AGE AND SEX RATIOS OF SEA DUCKS WINTERING IN THE STRAIT OF GEORGIA, BRITISH COLUMBIA: IMPLICATIONS FOR MONITORING

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SUMMARY

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In research on sea ducks, winter age and sex ratios provide valuable demographic data that are difficult to obtain by other means. Our objectives were to determine spatial, temporal, and density-related variability in (1) age and sex ratios for five sea duck species and (2) proportions of adult males for eight species that winter in the Strait of Georgia, British Columbia, Canada. Kilometre-long shoreline sections (n = 49–62) were surveyed in early February in three years: 2003, 2004, and 2014. Annual estimates for male age ratio (first year:adult male) varied significantly for Black Scoter *Melanitta americana* (0.071 to 0.170), Surf Scoter *M. perspicillata* (0.064 to 0.101) and Harlequin Duck *Histrionicus histrionicus* (0.068 to 0.138). Regional differences in male age ratio were found for Barrow's Goldeneye *Bucephala islandica* (0.034 to 0.197) and Common Goldeneye *B. clangula* (0.033 to 0.165), and more complex interactions were found between regions by year for Surf Scoter. Sex ratios were less variable than age ratios and varied consistently by year and region only for Common Goldeneye. Adult male proportions were correlated with but varied more than sex ratios and showed significant differences by year for Surf Scoter, Common Goldeneye and Bufflehead *B. albeola* and by region for Surf Scoter, Common Goldeneye, Bufflehead and Red-breasted Merganser *Mergus serrator*. Based on previous research that calculated expected confidence limits from different numbers of occupied survey sections, the sampling intensity for each species obtained in this study provided age ratio estimates with 95% confidence limits likely within ± 5% for Surf Scoters and ± 3% for Harlequin Ducks. Regional and density-related differences in age ratios, sex ratios and adult male proportions indicated segregation and emphasize the need for broad-scale sampling to achieve representativeness. Inter-annual differences may indicate demographic changes, but few comparative data exist, and several consecutive years of surveys are needed to provide baseline data.

Key words: age and sex segregation, age ratio, demographics, goldeneye, Harlequin Duck, immature plumage, Mergini, sea ducks, scoter, sex ratio, waterfowl

INTRODUCTION

Life history traits of delayed sexual maturity, high annual survival and low fecundity and recruitment rates make sea duck (taxonomic tribe Mergini) populations resilient to short-term fluctuations in reproductive performance but slow to recover from population impacts (Goudie *et al.* 1994, Iverson & Esler 2010, Wilson *et al.* 2012). Distributions at sea often overlap areas of human activity, and wintering populations are stressed by hunting, habitat loss and oil-spill-related mortality (Esler *et al.* 2000, De La Cruz *et al.* 2013). Although population dynamics are most sensitive to changes in adult survival rates, those rates may be relatively invariant. As a result, population trends may be most affected by variation in reproductive parameters and recruitment rates (Wilson *et al.* 2012). Estimating and monitoring recruitment is thus especially important for sea duck species (Flint 2015). Apparent declines in the 1990s of many Mergini led to heightened concern for Pacific populations (Goudie *et al.* 1994, Petersen & Hogan 1996) and to the formation of the Sea Duck Joint Venture (SDJV). More recently, British Columbia Coastal Waterbird Surveys (BCCWS) in the Strait of Georgia have indicated declines in five species since 1999 (Crewe *et al.* 2012). Population dynamics of sea ducks are generally poorly understood, and demographic data are needed to assist in the management of all species (Sea Duck Joint Venture 2008).

Age and sex ratios have long been used as demographic tools in the management of a variety of taxa (Bellrose *et al.* 1961, Harris *et al.* 2008, Citta *et al.* 2014). Obtaining demographic data using some common methods is more difficult for sea ducks than for other waterfowl species (Iverson *et al.* 2004). Consequently, the use of relatively easy-to-determine winter sex and age ratios to infer population demographics has particular value for this group of waterfowl, and models have been developed to estimate population trends from such data (Robertson 2008). However, spatial and temporal variation in these ratios may lead to differing conclusions, and most available data on age, sex ratios and survival rates yield a mismatch between inferred and observed population trends. It is therefore valuable to document potential variability in age and sex ratios in time and space, and, if possible, to relate them to independent measures of population status.

The Strait of Georgia in coastal British Columbia (BC) is an important wintering area for 11 Mergini species, many of which occur there in globally or continentally significant proportions (Vermeer 1982, Savard 1989, Campbell *et al.* 1990, Gaydos &

Pearson 2011, Crewe *et al.* 2012). A variety of long-term survey programs are underway to monitor numbers of wintering marine birds in the Strait of Georgia and the larger Salish Sea area (Fig. 1; Sauer *et al.* 1996, Anderson *et al.* 2009, Bower 2009, Crewe *et al.* 2012), but information on the demographic composition of wintering populations is poor (Smith *et al.* 2001, Rodway *et al.* 2003a, Iverson *et al.* 2004). Among Mergini that winter in the Strait of Georgia, first-year males can be reliably distinguished from adult males via field observation for Black Scoter *Melanitta americana*, Surf Scoter *M. perspicillata*, Harlequin Duck *Histrionicus histrionicus*, Barrow's Goldeneye *Bucephala islandica* and Common Goldeneye *B. clangula*, thereby allowing identification of three demographic classes (adult males, first-year males, and adult females and first-year females combined) and permitting estimation of age and sex ratios for these species. For other species, immature males are difficult to distinguish from females, making it practical only to separate adult males from all other demographic classes combined (adult females and first-year individuals of both sexes).

The objectives of this study were to (1) estimate demographic ratios and their temporal variability for wintering Mergini species; (2) relate variation in demographic parameters to local bird densities; (3) review available data on sea duck sex and age ratios from other studies; and (4) evaluate age ratios as an index of recruitment in light of reported population trends and survival rates. The Strait of Georgia is ideal for documenting and evaluating spatial and temporal variability in sex and age ratios of sea ducks because of its importance as a wintering area and its extensive sheltered marine waters, shorelines and estuaries that are well suited to shoreline surveys.

METHODS

Mid-winter surveys were conducted from the end of January to mid-February, when age class determinations are most reliable (Smith *et al.* 1998, Iverson *et al.* 2003, Leukering 2012) and winter distributions are stable (Rodway *et al.* 2003b). In 2003, we established 49 kilometre-long survey sections (hereafter, km-sections) with geo-referenced start and end points. These sections were first surveyed in 2003, then resurveyed, along with 13 additional sites, in 2004 (Iverson *et al.* 2006). Sample size was based on previous research in the study area indicating that about 60 km-sections containing about 1 000 males in total surveyed from land could provide age-ratio estimates with 95% confidence limits of ± 2% for Harlequin Ducks (Rodway *et al*. 2003a) and ± 5% for Surf Scoters (Iverson *et al*. 2004). In 2014, all established km-sections, except nine in the Lower Mainland region, were resurveyed. Survey sections were widely distributed across the Strait of Georgia (Fig. 1), but clustered logistically into three separated geographic areas that were used for regional comparisons: (1) Lower Mainland, including Boundary Bay, Fraser Delta, English Bay and Burrard Inlet (14 km-sections); (2) Sunshine Coast, from Gibsons to Powell River (12 km-sections); and (3) Vancouver Island, from French Creek to Campbell River, including Denman, Hornby and Quadra islands (36 km-sections).

Experienced observers walking the shoreline identified and counted birds within 500 m of shore using binoculars and 20–60× spotting scopes. The surveys were not conducted in fog, heavy rain or snow, or when sea conditions were Beaufort force 4 or higher.

First-winter (1Y) males of Black and Surf Scoter, Harlequin Duck, and Barrow's and Common Goldeneye were identified by their partial male plumage (Smith *et al.* 1998, 2001, Rodway *et al.* 2003a, Iverson *et al.* 2004, Alderfer 2006, Leukering 2012), and age and sex ratios were determined for these species in all years. Sub-sampling was only occasionally required for large flocks or those that were diving. Male age ratio was calculated as the ratio of 1Y males to adult males, which corresponds to the way recruitment is typically indexed in waterfowl (Cowardin & Blohm 1992) and the way age ratios have been used in population models (Robertson 2008), but differs from the way it has been reported by others (Smith *et al.* 2001, Mittelhauser *et al.* 2002, Caron & Paton 2007, Gardarsson 2008). The latter used the ratio of immature males to the total number of males (see also Rodway *et al.* 2003a, Iverson *et al.* 2004); in such cases we recalculated age ratio estimates as the ratio of 1Y male:adult male to allow comparison. Sex ratio was defined as the ratio of all males to all females. Ratios of adult males to all other birds have often been reported as sex ratios in previous studies, but that measure better corresponds to adult male proportions reported here. Female age ratio was calculated by assuming that the number of 1Y females was equivalent to the number of 1Y males, a reasonable assumption given that secondary sex ratios are generally equal and that survival rates do not differ between the sexes for subadults in waterfowl (Bellrose *et al.* 1961, Johnson *et al.* 1992, Blums & Mednis 1996, Sun *et al.* 2011).

Adult males were distinguished from birds in female-like plumage, which included females and 1Y males, for White-winged Scoter *Melanitta fusca*, Bufflehead *Bucephala albeola* and Red-breasted Merganser *Mergus serrator* in 2004 and 2014. Adult male proportion was calculated as the number of adult males divided by the total number of birds. Although likely correlated with sex ratios, adult male proportions were also determined in all years for Black and Surf Scoters, Harlequin Duck, and Barrow's and Common Goldeneye to allow comparisons of these parameters among all species. Other Mergini species wintering in the Strait of Georgia were not well sampled in our survey sections and are not included in this study.

Statistical analysis

Log-linear analyses were used to determine associations with year and region for age ratios, sex ratios and adult male proportions.

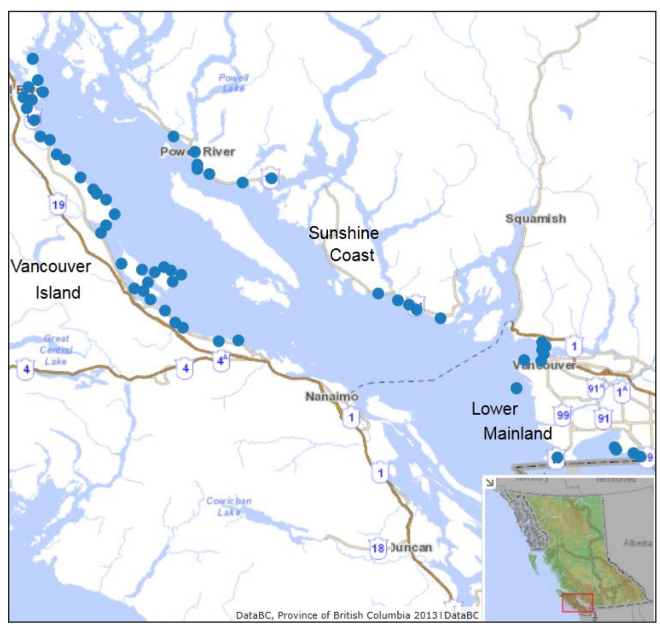

Fig. 1: Locations of one kilometre sections used to surveys sea ducks in the Strait of Georgia, British Columbia, 2003, 2004 and 2014.

Numbers of adult males relative to numbers of other birds (females plus 1Y males) were tabulated to analyze adult male proportions. Using SYSTAT 13, best-fitting models were chosen from a saturated model by excluding interaction terms that did not contribute significantly to model fit, based on changes in likelihood-ratio chi-square (*G*; Sokal & Rohlf 1995). The relationship of age ratios, sex ratios and adult male proportions to numbers of conspecifics per km-section was tested using *G*-tests in order to evaluate segregation in relation to abundance. The metric "numbers of conspecifics per km-section" rather than "flock size" was used in these analyses, as it was found to be difficult and arbitrary to define flock sizes because birds were relatively continuously distributed and because flock sizes and compositions changed during surveys.

RESULTS

Sampling intensity

Differences in percent occurrence and abundance of species within surveyed km-sections resulted in variation in sampling intensity among species. Percent occurrence was highest for Bufflehead and Surf Scoters and was lowest for Barrow's Goldeneye (Table 1). Numbers of individuals in all km-sections combined were highest for Surf and White-winged Scoters and Harlequin Ducks, and lowest for Red-breasted Mergansers and Barrow's Goldeneye (Tables 2 and 3). Regional distribution varied among species, and differences in numbers counted by year partly reflected the number of km-sections surveyed in each region. Low percent occurrence and low overall numbers of Barrows Goldeneye in 2014 likely reflected low survey effort in the Lower Mainland region in that year.

TABLE 1
Occurrence of sea duck species in surveys of the Strait of Georgia, British Columbia, 2003, 2004 and 2014

Species	% occurrence; year (number of km-sections surveyed)		
	2003 (49)	2004 (62)	2014 (53)
Black Scoter	59.2	48.4	39.6
White-winged Scoter	63.3	56.5	52.8
Surf Scoter	91.8	87.1	83.0
Harlequin Duck	77.6	80.6	75.5
Barrow's Goldeneye	42.9	43.5	24.5
Common Goldeneye	91.8	74.2	84.9
Bufflehead	95.9	93.5	86.8
Red-breasted Merganser	65.3	74.2	66.0

Male age ratios

Male age ratio (1Y males to adult males) was generally highest for Black Scoter and Common Goldeneye and lowest for Barrow's Goldeneye (Table 2). Log-linear models indicated significant associations between male age ratios and year for Black and Surf Scoter and Harlequin Duck, and between age ratios and region for Surf Scoter and Barrow's and Common Goldeneye (Appendix 1, available on the web site). Male age ratios were highest in 2003 and lowest in 2014 for Black Scoters, ranging from 0.071 to 0.170, and were highest in 2014 and lowest in 2003 for Harlequin Ducks, ranging from 0.068 to 0.138 (Table 2). Regional differences for Barrow's Goldeneye ranged from 0.034 on the Sunshine Coast to 0.197 on Vancouver Island, and for Common Goldeneye from 0.033 on the Sunshine Coast to 0.165 on Vancouver Island for all years combined. Male age ratio was lowest on the Sunshine Coast in all years for both species, and highest on Vancouver Island in most years (for Barrow's Goldeneye) or all years (for Common Goldeneye).

For Surf Scoter, the three-way interaction term of age class, year and region contributed significantly to model fit, making the interpretation of year and region effects more complicated. The interaction of year and region was significant for all species except Harlequin Duck (Appendix 1). This reflects expected variability in bird numbers in km-sections and indicates that, for four of the five species, yearly and regional variation in numbers of birds in survey sections had a major influence on cell frequencies in log-linear models. Harlequin Duck numbers showed little variation relative to the other species.

TABLE 2
Demographic ratios of five sea duck species surveyed in the Strait of Georgia, British Columbia, 2003, 2004 and 2014

Species	Year	Region[a]	Number					Ratio or proportion			
			Total[b]	Female[c]	Male	Adult male	1Y male	Male age	Sex (male/ female)	Adult male	Female age
Black Scoter	2003	LM	108	17	34	32	2	0.063	2.000	0.627	0.133
		SC	102	24	79	70	9	0.129	3.292	0.680	0.600
		VI	563	156	409	344	65	0.189	2.622	0.609	0.714
		Total	773	197	522	446	76	0.170	2.650	0.620	0.628
	2004	LM	6	2	4	3	1	0.333	2.000	0.500	1.000
		SC	61	17	44	43	1	0.023	2.588	0.705	0.063
		VI	744	204	540	485	55	0.113	2.647	0.652	0.369
		Total	811	223	588	531	57	0.107	2.637	0.655	0.343
	2014	LM	4	2	2	2	0	0.000	1.000	0.500	0.000
		SC	26	7	19	18	1	0.056	2.714	0.692	0.167
		VI	533	158	325	303	22	0.073	2.057	0.627	0.162
		Total	563	167	346	323	23	0.071	2.072	0.630	0.160

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Species	Year	Region[a]	Number					Ratio or proportion			
			Total[b]	Female[c]	Male	Adult male	1Y male	Male age	Sex (male/ female)	Adult male	Female age
Surf Scoter	2003	LM	1039	280	473	438	35	0.080	1.689	0.582	0.143
		SC	225	71	154	152	2	0.013	2.169	0.676	0.029
		VI	1036	288	743	698	45	0.064	2.580	0.677	0.185
		Total	2300	639	1370	1288	82	0.064	2.144	0.641	0.147
	2004	LM	521	180	341	282	59	0.209	1.894	0.541	0.488
		SC	253	85	168	164	4	0.024	1.976	0.648	0.049
		VI	839	247	592	574	18	0.031	2.397	0.684	0.079
		Total	1613	512	1101	1020	81	0.079	2.150	0.632	0.188
	2014	LM	93	26	67	55	12	0.218	2.577	0.591	0.857
		SC	173	49	124	120	4	0.033	2.531	0.694	0.089
		VI	1643	679	821	744	77	0.103	1.209	0.496	0.128
		Total	1909	754	1012	919	93	0.101	1.342	0.520	0.141
Harlequin Duck	2003	LM	55	28	27	23	4	0.174	0.964	0.418	0.167
		SC	58	25	33	32	1	0.031	1.320	0.552	0.042
		VI	896	378	518	486	32	0.066	1.370	0.542	0.092
		Total	1009	431	578	541	37	0.068	1.341	0.536	0.094
	2004	LM	56	29	27	25	2	0.080	0.931	0.446	0.074
		SC	77	31	46	37	9	0.243	1.484	0.481	0.409
		VI	1154	490	664	610	54	0.089	1.355	0.529	0.124
		Total	1287	550	737	672	65	0.097	1.340	0.522	0.134
	2014	LM	52	25	27	24	3	0.125	1.080	0.462	0.136
		SC	62	26	36	33	3	0.091	1.385	0.532	0.130
		VI	967	402	565	495	70	0.141	1.405	0.512	0.211
		Total	1081	453	628	552	76	0.138	1.386	0.511	0.202
Barrow's Goldeneye	2003	LM	191	83	108	101	7	0.069	1.301	0.529	0.092
		SC	180	83	98	93	5	0.054	1.181	0.514	0.064
		VI	41	13	28	26	2	0.077	2.154	0.634	0.182
		Total	412	179	234	220	14	0.064	1.307	0.533	0.085
	2004	LM	253	101	152	144	8	0.056	1.505	0.569	0.086
		SC	75	29	46	46	0	0.000	1.586	0.613	0.000
		VI	59	18	41	31	10	0.323	2.278	0.525	1.250
		Total	387	148	239	221	18	0.081	1.615	0.571	0.138
	2014	LM	2	0	2	1	1	1.000		0.500	
		SC	66	28	38	37	1	0.027	1.357	0.561	0.037
		VI	28	12	16	14	2	0.143	1.333	0.500	0.200
		Total	96	40	56	52	4	0.077	1.400	0.542	0.111
Common Goldeneye	2003	LM	100	27	73	69	4	0.058	2.704	0.690	0.174
		SC	57	23	34	33	1	0.030	1.478	0.579	0.045
		VI	461	197	258	231	27	0.117	1.310	0.508	0.159
		Total	618	247	365	333	32	0.096	1.478	0.544	0.149
	2004	LM	49	8	41	38	3	0.079	5.125	0.776	0.600
		SC	68	22	46	45	1	0.022	2.091	0.662	0.048
		VI	515	170	345	295	50	0.169	2.029	0.573	0.417
		Total	632	200	432	378	54	0.143	2.160	0.598	0.370
	2014	LM	59	24	35	32	3	0.094	1.458	0.542	0.143
		SC	111	34	77	74	3	0.041	2.265	0.667	0.097
		VI	489	201	288	239	49	0.205	1.433	0.489	0.322
		Total	659	259	400	345	55	0.159	1.544	0.524	0.270

[a] Regions are Lower Mainland (LM), Sunshine Coast (SC) and Vancouver Island (VI).
[b] Totals do not always equal the sum of females and males because in some cases not all birds were sexed.
[c] Female includes first-year males for species in which first-year males were not distinguished.

Two-way analyses at each level of the third factor were used to investigate the significant three-way interaction for Surf Scoter: differences by year were significant in the Lower Mainland ($G_2 = 20.9$, $P < 0.001$) and Vancouver Island ($G_2 = 24.5$, $P < 0.001$) regions, but not on the Sunshine Coast ($G_2 = 1.23$, $P = 0.54$), where the age ratio was low in all three years (Table 2). Regional differences for Surf Scoter were consistent in 2003 ($G_2 = 10.3$, $P = 0.006$), 2004 ($G_2 = 65.4$, $P < 0.001$) and 2014 ($G_2 = 11.8$, $P = 0.003$), tending to be highest on the Lower Mainland and lowest on the Sunshine Coast in all years.

Male age ratio varied in relation to the total number of conspecifics present in a km-section for Surf Scoter but not for other species (Table 4). Surf Scoter age ratio was higher where there were larger numbers of birds.

TABLE 3
Adult male proportions of three sea duck species surveyed in the Strait of Georgia, British Columbia, 2003, 2004 and 2014

Species	Year	Region[a]	Total[b]	Female[c]	Adult male	Adult male proportion
White-winged Scoter	2004	LM	542	245	297	0.548
		SC	65	35	30	0.462
		VI	1628	775	853	0.524
		Total	2235	1055	1180	0.528
	2014	LM	18	12	6	0.333
		SC	17	9	8	0.471
		VI	685	328	357	0.521
		Total	720	349	371	0.515
Bufflehead	2004	LM	117	60	57	0.487
		SC	59	24	35	0.593
		VI	719	360	359	0.499
		Total	895	444	451	0.504
	2014	LM	76	52	24	0.316
		SC	107	52	55	0.514
		VI	962	584	378	0.393
		Total	1145	688	457	0.399
Red-breasted Merganser	2004	LM	38	25	13	0.342
		SC	22	10	12	0.545
		VI	187	109	78	0.417
		Total	247	144	103	0.417
	2014	LM	28	25	3	0.107
		SC	20	13	7	0.350
		VI	237	143	94	0.397
		Total	285	181	104	0.365

[a] Regions are Lower Mainland (LM), Sunshine Coast (SC) and Vancouver Island (VI).
[b] Totals do not always equal the sum of females and males because in some cases not all birds were sexed.
[c] Female includes first-year male for species in which first-year males were not distinguished.

Sex ratios

Sex ratios (all males to all females) tended to be highest for the two scoter species, and annual estimates ranged from 1.3 for Harlequin Ducks and Barrow's Goldeneye to 2.6 for Black Scoters (Table 2). Log-linear models indicated significant associations between sex ratio and year and between sex ratio and region only for Common Goldeneye (Appendix 1). Male bias in the Common Goldeneye sex ratio was highest in 2004 and in the Lower Mainland region (Table 2). The three-way interaction between sex class, year and region contributed significantly to model fit for Surf Scoter (Appendix 1). Two-way analyses for Surf Scoter revealed significant annual differences in the Vancouver Island ($G_2 = 100.7$, $P < 0.001$) region but not in the Lower Mainland ($G_2 = 3.53$, $P = 0.17$) or Sunshine Coast ($G_2 = 1.33$, $P = 0.51$) regions, and significant regional differences in 2003 ($G_2 = 17.1$, $P < 0.001$) and 2014 ($G_2 = 28.0$, $P < 0.001$) but not in 2004 ($G_2 = 4.34$, $P = 0.11$). In the Vancouver Island region, male bias in the Surf Scoter sex ratio was lower in 2014 than in 2003 and 2004 (Table 2). Because of these annual differences in the Vancouver Island region, regional differences for Surf Scoter were not consistent across years: the Vancouver Island region had the overall highest male bias in 2003 and the lowest in 2014. The interaction of year and region was again significant for all species except Harlequin Duck (Appendix 1).

Sex ratio varied in relation to the total number of conspecifics present in a km-section for Black and Surf Scoter and Common Goldeneye (Table 4). Trends were contrary for Black Scoter, which had the highest male-biased sex ratio where the density of birds was highest, and for Surf Scoter and Common Goldeneye, for which male bias was lowest where there were larger numbers of birds.

Adult male proportions

Adult male proportions (adult males to total birds) were generally highest for Black and Surf Scoters and lowest for Red-breasted Mergansers and Buffleheads (Tables 2 and 3). As expected, samples from each year and region showed a high correlation between adult male proportion and sex ratio ($r_s = 0.84$, $P < 0.001$, n = 44) for the five species for which sex ratios were estimated. However, results of analyses for adult male proportions differed somewhat from those for sex ratios for these species, especially for Surf Scoter (Appendices 1 and 2, available on the web site).

Log-linear models indicated a significant association between adult male proportions and year for Surf Scoter, Common Goldeneye and Bufflehead, and between adult male proportions and region for Surf Scoter, Common Goldeneye, Bufflehead and Red-breasted Merganser (Appendix 2). The three-way interaction between sex class, year and region was significant for Surf Scoter. The interaction of year and region was significant for all species except Harlequin Duck and Red-breasted Merganser, indicating relatively consistent numbers in km-sections for these two species among regions and years. Adult male proportions were highest in 2004 and lowest in 2014 for Common Goldeneye and Bufflehead (Tables 2 and 3). Regionally, adult male proportions were lowest on Vancouver Island for Common Goldeneye and on the Lower Mainland for Bufflehead and Red-breasted Merganser.

Two-way analyses were again used to interpret the significant three-way interaction for Surf Scoter. As with sex ratios, there were significant yearly differences in adult male proportions in the Vancouver Island region (G_2 = 117.8, P < 0.001) but not in the Lower Mainland (G_2 = 2.29, P = 0.32) or Sunshine Coast (G_2 = 1.01, P = 0.60) regions (Table 2). There were significant regional differences in adult male proportions in all three years: 2003 (G_2 = 18.4, P < 0.001), 2004 (G_2 = 28.3, P < 0.001) and 2014 (G_2 = 26.9, P < 0.001), unlike sex ratios, which differed only in 2003 and 2014. In the Vancouver Island region, adult male proportions were lower in 2014 than in 2003 and 2004 (Table 2). As a result of these annual differences in the Vancouver Island region, regional differences for Surf Scoters were not consistent across years: the Vancouver Island region had the overall highest proportions in 2003 and 2004, and the lowest in 2014.

Adult male proportions varied in relation to the total number of conspecifics present in a km-section for Black and Surf Scoters, Common Goldeneye and Red-breasted Merganser (Table 5). As with sex ratios, trends in adult male proportions were contrary for Black Scoter, which had the highest adult male proportion where densities were highest (> 100 birds/km), although adult male proportion was lowest at intermediate densities (51–100 birds/km), and for Surf Scoter, Common Goldeneye and Red-breasted Merganser, for which adult male proportions were lowest where there were larger numbers of birds.

Female age ratios

Calculated female age ratios (1Y females to adult females) were sensitive to differences in sex ratios and varied more than observed male age ratios (Table 2). Similar to male age ratios, female age ratios were generally highest for Black Scoter and Common Goldeneye, and lowest for Barrow's Goldeneye. As well, they showed considerable variability among years and regions.

DISCUSSION

Results of this study indicate spatial and temporal variability in age ratios for most sea duck species surveyed, which has implications for temporal replication and spatial scale of a monitoring program. Male age ratios varied by year for Black and Surf Scoters and Harlequin Duck, and by region for Surf Scoter, and Barrow's and Common Goldeneye. The magnitude of variation was substantial in some cases, such as the temporal range observed for Black Scoter (0.071 to 0.170) and the spatial variation found for all species for which regional differences were documented (e.g., 0.034 to 0.197 for Barrow's Goldeneye). Few data allow comparison of these results with other years and areas or evaluation of potential causes of variability; such data are available only for Surf Scoters and Harlequin Ducks. Iverson *et al.* (2004) also found significant yearly variation in Surf Scoter age ratios on the Pacific Coast, with overall averages somewhat higher than in this study (male age ratio of 0.110 and female age ratio of 0.230), indicating that high variability is common for this species and must be considered in monitoring design. For Harlequin Ducks, previously observed male age ratios on the Pacific coast ranged from 0.073 to 0.098 (Rosenberg & Petrula 1998, Smith *et al.* 2001 [recalculated], Rodway *et al.* 2003a, Rosenberg *et al.* 2005), which are lower than those from our study but similar to those from Iceland (0.099; recalculated from data in Gardarsson 2008). Somewhat higher and increasing age ratios were associated with historically increasing populations of Harlequin Ducks in Maine (overall age ratio of 0.128 from 1989 to 1999;

TABLE 4
Variation in age and sex ratio in relation to density of conspecifics in the Strait of Georgia, British Columbia, 2003, 2004 and 2014

Species	Number of conspecifics per km-section	First-year male	Adult male	Female	Age ratio	Sex ratio	Age ratio *G*-test	Sex ratio *G*-test
Black Scoter	1–20	20	233	115	0.086	2.20	G_3 = 2.79, P = 0.43	G_3 = 14.9, P = 0.002
	21–50	32	245	120	0.131	2.31		
	51–100	33	251	145	0.131	1.96		
	101–200	71	571	207	0.124	3.10		
Surf Scoter	1–20	30	448	227	0.067	2.11	G_4 = 26.0, P < 0.001	G_4 = 47.6, P < 0.001
	21–50	27	700	303	0.039	2.40		
	51–100	70	808	430	0.087	2.04		
	101–200	58	629	466	0.092	1.47		
	201–600	71	642	479	0.111	1.49		
Harlequin Duck	1–20	33	307	267	0.107	1.27	G_3 = 1.40, P = 0.71	G_3 = 1.82, P = 0.61
	21–50	68	722	598	0.094	1.32		
	51–100	68	621	479	0.110	1.44		
	101–200	9	115	90	0.078	1.38		
Barrow's Goldeneye	1–20	12	154	118	0.078	1.41	G_2 = 2.18, P = 0.34	G_2 = 2.54, P = 0.28
	21–50	15	160	104	0.094	1.68		
	51–100	9	179	145	0.050	1.30		
Common Goldeneye	1–20	59	481	300	0.123	1.80	G_2 = 1.03, P = 0.60	G_2 = 23.7, P < 0.001
	21–50	56	374	206	0.150	2.09		
	51–100	26	201	200	0.129	1.14		

recalculated from Table 1 in Mittelhauser *et al.* 2002) and Rhode Island (0.15; recalculated from Caron & Paton 2007). A high male age ratio (0.382), indicative of a local hot spot, was reported from a small population on the Wolves Archipelago, Bay of Fundy (Hicklin & Barrow 2008). Such unusually high values likely reflect unusual population parameters (e.g., population growth) or sampling scale, similar to the 0.243 reported for the Sunshine Coast in 2004 in our study. Given that Harlequin Ducks were well represented in km-sections surveyed in all years, annual differences from this study likely reflect variation in productivity.

In contrast to age ratios, sex ratios were relatively constant in this study, and significant variability was observed only for Common Goldeneye and Surf Scoter. As expected, adult male proportions were correlated with sex ratios, and the two measures showed similar variability. We therefore suggest that adult male proportions can serve as a surrogate measure for sex ratio when 1Y males cannot be reliably distinguished, although adult male proportions will be more sensitive than sex ratios to the proportion of immature birds in the population. For example, male bias in Black Scoter sex ratio was higher and adult male proportion was lower in 2003 than 2014, likely because age ratio was higher in 2003 than 2014 (Table 2). Sex ratios estimated in this study are similar to those previously reported on the Pacific coast for Surf Scoter (1.9, Iverson *et al.* 2004) and Harlequin Duck (1.4–1.5, Smith *et al.* 2001, Rodway *et al.* 2003a, Rosenberg *et al.* 2005). Mid-winter surveys conducted throughout the Strait of Georgia in 1951–1952 by Mitchell (1952) and in the Lower Mainland region in 1980–1983 by Savard (1989) provide some comparisons of adult male proportions (reported as sex ratios in original sources and recalculated to allow comparisons). Estimates from Mitchell (1952), Savard (1989) and this study for Black Scoter (0.51, 0.65, 0.64, respectively), Surf Scoter (0.71, 0.68, 0.60), Harlequin Duck (0.68, 0.62, 0.52) and Barrow's Goldeneye (0.52, 0.60, 0.55) indicate possible declines in adult

TABLE 5
Variation in adult male proportions[a] in relation to density of conspecifics in the Strait of Georgia, British Columbia, 2003, 2004 and 2014

Species	Number of conspecifics per km-section	Adult male	Female plus first-year male	Adult male proportion	G-test
Black Scoter	1–20	233	135	0.633	
	21–50	245	152	0.617	$G_3 = 10.3$, $P = 0.016$
	51–100	251	178	0.585	
	101–200	571	278	0.673	
White-winged Scoter	1–20	178	157	0.531	
	21–50	118	120	0.496	
	51–100	204	192	0.515	$G_4 = 2.66$, $P = 0.62$
	101–200	514	483	0.516	
	201–600	537	452	0.543	
Surf Scoter	1–20	448	257	0.635	
	21–50	700	330	0.680	
	51–100	808	500	0.618	$G_4 = 65.9$, $P < 0.001$
	101–200	629	524	0.546	
	201–600	642	550	0.539	
Harlequin Duck	1–20	307	300	0.506	
	21–50	722	666	0.520	$G_3 = 1.30$, $P = 0.73$
	51–100	621	547	0.532	
	101–200	115	99	0.537	
Barrow's Goldeneye	1–20	154	130	0.542	
	21–50	160	119	0.573	$G_2 = 0.90$, $P = 0.64$
	51–100	179	154	0.538	
Common Goldeneye	1–20	481	359	0.573	
	21–50	374	262	0.588	$G_2 = 16.1$, $P < 0.001$
	51–100	201	226	0.471	
Bufflehead	1–20	271	311	0.466	
	21–50	352	431	0.450	$G_2 = 2.49$, $P = 0.29$
	51–100	285	390	0.422	
Red-breasted Merganser	1–20	163	222	0.423	$G_1 = 7.05$, $P = 0.008$
	21–50	44	103	0.299	

[a] Analysis of frequency of adult males to females and first-year males.

male proportions for Surf Scoter and Harlequin Duck. However, inter-annual variation in this study was similar to variation among studies, and inference of long-term trends is unwarranted without additional evidence. Mitchell (1952) also documented higher adult male proportions for White-winged Scoter (0.60), Common Goldeneye (0.73) and Bufflehead (0.62) than found in this study.

The target sample size of 62 km-sections was based on previous studies of Harlequin Ducks and Surf Scoters that calculated expected confidence limits for estimating age ratios from different numbers of occupied km-sections (Rodway *et al*. 2003a, Iverson *et al*. 2004). Because of the high percent occurrence in km-sections (83% to 92%) in this study, sampling intensity reached our desired target for Surf Scoters of over 1 000 males in each year, predicted to produce age-ratio estimates with 95% confidence limits of ± 5% (Iverson *et al*. 2004). For Harlequin Ducks, percent occurrence of 75% to 81% resulted in sampling of only 600 to 700 males per year rather than the target 1 000, providing estimates with 95% confidence limits likely within ± 3% (Rodway *et al*. 2003a). Reduced percent occurrence of individual species is a consequence of including multiple species in a single monitoring program, owing to the need to include habitats occupied by each species. The overall number of samples must therefore be increased to compensate. Alternatively, sampling greater lengths of shoreline would increase habitat and species representation within individual samples but would present greater accessibility problems and reduce feasible sample sizes, given budget constraints. Kilometre-long sections, as used in this study, are recommended as a good compromise, considering desired sample sizes, occurrence and abundance of different species, and accessibility and other logistical constraints.

Regional differences in age and sex ratios most likely reflect segregation and emphasize the need for broad-scale sampling to provide representative estimates. Age ratios were lowest on the Sunshine Coast for all three species that showed regional differences, and surveys conducted only in that region would have yielded biased estimates. Sexual segregation is common in diving ducks (summarized in Rodway 2007), and local sex or age segregation during mid-winter in the Strait of Georgia has previously been reported for Surf Scoters (Iverson *et al.* 2004), Harlequin Ducks (Smith *et al.* 2001, Rodway *et al.* 2003a), Barrow's Goldeneye (Eadie *et al.* 2000) and Red-breasted Mergansers (Kahlert *et al.* 1998, Coupe & Cooke 1999). Because the choice and size of the survey area can have major implications for our understanding of age and sex ratios, sampling should consider the scale of segregation for each species. The scale of this study was adequate to accommodate local age- and sex-related segregation, such as reported for Harlequin Ducks (Smith *et al.* 2001, Rodway *et al.* 2003a), but more robust estimates for species that may exhibit broad-scale segregation would be obtained by widening the sampling area. Further data on age and sex segregation in sea duck species would help evaluate potential scale-related biases for monitoring.

Differences in ratio estimates in relation to bird densities provide evidence of population structuring at finer scales. Surf Scoter age ratios were higher where there were larger numbers of birds, concurring with the findings of Iverson *et al.* (2004) that 1Y males cluster in larger flocks. Sex ratios or adult male proportions or both varied in relation to abundance for Black and Surf Scoters, Common Goldeneye and Red-breasted Merganser. For Black Scoter, sex ratios and adult male proportions were highest where densities were highest, while for Surf Scoter, Common Goldeneye and Red-breasted Merganser sex ratios or adult male proportions or both were lowest where there were larger numbers of birds. Iverson *et al.* (2004) also found that female proportions were higher in larger flocks of Surf Scoters. Structuring in relation to bird density and the highly clumped distribution of large flocks, especially for scoter species, presents a sampling challenge. For example, in one km-section in the Lower Mainland region, a large flock of scoters was present in all years, but in 2014 it occurred too far offshore to be included in the count. Thus, for scoter species especially, numbers of sections surveyed need to be large enough to accommodate such variability and provide representative samples from highly clumped distributions (Iverson *et al.* 2004).

Age ratios in relation to survival rates can be used to estimate population growth rates for sea duck species. Robertson's (2008) model suggests that survival rates of 75% and 65% require female age ratios of approximately 0.35 and 0.60 for population stability, respectively. Results of this study indicate that only Black Scoters have a female age ratio (0.362 over all regions and years) that approaches the magnitude required for population stability according to estimated female survival rates (77%; summarized in Rodway 2007). For other species, either age-ratio or female survival estimates or both are biased, or the populations are declining. Common Goldeneye had the second-highest female age ratio in this study (0.250 over all regions and years), consistent with a relatively low survival rate (66%), but still exhibits a declining population according to the model. Other studies have found higher survival rates for Common Goldeneye (80%, 83%; Barker & White 2001, Ludwichowski *et al.* 2002), but those studies were conducted where hunting was absent.

Population parameters such as survival rates, age ratios and population trends are estimates with many sources of error. Two potential sources of bias are particularly relevant when interpreting population dynamics from age ratios and survival rates. First, female survival rates are typically biased low because mortality is frequently confounded with emigration (Clobert & Lebreton 1991). Second, juvenile age ratios are typically underestimated owing to factors such as juvenile misidentification (e.g., Rodway *et al.* 2003a), segregation (Rodway *et al.* 2003a, Iverson *et al.* 2004, this study) and greater mobility (e.g., Rodway *et al.* 2003a, Regehr 2011). For Harlequin Ducks, attempts have been made to correct biases in female survival rates and age ratios. Rodway *et al.* (2003a) developed a correction factor for misidentification of juveniles at greater distances offshore (resulting in a corrected female age ratio of 0.152) and compared this to a survival rate calculated from paired females only (76%), which are thought to be highly site-faithful (Cooke *et al.* 2000). However, in spite of attempted corrections, population stability was not indicated. Nevertheless, stable or increasing populations have been reported for Maine (Mittelhauser 2008) and Alaska (Rosenberg *et al.* 2005) in association with age ratios and survival estimates similar to those estimated elsewhere, indicating that stable Harlequin Duck populations exhibit some discrepancy between recruitment estimated by age ratios and survival rates. Although accuracy of survival and recruitment estimates could likely be improved by more intensive study, such discrepancies may be inevitable at the practical scale of most studies, and winter age ratios may generally underestimate recruitment. However, they can still serve to monitor changes as long as there are adequate baseline data, collected in standardized fashion.

Changes in winter age and sex ratios, especially when associated with trends or supported by observations from other monitoring programs, can function as warning signals. However, a number of challenges exist in monitoring sea duck demographics using ratio estimates. First, it can be difficult to distinguish between alternative explanations for changes in ratio estimates (Harris *et al.* 2008). For example, an increase in age ratio may indicate either increased recruitment or reduced male survival, and a change in the proportion of adult males may be caused by changes in male survival or female survival or in recruitment. Thus, although our ability to interpret observed changes is superior when we can compare among ratios (e.g., analysis of sex ratios may permit distinction of the roles of recruitment and adult survival in age ratios), additional information, such as that provided by other monitoring programs, improves interpretation of results regardless of whether two or three demographic classes can be distinguished. Second, differences in survey timing, survey locations and habitats sampled, and quality of species detection and identification among monitoring programs may limit their comparability (Anderson *et al.* 2009, Bower 2009). Finally, the effectiveness of monitoring studies may differ by species owing to distribution characteristics, the ability to distinguish demographic classes, and demographic segregation. We therefore recommend that (1) numbers for all demographic classes that can be distinguished be reported (Smith *et al.* 2001, Robertson 2008), (2) standardized definitions for age and sex ratios be adopted, (3) limitations and biases in survey methods be evaluated, (4) broad-scale sampling be conducted to account for spatial segregation, and (5) several consecutive years of surveys be conducted to provide baseline data.

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