock and Point Roberts were combined as the sixth colony with a joint population of 200 birds.

Harmonic mean of colony population sizes (Wright 1969) was taken, and census population size was adjusted for male-biased sex ratio (1.51; Rodway *et al.* 2003b), variance in offspring number, and overlapping generations (Wright 1938; Crow and Kimura 1970). To adjust for male-biased sex ratio Ne was set equal to twice the number of females (Wright 1938). Variance in offspring number is high (Robertson and Goudie 1999), and assuming that two-thirds of females produce no young, and the remainder produce between one and six, the variance in offspring number ($\sigma^2_{offspring}$) was estimated at three and Ne was calculated as $4N_{census}/(\sigma^2_{offspring} + 2)$ (Meffe and Carroll 1994). The effect of overlapping generations was adjusted with the same correction factor (0.982) that was calculated from the life history schedules of the Lesser Snow Goose (*Anser caerulescens caerulescens*) (Rockwell and Barrowclough 1987), a species with very similar demographic characteristics as the Harlequin Duck. Fluctuations in population size over time also reduce Ne relative to N_{census}, however, Harlequin Duck populations are not likely prone to large size fluctuations and constant population size was assumed.

Statistical Analyses

Kruskal-Wallis tests (Sokal and Rohlf 1995) were used to determine the effects of sex and age on movement distances and *G* tests were used to compare proportions. Type I error rate at was set at 0.05. Means ± SE are reported.

RESULTS

Movement Distances

Of 220 birds marked with nasal discs in the northern SOG during fall 1999 and with transmitters in 2000, 88% were resighted the following winter. Movement distances did not differ by sex for the full wintering season (males: 11.6 ± 1.6 km, N = 65; females: 16.6 ± 1.6 km, N = 128; Kruskal-Wallis: $H_1 = 2.52$, $P = 0.11$) or the mid-winter period (males: 9.5 ± 1.8 km, N = 53; females: 11.0 ± 1.4 km, N = 104; Kruskal-Wallis: $H_1 = 0.11$, $P = 0.74$) but did differ by age, with subadult birds moving greater distances than older ones (Fig. 2; full wintering season: Kruskal-Wallis: $H_3 = 20.35$, $P < 0.001$; mid-winter: Kruskal-Wallis: $H_3 = 10.61$, $P = 0.014$).

Annual Movement Rates

Sex and Distance Between Locations—Annual movement rates within the SOG were similar for males and females and declined with distance between locations. The most parsi-

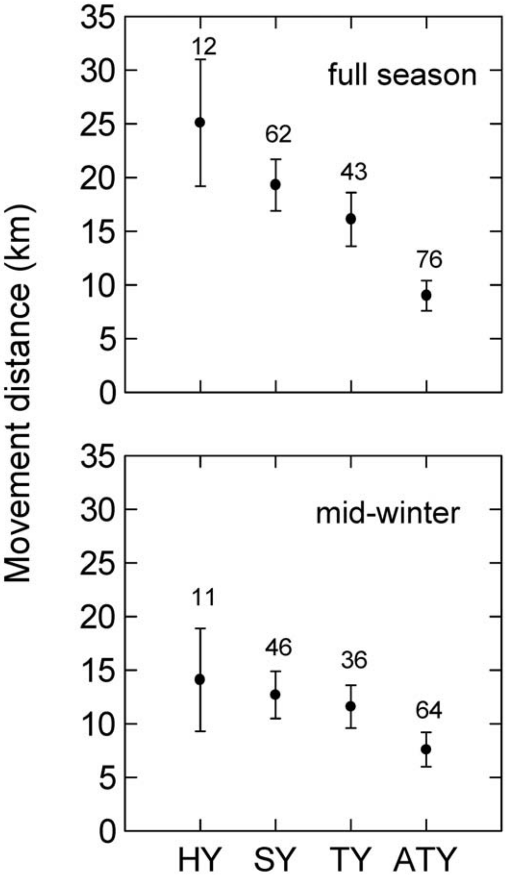

Figure 2. Full winter season (November to April) and mid-winter (November to February) mean maximum movement distances (km ± SE) from capture locations of hatch year (HY), second year (SY), third year (TY) and after-third year (ATY) Harlequin Ducks in the northern Strait of Georgia, 1999-2001. Sample sizes are shown above points.

monious model (of 21), which included only distance in the estimation of movement rates, received six times the support of the second highest ranking model which included the effect of sex in addition to distance (Table 2). Movement rates ranged from 5 in 100 individuals per year to 1 in 1,000 individuals per year (Table 3). Sex-specific movement rates generated by the second highest ranking model indicated that point estimates for males were slightly higher than those for females for all distance classes (Table 3).

Age—When models with and without age effects on annual movement rates were compared between locations within the northern SOG, the two highest ranking models (of 23) received similar support ($\Delta QAIC_c = 0.62$) and both included an age effect in the estimation of movement rates (Table 2). Models without an age effect on movement received virtually no support. Model-averaged movement rates among locations ranged from 0.072 to 0.105 per year for subadults, and from 0.022 to 0.037 per year for adults, and were best parameterized as equal regardless of the direction of movement (Fig. 3).

Paired Status—The most highly parameterized model among the four highest ranking models with similar $QAIC_c$ values (Table 2) estimated separate movement rates for each paired status group in the northern SOG: 0.000 ± 0.000 for paired males, 0.050 ± 0.055 for unpaired males, and 0.018 ± 0.017 for paired females, for all locations combined. Similarly, 5% (N = 39) of unpaired males, 5% (N = 138) of paired females, and 0% (N = 51) of paired males ($G_2 = 4.66$, $P = 0.10$) within the entire SOG were observed to change locations from one molt season to the next when their location was known in two consecutive years.

Seasonal Movement Rates

Sex - When models with and without a sex effect on movement between locations in the northern SOG from the molt to the winter season or from the winter to the spawn season were compared, models that included a sex effect received little support. The best supported model (of 20) for both molt to winter and winter to spawn seasons included only location and season as effects in the estimation of movement rates (Table 4). Movement rates between locations from the molt to the winter season were best parameterized as equal regardless of the direction of movement (CR-CX: 0.039 ± 0.025, CX-HO: 0.030 ± 0.009, CR-HO: 0.000 ± 0.000), whereas movement rates from winter to spawn were best parameterized as direction-specific for each location, with greatest movement to Hornby Island (Fig. 4A).

Age—When models with and without age effects on movement rates from the molt to the winter season were compared between

Table 2. Model selection statistics for effects of sex, distance between locations, age and paired status on annual movement rates for Harlequin Ducks in the Strait of Georgia (SOG), 1994-2000. Effects of time (*t*), sex (*sx*), location (*l*), distance between locations (*d*), age (*a*) and paired status (*ps*) are indicated for survival (ϕ), sighting (*p*) and movement (ψ) rates; the '/' notation separates time effects (time dependence ['*t*'], or time held constant ["*c*"]) for subadult and adult age classes, respectively; l_c indicates that movement rates are constrained to be the same regardless of direction, and l_j indicates that the location effect on survival rates are specific to the subadult age class. Highest ranking models up to $\Delta QAIC_c < 10$ are presented.

Model	No. of parameters	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight
1) Sex and distance between locations, entire SOG ($\hat{c}$ = 3.32):				
$\phi(sx)\ p(l * t)\ \psi(d)$	34	2713.45	0.00	0.7763
$\phi(sx)\ p(l * t)\ \psi(sx * d)$	36	2716.87	3.43	0.1400
$\phi(l * sx)\ p(l * t)\ \psi(d)$	42	2718.24	4.79	0.0707
$\phi(l * sx)\ p(l * t)\ \psi(sx * d)$	44	2721.78	8.33	0.0121
2) Age, within the northern SOG ($\hat{c}$ = 2.87):				
$\phi(a\text{-}c/c)\ p(l * t)\ \psi(a)$	22	2614.25	0.00	0.5609
$\phi(l_j * a\text{-}c/c)\ p(l * t)\ \psi(l_c * a)$	28	2614.87	0.62	0.4124
$\phi(a\text{-}c/t)\ p(l * t)\ \psi(a)$	26	2620.99	6.74	0.0193
$\phi(l_j * a\text{-}c/c)\ p(l * t)\ \psi(a)$	23	2622.91	8.65	0.0074
3) Paired status, within the northern SOG ($\hat{c}$ = 2.60):				
$\phi()p()\psi()$	3	211.03	0.00	0.4382
$\phi()p()\psi(ps)$	4	212.33	1.29	0.2293
$\phi()p()\psi(sx)$	4	213.09	2.06	0.1568
$\phi()p()\psi(ps * sx)$	5	213.55	2.52	0.1244
$\phi(sx)p(l)\psi(ps)$	7	217.58	6.55	0.0166
$\phi()p()\psi(l)$	8	217.82	6.79	0.0147
$\phi(sx)p(l)\psi(sx)$	7	218.47	7.44	0.0106
$\phi(sx)p(l)\psi(ps * sx)$	8	218.82	7.79	0.0089

locations within the northern SOG, the two highest ranking models (of 20) received similar support (Table 4). Model averaging generated age-specific movement rates in which estimates between location pairs from the molt to the winter season were higher for subadults than for adults and were equal regardless of the direction of movement (Fig. 4B). Models that included age in the estimation of movement rates between locations from the winter to the spawn season received virtually no support (Table 4). The highest ranking model (of 20) generated direction-specific movement rates for each location pair, and given that highest ranking models in this analysis and in that testing for sex effects (above) included the same effects in the generation of movement rates from winter to spawn, rates were virtually identical in both analyses (Fig. 4A).

Estimating F_{ST}

The average movement rate to one adjacent colony for the subadult age class in the northern SOG was estimated at 0.081 ± 0.035 (Fig. 3). Twice this rate (one colony on either side) was taken to represent gene flow from adjacent colonies (m_{adj} = 0.16 per year). Harmonic mean of colony census population sizes, given six colonies within the entire study area (Fig. 1), was calculated to be 404, and *Ne* was estimated at 206 due to male-biased sex ratio, variance in offspring number, and overlapping generations. F_{ST} was estimated at 0.005 after correction for a finite number of colonies in a reduced portion of the species range.

The number of colonies was increased from six to 150 to approximately represent the entire species range in western North America as estimated from wintering numbers (Robertson and Goudie 1999) and on the geographical extent of the range, assuming roughly similar spacing and colony sizes as in this study area. With this increase in number of colonies, F_{ST} increased to 0.11. F_{ST} was robust to decreases in *Ne* and to changes in m_{adj}. Reducing *Ne* from 206 to 30 only increased F_{ST} from 0.11 to 0.15, given m_{adj} of

Table 3. Annual movement rates (proportion of individuals per year) for Harlequin Ducks between pairs of locations in the Strait of Georgia (White Rock [WR], Point Roberts [PR], Hornby [HO], Comox [CX], Campbell River [CR]), 1994-2000. Estimates for the sexes combined, and for the sexes separately, were generated by the models ϕ (sex) p (location*time) ψ (distance) and ϕ (sex) p (location*time) ψ(sex*distance), respectively (see Table 2).

			Movement rates for the sexes combined			Sex-specific movement rates	
First Location	Second Location	Distance apart (km)	Estimate ± SE	Lower CI	Upper CI	Males	Females
WR	PR	15	0.046 ± 0.009	0.031	0.066	0.048 ± 0.011	0.040 ± 0.015
HO	CX	30	0.034 ± 0.006	0.024	0.047	0.036 ± 0.007	0.029 ± 0.001
CX	CR	35	0.031 ± 0.005	0.022	0.042	0.032 ± 0.006	0.026 ± 0.008
HO	CR	65	0.017 ± 0.003	0.012	0.023	0.018 ± 0.003	0.013 ± 0.005
PR	HO	140	0.004 ± 0.001	0.002	0.007	0.004 ± 0.002	0.002 ± 0.002
WR	HO	155	0.003 ± 0.001	0.001	0.006	0.003 ± 0.001	0.002 ± 0.002
PR	CX	170	0.002 ± 0.001	0.001	0.005	0.002 ± 0.001	0.001 ± 0.001
WR	CX	180	0.002 ± 0.001	0.001	0.004	0.002 ± 0.001	0.001 ± 0.001
PR	CR	210	0.001 ± 0.000	0.000	0.003	0.001 ± 0.001	0.000 ± 0.001
WR	CR	220	0.001 ± 0.000	0.000	0.002	0.001 ± 0.001	0.000 ± 0.001

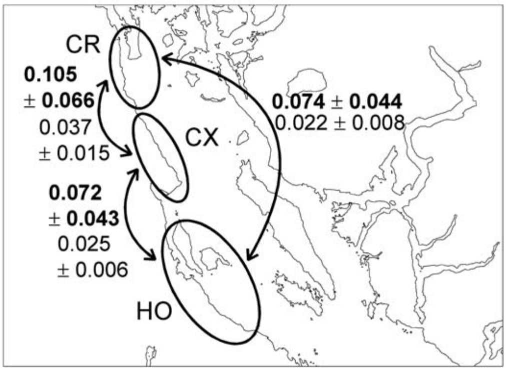

Figure 3. Annual movement rates (proportion of individuals per year ± SE) between pairs of locations in the northern Strait of Georgia (Campbell River [CR], Comox [CX], Hornby [HO]) for subadult (hatch year and second year) and adult (third year and after-third year) Harlequin Ducks. Movement rates of subadult birds are shown in bold text above those of adults.

0.16 and 150 colonies in the species range. Changing m_{adj} from 0.16 to 0.10 and 0.22 (in accordance with error around the average point estimate) resulted in F_{ST} values for the SOG of 0.006 and 0.004, respectively.

DISCUSSION

Low estimates of F_{ST} generated from Harlequin Duck movement rates in this study were comparable to those estimated from genetic analyses of two wintering populations in Alaska (Lanctot *et al.* 1999). Thus, movement of subadults at wintering areas can sufficiently explain the reported lack of genetic structuring. In this study F_{ST} was estimated from movement at wintering areas alone, thus it conservatively assumed that no genetic mixing occurred at breeding areas and that all juveniles arrived at wintering areas with their mothers. Pairs are dispersed at breeding areas, survival of males is high, and males depart once incubation begins, thus little genetic exchange outside of the pair bond is likely. However, some juveniles migrate without their biological mothers (Regehr *et al.* 2001) which might result in additional genetic mixing similar to that of winter dispersal. F_{ST} also could have been overestimated if movement outside of the study area occurred or if movement rates per gener-

Table 4. Model selection statistics for effects of sex and age on seasonal movement rates (molt to winter and winter to spawn seasons) for Harlequin Ducks in the northern Strait of Georgia, 1994-2000. Effects of time (*t*), sex (*sx*), location (*l*), age (*a*) and season (*s*) are indicated for survival (ϕ), sighting (*p*) and movement (ψ) rates; the '/' notation separates time effects (time dependence ['*t*'], or time held constant ["*c*"]) for subadult and adult age classes, respectively; l_c indicates that movement rates are constrained to be the same regardless of direction, and l_j indicates that the location effect on survival rates are specific to the subadult age class. Highest ranking models up to ΔQAIC$_c$ < 10 are presented.

Model	No. of parameters	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ weight
1) Sex: molt to winter ($\hat{c}$ = 4.23):				
$\phi(sx)\ p(l*t)\psi(l_c*s)$	47	2599.29	0.00	0.6254
$\phi(sx)\ p(l*t)\psi(l*s)$	53	2602.33	3.04	0.1371
$\phi(sx)\ p(l*t)\psi(sx)$	43	2602.49	3.20	0.1261
$\phi(sx)\ p(l*t)\psi(l_c*sx)$	47	2603.11	3.82	0.0926
$\phi(l*sx)\ p(l*t)\psi(l_c*s)$	51	2607.18	7.89	0.0121
2) Sex: winter to spawn ($\hat{c}$ = 3.78):				
$\phi(sx)\ p(l*t)\psi(l*s)$	52	2408.13	0.00	0.8783
$\phi(l*sx)\ p(l*t)\psi(l*s)$	56	2412.11	3.97	0.1205
3) Age: molt to winter ($\hat{c}$ = 4.17):				
$\phi(a-c/c)\ p(l*t)\psi(a-c/c)$	43	2602.85	0.00	0.4280
$\phi(a-c/c)\ p(l*t)\psi(l_c*s)$	47	2603.50	0.65	0.3092
$\phi(l_j*a-c/c)\ p(l*t)\psi(a-c/c)$	45	2606.14	3.29	0.0826
$\phi(a-c/c)\ p(l*t)\psi(l*s)$	53	2606.56	3.71	0.0669
$\phi(l_j*a-c/c)\ p(l*t)\psi(l_c*s)$	49	2607.01	4.16	0.0533
$\phi(l_j*a-c/c)\ p(l*t)\psi(l_c*a-c/c)$	49	2607.24	4.39	0.0477
$\phi(l_j*a-c/c)\ p(l*t)\psi(l*s)$	55	2610.09	7.24	0.0114
4) Age: winter to spawn ($\hat{c}$ = 3.62):				
$\phi(a-c/c)\ p(l*t)\psi(l*s)$	52	2474.19	0.00	0.7972
$\phi(l_j*a-c/c)\ p(l*t)\psi(l*s)$	54	2476.94	2.75	0.2015

ation are higher than the annual rates used. F_{ST} estimates from gene flow models are typically considered rough order of magnitude only due to simplifying model assumptions, potential for sampling error in movement statistics, and limited study time scale (Rockwell and Barrowclough 1987; Slatkin 1987). Sensitivity analyses concluded that F_{ST} was robust to potential error in factors used in the estimation of *Ne* and m_{adj}.

F_{ST} increased substantially when the number of colonies was increased to roughly approximate the entire western species range (F_{ST} = 0.11). Birds typically have low F_{ST} values, likely due to their extensive dispersal capabilities (Evans 1987). However, Kimura and Weiss (1964) demonstrated that populations diverge rapidly with increasing number of steps in a single dimension, and Barrowclough (1980) found that the one species most likely to show any genetic differentiation was the Silver Gull (*Larus novaehollandiae*) with a one-dimensional distribution along the Australian coastline. Similarly, genetic differences could develop in Harlequin Ducks because they are distributed along an extensive stretch of the western coastline of North America. Some indication of genetic structuring at this scale has been reported (Goatcher *et al.* 1999).

The lack of detectable difference in movement by sex was unexpected. Although the observed extreme philopatry (100%) of paired males likely reflects requirements of maintaining a multi-year pair bond and its value to the male (Savard 1985; Robertson and Cooke 1999), dispersal of unpaired males was expected to drive an overall difference between the sexes. Rather, unpaired males also showed high rates of philopatry (95%). Unpaired males may choose to court familiar females persistently rather than search for mates widely, especially because ecological benefits of philopatry and costs of dispersal are likely (Greenwood 1987; Anderson *et al.* 1992). Development of liai-

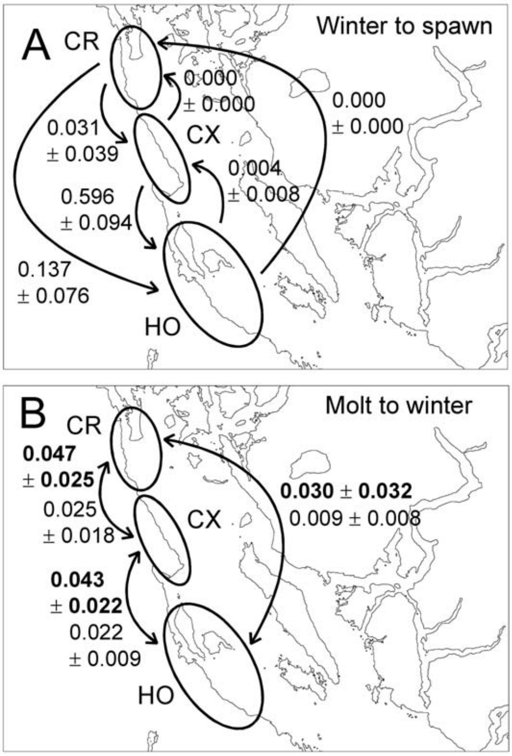

Figure 4. Seasonal movement rates (proportion of individuals per season ± SE) of Harlequin Ducks between pairs of locations in the northern Strait of Georgia (Campbell River [CR], Comox [CX], Hornby [HO]) for: A) from the winter to the spawn season for all age groups combined, and B) from the molt to the winter season for subadults (hatch year and second year) and adults (third year and after-third year). Movement rates of subadults are shown in bold text above those of adults.

sons to improve chances of future pairing has been suggested for males in other waterfowl species (Anderson 1985; McKinney 1992). Courtship of paired females by unpaired males is common in Harlequin Ducks (Rodway 2006) and some unpaired philopatric males were observed to pair within one to three years. Movement by paired females may reflect mate-sampling strategies and, in some cases, may facilitate divorce (Rodway 2006). Slightly higher point estimates in movement rates for males than females overall were consistent with slightly elevated levels of differentiation for maternally inherited mtDNA in comparison to nuclear microsatellite DNA in genetic studies (Lanctot *et al.* 1999).

Results of this study suggest that subadult Harlequin Ducks move farther and are more likely to move than adults of both sexes which tend to become site faithful regardless of their pairing success. Greater mobility of young than older individuals has been observed among birds in general (Greenwood and Harvey 1982) and in some species of waterfowl at breeding (Anderson *et al.* 1992) and wintering (Nichols and Hines 1987; Rienecker 1987; Baldassarre *et al.* 1988) areas. Younger individuals are less likely than older ones to be constrained to site faithfulness by the need to reunite with a mate, and they may gain less from ecological benefits because they have invested less time becoming familiar with an area (Nichols and Hines 1987). No difference by age found in Alaska (Iverson and Esler 2006) suggests that movement patterns of Harlequin Ducks may vary geographically, however sample size of subadult birds in that study was much smaller than in this study (62 *vs* 343).

Movement rates between the molt and winter seasons in the northern SOG were low, especially for adults (Fig. 4), with less than 5% of all individuals leaving each location. Similarly, studies in White Rock found that 96% of males wintered close to their molting sites (Breault and Savard 1999), and reports of higher rates of departure (Robertson *et al.* 2000) were likely due to a smaller search area. These results, and those from Alaska (Iverson and Esler 2006), all indicate that, unlike in eastern North America where molting and wintering sites are separated by great distances (Brodeur *et al.* 2002; Robert *et al.* 2008), Harlequin Ducks in western North America mainly spread out over a wider area following molt.

Results indicate that there is little difference in participation by sex or age in the annual aggregation by Harlequin Ducks at herring spawning sites in the northern SOG each spring. Movements to spawning sites do not represent dispersal or affect annual movement rates because most birds return to their wintering locations following spawn (Rodway *et al.* 2003a), however, they do have implications for genetic and demographic population structure. Pairing at spawning sites by individuals from different locations would lead to a change in wintering location by at least one partner, and therefore, pending successful reproduction, to gene flow. In fact, higher annual movement rates for subadults than adults may partly reflect the fact that half of subadult females pair in spring, whereas most mature females pair during winter (Rodway 2007b). Further, the potential for demographic independence, which implies no correlation in vital rates (Hanski 1991), is reduced if normally separate populations mix at some time. In the northern SOG herring spawn likely is an important late winter food source (Rodway and Cooke 2002) that may benefit survival, and thus demographic independence is unlikely. Where no such seasonal aggregation occurs, demographic independence is more likely (e.g. Esler *et al.* 2006; Iverson and Esler 2006). At the scale of the entire study area, low but quantifiable movement rates between the northern and southern SOG (Table 3), little mixing between these regions during the spawn season (Rodway *et al.* 2003a), and dispersal by both sexes (Avise 1995; Regehr 2003) suggests that a metapopulation distribution (MacArthur and Wilson 1967; Lande 1988) may function for Harlequin Ducks between the north and south ends of the study area and at a larger scale within the Pacific Coast of North America.

Conservation concern exists for Harlequin Ducks partly due to increasing human disturbance to their wintering and breeding areas. In addition, there appears to be an imbalance between recruitment and mortality; however, some uncertainty remains as estimates of apparent survival are likely biased low due to emigration (Rodway *et al.* 2003b). Higher movement rates and distances for subadults than adults in this study suggest that subadult survival rates are more likely to be underestimated and are best generated using radio telemetry or large search areas. Further, survival rates estimated from paired individuals, because they were thought most likely to be philopatric (Cooke *et al.* 2000), are likely to be accurate for males but may be underestimated for females. Although many variables, such as the spatial and temporal distribution of suitable habitat, likely influence movement rates, age and distance-specific movement rates estimated in this study should aid in the correction of local survival rates due to emigration in future studies.

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