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Resource selection and space use by sea ducks during the non-breeding season: Implications for habitat conservation planning in urbanized estuaries

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ABSTRACT

Wide-ranging marine birds rely on multiple habitats for wintering, breeding, and migrating, and their conservation may be dependent on protecting networks of key areas. Urbanized estuaries are critical wintering and stopover areas for many declining sea ducks in North America; however, conservation measures within estuaries are difficult to establish given lack of knowledge about habitat use by these species and the variety of competing human interests. We applied hierarchical modeling to evaluate resource selection of sea ducks (surf scoters, *Melanitta perspicillata*) wintering in San Francisco Bay, California, USA, a large and highly urbanized estuary. We also examined their distribution, home range, and movements with respect to key habitat features and regions within the estuary. Herring roe was the strongest predictor of bird locations; however, eelgrass, water depth and salinity were also highly-ranked, with sea ducks using deeper areas of higher salinity associated with herring roe and eelgrass presence during mid-winter. Sea ducks were also strongly associated with ferry routes, suggesting these areas may contain resources that are too important to avoid and emphasizing the need to better understand water traffic effects. Movements and home range size differed between males and females in early winter but became more similar in late winter. Birds traveled farther and used several sub-bays in early winter compared to mid-winter when herring roe availability peaked in the Central Bay. Our findings identified key environmental variables, highlighted core use areas, and documented critical periods for consideration when developing conservation plans for sea ducks in urbanized estuaries.

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1. Introduction

Designing effective conservation plans is challenging for wide-ranging marine birds that rely on multiple habitats over their annual cycle for wintering, breeding, and migration. Recent studies have investigated the feasibility of establishing networks of marine protected areas to conserve mobile marine predators including migratory birds (Agardy et al., 2003; Amorim et al., 2009; Hyrenbach et al., 2000). Such species are often associated with dynamic habitat features (Louzao et al., 2006), and their habitat associations may change as individuals move among and within regions throughout their annual cycle (Kobayashi et al., 2008). In order to identify areas to protect for these species, it is essential to have a thorough understanding of the timing of their movements and associations with habitat features during all their life stages (Hyrenbach et al., 2000; Newbold and Eadie, 2004; Norse et al., 2005).

Many avian species rely on urbanized coastal estuaries during part of their annual cycle. For example, most North American sea duck species spend several months each year wintering and migrating along the Pacific and Atlantic coasts, where they concentrate in estuaries (Bellrose, 1980; Savard et al., 1998). During these periods, sea ducks are often in close proximity to dense human populations, and may be influenced by disturbance, contaminant exposure, aquaculture, non-native species invasions, or physical

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habitat alteration (Carlton et al., 1990; Cohen and Carlton, 1995; Linville et al., 2002; Merkel et al., 2009; Savard et al., 1998). In addition, the projected effects of sea-level rise and extreme storm events associated with climate change may further alter coastal habitats relied upon by these species (Crooks, 2004; Morris et al., 2002; Galbraith et al., 2002). Since urbanized estuaries figure prominently in the annual cycles of many migratory species, these areas should be considered as essential components of any comprehensive conservation strategy. However, criteria for determining protective zones within estuaries are difficult to establish given the variety of competing human interests.

San Francisco Bay (SFB) is the largest estuary on the Pacific coast of North America and one of the most urbanized estuaries in the United States; its intertidal and subtidal habitats have been greatly altered over the past century (Nichols et al., 1986). The human population surrounding the estuary exceeds 7.5 million and is expected to grow to 9 million by 2035 (Association of Bay Area Governments, 2009 http://www.abag.ca.gov/planning/currentfcst/regional.html). However, the estuary has great significance to waterfowl of the Pacific Flyway and is a major migration and wintering area for benthic foraging bay and sea ducks, many of which have declined precipitously in the past several decades (Dickson and Gilchrist, 2002; Hodges et al., 1996; Savard et al., 1998; Sea Duck Joint Venture, 2001). In midwinter surveys, >39% of all surf scoters (*Melanitta perspicillata*) counted in the lower Pacific Flyway (32°–49° latitude) are found in SFB where peak counts have exceeded 72,000 individuals (Accurso, 1992; Collins and Trost, 2009).

Sea ducks are long-lived with low but variable annual productivity, and their populations are particularly sensitive to changes in adult female survival (Goudie et al., 1994; Schamber et al., 2010). Habitat quality on wintering areas is vital to waterfowl since it can influence survival (Moon and Haukos, 2006), body condition (Miller, 1986), migration timing (Prop et al., 2003; Black et al., 2007), and reproductive success in subsequent breeding seasons (Baldassarre and Bolen, 2006). Many sea duck species, such as surf scoters, overwinter in urbanized estuaries and display strong winter site fidelity (De La Cruz et al., 2009; Kirk et al., 2008; Robertson and Cooke, 1999; Robertson et al., 2000); thus, efforts to protect and enhance these coastal habitats could benefit large segments of their populations.

Despite the importance of urbanized estuaries as migration and wintering areas for sea ducks, little is known about their habitat associations with intertidal and subtidal resources in these regions. Previous work suggests that benthic prey distribution and availability, depth, and structural habitat may influence the distribution and movements of sea ducks and more broadly, diving ducks (Kirk et al., 2007, 2008; Lewis et al., 2007a; Lovvorn and Gillingham, 1996; Vaitkus and Bubinas, 2001; Zydelis et al., 2006). Pacific herring (*Clupea pallasi*) roe also is an important prey that influences sea duck distributions at spring stop-over sites (Anderson et al., 2009; Lewis et al., 2007b; Lok et al., 2011, 2008) and could influence movements in estuaries during the winter. Remnant native seagrass (eelgrass: *Zostera marina*) beds, once extensive in SFB and other estuaries, serve as Pacific herring spawning substrate and also are a source of epibenthic and epifaunal prey (Anderson et al., 2008; Carr et al., 2011; Zimmerman et al., 1991). In addition, disturbance in urbanized estuaries may alter the behavior and habitat use of open water birds (Larsen and Laubek, 2005), and is likely to have the greatest effect on waterfowl during late winter when food has been depleted and energy demands are high (Madsen, 1994).

Limited knowledge of sea duck resource selection has constrained development of strategies for managing and restoring their urbanized habitats. Thus, the primary goal of our study was to identify how relationships of sea ducks with broad scale habitat features may influence their distribution and movements during the non-breeding season. Further, we used these results to help define a suite of seasonal habitats that could be targeted for protection and conservation. Specifically, we modeled resource selection from a sample of radio-marked individuals to define their associations with estuarine features, disturbances, and sub-regions. In addition, we evaluated seasonal and annual changes in their collective distribution, individual home ranges, and movements. We then related these findings to changing habitat conditions and possible management practices that could ultimately improve the overwinter condition and survival of sea ducks in urbanized estuaries.

2. Methods

2.1. Radio-marking and data collection

We captured wintering surf scoters with floating mist nets (Kaiser et al., 1995) or from a boat with a netgun (Coda Enterprises, Inc., Mesa, AZ) in both San Pablo Bay and the Central Bay (Fig. 1) during November and December 2003–2004. Of all scoters wintering in SFB, 19–35% were counted in San Pablo Bay and 46–50% in the Central Bay via systematic transect based surveys of SFB during 1988–1990 (Accurso, 1992), and our capture efforts were distributed in order to obtain similar proportions of birds from each sub-bay. We banded, weighed, and measured each captured bird, and then used a combination of plumage characteristics and cloacal examination to determine sex and bursal depth measurements to estimate age (Mather and Esler, 1999). A veterinarian surgically implanted coelomic radio transmitters with external whip antennas (22 to 24-g, model A2310, Advanced Telemetry Systems, Insanti, MN, USA) in juvenile and after second year (ASY) males and females (Korschgen et al., 1996; Mulcahy and Esler, 1999). Implant transmitters are less disruptive to diving birds, cause fewer behavioral modifications than externally attached transmitters, and are preferred for studies of longer duration (Hupp et al., 2003; Iverson et al., 2006; Rotella et al., 1993). In total, birds were held between 5–24 h for the radio-marking procedure, including a post-surgical recovery period that lasted between 2 and 8 h. We administered subcutaneous fluids every 4–5 h to prevent dehydration and released recovered birds within 2 km of their capture location.

We tracked marked birds daily from 500 to 2100 h during 12 November 2003 to 26 April 2004 and 5 November 2004 to 8 April 2005 with vehicle-mounted, dual-null-peak, 4-element-Yagi antenna systems (AVM Instrument Co., Livermore, California, USA). We surveyed the entire study area (all of SFB) each day, alternating between two different routes to obtain locations on each individual during targeted time periods across the week. We divided each day into 3 time periods following U.S. Naval Observatory definitions (http://aa.usno.navy.mil/faq/docs/RST_defs.php): *crepuscular* – dawn (the hour before the onset of civil twilight) to dusk (the hour after civil twilight ends); *day* – the hours of civil twilight; and *night* – dusk to dawn. We obtained at least one location per individual in each time period each week. To avoid autocorrelation, locations from the same individual were collected at least 2 h apart, the estimated time for a bird to fly across our study area (Otis and White, 1999); however, typically we obtained no more than one location per individual per day. Azimuth error for the null-peak systems was previously established as 1.5° with an associated mean linear distance between calculated and true locations of 58 ± 35 (standard error; SE) m (Warnock and Takekawa, 1995) when tested at a distance of approximately 1 km from the observer. Test transmitters on buoys in the centers of the San Pablo and Central Bays were detectable with our null-peak system from all observation sites used in our study. We determined Universal Transverse Mercator (UTM) locations by collecting 2–3 bearings and using triangulation

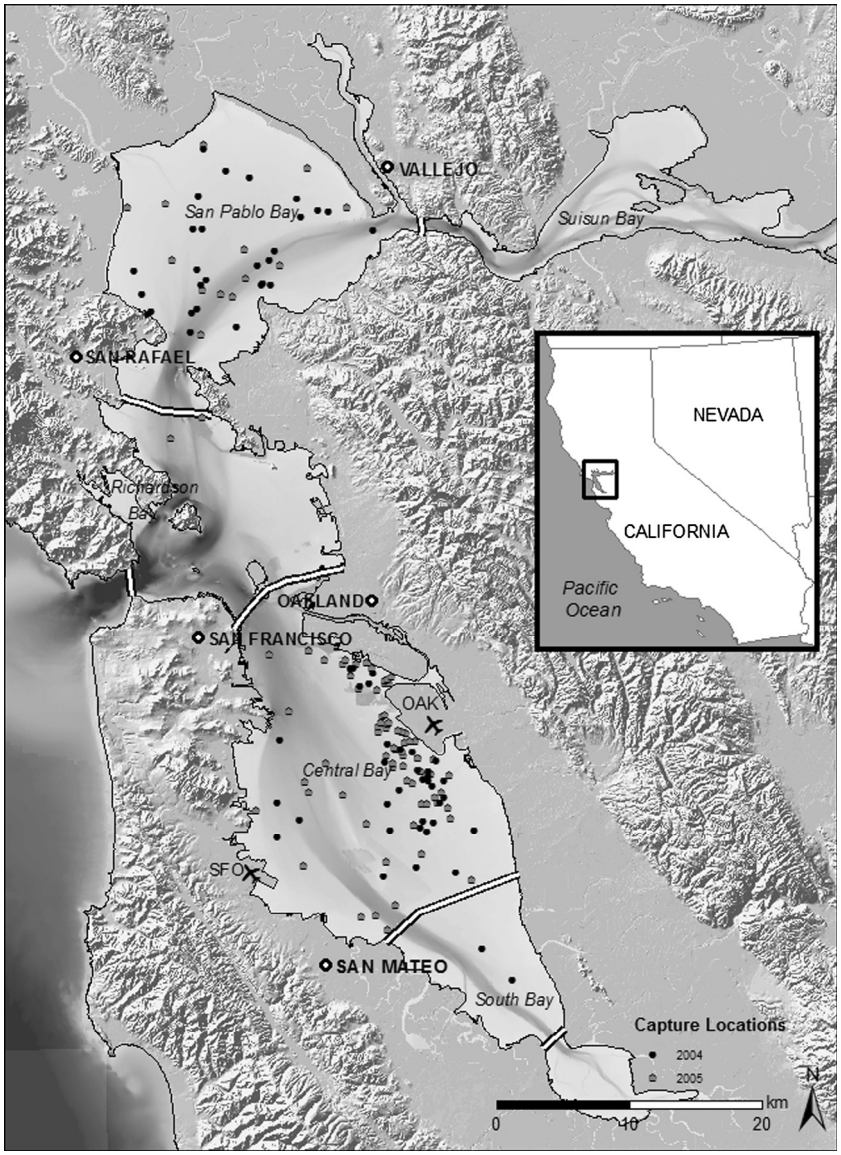

Fig. 1. Map of the urbanized estuary of San Francisco Bay, California, USA including major cities, airports, bridges, and sub-bays. Surf scoters were captured throughout the Central Bay and San Pablo Bay (see Section 2).

software (Location of a Signal, version 3.0.1, Ecological Software Solutions, Schwägalpstrasse 2, 9107 Urnäsch, Switzerland). Telemetry flights from aircraft affixed with two antennas and a left–right switchbox were conducted weekly to locate birds that were missing or had weak signals (Gilmer et al., 1981). Locations were included in our analyses after a 7-day adjustment period to control for capture, handling and attachment effects.

2.2. Resource selection models

2.2.1. Environmental variables

We assembled existing Geographic Information System (GIS) data layers of resource variables that we considered potentially important for sea ducks. Benthic prey availability can influence distributions of sea ducks (e.g. Kirk et al., 2008), and sea and bay duck diets in SFB are dominated by the invasive overbite clam (*Corbula amurensis*) in the brackish northern reach while consisting mainly of the invasive Japanese littleneck clam (*Venerupis phillipinarium*) in the more marine central section (De La Cruz, 2010; Lovvorn et al., 2013). Soft-bottom, invertebrate prey assemblages in SFB can be qualitatively defined using salinity during normal hydrologic years (NOAA, 2007) and are known to shift geographically with salinity both seasonally and annually (Peterson and Vayssieres, 2010; Nichols and Thompson, 1985). We created monthly salinity profiles from December through April 2003–2004 and 2004–2005 from 39 U.S. Geological Survey water quality monitoring stations (http://sfbay.wr.usgs.gov/access/wqdata). We created salinity surfaces by interpolating monthly averages with the Spatial Analyst Inverse Distance Weighting (IDW) function and a fixed radius of 1200-m in ArcGIS v 9.2 (ESRI, Redlands, CA). We accounted for a potential short-term lag in the response of some invertebrate species distributions to salinity (Peterson and Vayssieres, 2010; Nichols and Thompson, 1985) by including salinity from the previous month as an independent variable.

Foraging efficiency of diving ducks is sensitive to depth (Lovvorn and Gillingham, 1996); thus, the available area and depth of tidal mudflats and shallow subtidal shoals are potential predictors of sea duck presence. To determine depth in SFB, we used a continuous bathymetric surface grid generated by Jaffe et al. (1998) with the IDW function in ArcInfo (ESRI, Redlands, CA) based on an existing

National Oceanographic and Atmospheric Administration/National Ocean Services database of depth soundings. The tidal datum used as the base elevation reference for the grid was mean lower low water (MLLW) representing the average of the lower low water height of each tidal day observed over the National Tidal Datum Epoch (http://tidesandcurrents.noaa.gov/datum_options.html). Each grid square measured 100 m × 100 m with a depth resolution considered accurate to 0.1 m.

Herring spawn between November and March in SFB with peak activity in January (O'Farrell and Larson, 2005; Watters et al., 2004). Spawning substrates include pilings, rip-rap retaining walls, and submerged vegetation, including native seagrass (eelgrass; Hay, 1985; Watters et al., 2004). We obtained data on the location, extent, and timing of herring spawning events during the winters of 2003–2004 and 2004–2005 (Wantanabe et al., California Department of Fish and Game, unpublished data). We used the eelgrass distribution coverage of Merkel and Associates (2004), which was produced using in-water surveys conducted during June–October 2003 from a combination of side-scan sonar and single-beam sonar integrated with a differential global positioning system (dGPS). Aerial and diver ground-truthing surveys were used to confirm the presence of eelgrass (Merkel and Associates, 2004).

Waterbirds may be influenced by existing SFB water transit and recreational access systems and their planned expansions (Water Emergency Transit Authority, <http://www.watertransit.org>; California State Coastal Conservancy, http://scc.ca.gov/2010/07/30/san-francisco-bay-area-water-trail/). To evaluate distributions in relationship to one type of potential disturbance, ferry traffic, we mapped existing ferry routes and used the buffer wizard in ArcMap v 9.2 to create a 400 m zone on either side of each route to depict potential disturbance areas. This disturbance zone width was based on on-board ferry surveys in SFB to determine behavioral response (fly, dive, swim, alert posture) distances for sea ducks (Takekawa et al., unpublished data). Mean response distance for all behaviors was 206.35 ± 5.91 m (range 30–900 m, $n = 2512$). We added 200 m to the rounded mean response distance to account for GPS measured variation in the published ferry route (Takekawa et al., unpublished data).

We used the "create fishnet" command in ArcToolbox (ArcMap v. 9.2) to divide the Bay into 1278 1-km^2 grids based on USGS 1:24,000 topographic maps with NAD27 UTM demarcations. The 1-km^2 scale provided the best resolution for integrating data sets from a variety of spatial scales. Grid cells were identified by a unique number and unique UTM coordinates representing the cell center point, and all data layers were joined to the grid. Grid cells were assigned a numerical value for continuous variables (month, current salinity, previous month salinity, and depth), and a value of 1 (present) or 0 (absent) for binary variables (herring, seagrass, ferry route). We lacked information on the density of herring spawn at the grid spatial scale, and therefore considered spawn as a binary variable. We presumed the eelgrass data layer, produced the summer prior to the commencement of our study, was representative of eelgrass distribution during the entire study period. We coded all grids with ⩽1% mean cover ($n = 75$) as 0, in recognition that such small patches may not provide adequate habitat to attract scoters. Based on measurements taken in June–October 2003 (Merkel and Associates, 2004), mean percent cover in grids containing >1% seagrass was 22.3 ± 3.45%.

2.2.2. Statistical analyses

We examined resource selection by modeling differences between grids where radio-marked birds were present and where we did not locate marked birds (pseudo-absence) and related them to the environmental variables (Wisz and Guisan, 2009). We did not apply a traditional resource selection function (RSF, sensu Manly et al., 2002) framework for two reasons. First, our resources were measured in 1-km^2 grids which set the scale at which we could reliably investigate habitat relationships. By aggregating telemetry data to the grid level, we set our units of analysis to grids instead of to individual locations. This enabled us to relate the influence of environmental variables on presence vs. pseudo-absence, and also on the relative numbers associated with that particular resource. Second, implicit to this framework, we did not have to assume that resource selection was independent among individuals. Instead, our analysis allowed for the consideration that wintering sea ducks may aggregate based on social cues (Wormington and Leach, 1992; LaCroix et al., 2005).

Because our telemetry dataset showed evidence of spatial autocorrelation (Moran's $I = 0.04$, Z-score = 332.7, $\alpha = 0.01$, critical value 2.58; Sokal and Oden, 1978; ArcToolbox, ArcMap v. 9.2) we accounted for its effects in our modeling efforts. To determine the most appropriate spatial covariance structure for our data, we tested different models of spatial structure (spherical, exponential, power, and Gaussian) with PROC MIXED (SAS Institute, 2004) for the full set of explanatory variables (Diniz-Filho et al., 2003; Littell et al., 1996). The exponential spatial covariance structure was identified as the best fitting model with Akaike's Information Criterion (AIC_c).

Our telemetry data contained a greater number of zero observations than would be predicted with standard, unimodal statistical distributions (Potts and Elith, 2006); therefore, we used a two-part modeling approach. We first applied a binomial distribution to model presence and pseudo-absence, and then we used a truncated dataset in the second part of the analysis to model densities in grids where marked birds were present (Cunningham and Lindenmayer, 2005). In the first part of our analysis, we used a generalized linear mixed model (PROC GLIMMIX, SAS Institute, 2004; Littell et al., 1996) with the logit-link function to evaluate effects on presence/pseudo-absence of depth, current and previous month salinity, seagrass or herring spawn presence, and month. The log pseudo-likelihood values produced in the generalized linear mixed models with R-side covariance were not comparable among different statistical models (GLIMMIX documentation, SAS Institute, 2004). Therefore, we could not use an AIC approach for model selection. Instead, we evaluated a full model including all habitat variables, interactions of all variables with month, and the interaction of herring spawn presence with seagrass presence. We considered ferry route presence and the interaction of ferry route with month in a separate GLIMMIX model, because it was confounded with depth. Grids in which ferry routes were present had depths that were greater (1.38 ± 0.02 m), and did not overlap with depths of grids where ferry routes were absent (0.46 ± 0.004 m). To examine which variables were the strongest predictors of marked bird presence, we used the LSMEANS statement to construct *t*-tests, and we considered the odds ratios by calculating the percent change in odds for every unit increase in covariate. Positive or negative percent differences indicate that the odds of encountering a bird in a cell is increasing or decreasing, respectively.

In the second part of our analysis, we modeled marked bird counts with a mixed linear model (PROC MIXED, SAS Institute, 2004; Littell et al., 1996). We used the buffer command in ArcToolbox (ArcMap v. 9.2) to create 1-km^2 (one grid) buffer zones around all grids containing birds. The resulting dataset was exported and normalized by log-transforming numbers in each grid cell and zero values in buffer grids to log(0.5). We used an information theoretic approach (Burnham and Anderson, 2002) to determine environmental factors that best explained observed marked bird counts. We calculated second-order, AIC_c values for a candidate set of 21 index models. We chose models to evaluate the predictive power of each habitat variable individually, the interaction of variables with time (months), and potentially important biological relationships (e.g. the interaction effects of seagrass and herring). Our

candidate set also included the null and full (all variables and interactions) models. We compared ΔAIC_c values of each model to that of the best-fitting model, and calculated Akaike weights to assess the relative importance of each model (Burnham and Anderson, 2002). We also calculated evidence ratios (w_1/w_j), where w_1 is the Akaike weight of the top ranked model and the w_j weight is used to calculate the evidence ratio of the jth-ranked model in the candidate set (Burnham and Anderson, 2002), to further compare models. We averaged the best supported models to obtain weighted parameter estimates for each explanatory variable.

2.3. Collective range, individual home range and movement analyses

To evaluate space use over time, we calculated monthly fixed kernel densities at the collective and individual levels. We defined collective range size as the overall distribution for all radio-marked birds (e.g. Ackerman et al., 2006; Adams et al., 2004). To estimate monthly collective range size, we used Hawth's Analysis Tools (Beyer, 2004) for ArcGIS to randomly select five locations per bird per month to ensure equal weighting. We then pooled data from these birds and used the CVh (likelihood cross-validation) method in Animal Space Use 1.1 (Horne and Garton, 2006) to select smoothing parameters. We calculated monthly 50% (core use area), 65%, 75%, 85%, and 95% fixed kernel densities in Home Range Tools version 1.1 (Rodgers et al., 2007) for ArcGIS (ESRI, Redlands, CA). To calculate monthly home ranges for individuals, we used Hawth's Analysis Tools (Beyer, 2004) for ArcGIS to randomly choose ten locations from each bird during each month in order to avoid bias towards birds with more locations (Börger et al., 2006; Kirk et al., 2008), and calculated monthly 50% and 95% fixed kernel densities as indicated above.

To assess changes in movement patterns over winter, we used monthly average distances between consecutive telemetry locations for individuals, which we identified using Hawth's Analysis Tools for ArcGIS (Beyer, 2004). To avoid bias associated with different numbers of locations per individual, we included only birds with 10 or more locations collected in each specified month. In addition, while this measure could be influenced by variable times between locations, our radio-telemetry sampling scheme was designed to result in regularly spaced time intervals. The mean number of days (±SE) between consecutive locations was 2.21 (±0.06) during 2003–2004 and 2.46 (±0.06) in 2004–2005.

We used mixed linear models (PROC MIXED, SAS Institute, 2004) to evaluate whether individual home range sizes and mean distance between consecutive locations differed across the fixed effects of month, year and sex. In each model, individual birds were treated as a random effect by including them as a repeated measure to account for interdependence of their locations across time. The effect of age was not tested because of insufficient location data on juvenile birds. We $\log_e$-transformed distances moved between locations to improve normality and reported back-transformed least-squares means ± SE derived from the most parsimonious model for distance. Standard errors were calculated by the delta method (Powell, 2007; Williams et al., 2002). We employed an information theoretic approach (Burnham and Anderson, 2002) as described above to select among models.

3. Results

3.1. Resource selection

We radio-marked 151 birds and obtained 2726 locations during the winters of 2003–2004 and 2004–2005 (Table 1) for our resource selection analysis. Of all birds, 27% were captured in San Pablo Bay and 73% in the Central Bay; reflecting the typical annual abundance of sea ducks in both these regions (Accurso, 1992; Table 1). Sea duck distribution was nonrandom and was most influenced by the presence of herring roe, seagrass, herring ∗ seagrass, current salinity ∗ month, salinity from previous month, depth and depth ∗ month, (Table 2).

Herring roe presence had the greatest explanatory power; however, seagrass and particularly the interaction of herring ∗ seagrass were also important predictors (Table 2). Current salinity was not a significant predictor of locations; but the odds of locating a bird in a grid increased by 10.01% with every 1 g/L increase in salinity from the previous month (Table 2). The interaction of current salinity ∗ month was significant only in December, January and March, and odds ratios generally increased over winter which indicated birds were increasingly associated with higher current salinity as winter progressed (Table 2).

Water depth was a strong predictor of locations, as marked birds were distributed in shallower waters and were 2.45% less likely to occur with every meter increase in depth (Table 2). Birds were associated with the deepest water depth in mid-winter; however, the interaction of depth ∗ month was significant only in April, when they were 9.41% less likely to occur with each unit increase in depth (Table 2). Sea ducks were 33.22% (odds ratio ± SE: 1.33 ± 0.11) more likely to be located in grid cells where ferry routes were present ($F_{1,12660} = 11.71$, $p = 0.0006$). The interaction of ferry route and month was not significant ($F_{4,12660} = 0.72$, $p = 0.675$).

The model containing the additive effect of herring roe and seagrass best explained bird counts (Table 3). Models including herring roe and the interaction of herring roe ∗ seagrass had appreciable model weights, but were 1.3 and 3.2 times, respectively, less likely to explain counts than the top ranked model (Table 3). After averaging the three top models representing 0.93 of the Akaike weight, the parameter estimates and SE for herring, seagrass, and herring ∗ eelgrass were 0.252 ± 0.025, 0.071 ± 0.021, and 0.031 ± 0.001, respectively, indicating support for each as predictors of increasing bird density.

3.2. Distributions, home ranges, and movements

Overall, we used 105 marked birds that had five or more locations in at least 1 month in our collective range assessment. Very few birds met our criteria for 5 locations in April, thus we did not consider that month in our analyses. Monthly collective ranges (Fig. 2) indicated that birds distributed in a consistent overall pattern and had similar defined core use areas during 2004 and 2005. Birds were concentrated in San Pablo Bay during December and January of both years. In January, individuals began to disperse from San Pablo Bay, and their distribution shifted to the Central Bay during February and March. In contrast, the western shoreline of the Central Bay below Oakland and the eastern shoreline north of the San Mateo Bridge were used as core areas during all study months. Birds used Suisun Bay during January and February 2004 and January 2005. We also identified Richardson Bay on the west side of the Central Bay as a core use area during January 2004 and January–March 2005 (Fig. 2).

Fifty-two marked individuals had ⩾10 locations in at least 1 month and were used in individual home range and movement distance analyses. April was excluded from our analyses because of the low number of birds with 10 locations. Sex and the interaction of month and year were identified as the most important predictors of both 95% and 50% fixed kernel density home range sizes (Table 4). The interaction of month and sex also was supported as a predictor of the 50% fixed kernel size (Table 4). Home range sizes of both males and females were slightly smaller in December and January 2004 than in the same months in 2005 (Fig 3). December home ranges of females (2004: 51.01 ± 19.68

Table 1
Summary of birds marked and total locations in two sub-bays of San Francisco Bay during the winters of 2003–2004 and 2004–2005. AHY (after hatch year) denotes birds captured at least a year after hatching and HY (hatch year) denotes birds captured in the year they were hatched.

Year	San Pablo Bay				Central Bay				Total marked	Total locations
	M		F		M		F			
	AHY	HY	AHY	HY	AHY	HY	AHY	HY		
2003–2004	10	13	0	5	11	11	10	5	65	1193
2004–2005	10	1	2	0	18	5	38	12	86	1533
Totals	20	14	2	5	29	16	48	17	151	2726

Table 2
Fixed effects results from general linear mixed model analysis of surf scoter locations in relation to key habitat variables in San Francisco Bay during the winters of 2003–2004 and 2004–2005. Odds ratios, percent difference, standard error (SE), and *t*-values are presented when *F*-value probabilities are significant.

Predictor variable	*F*-value	df	Pr > *F*	Odds ratio	Percent difference	SE	*t*-value	Pr > [*t*]
Herring	38.34	1, 12660	<0.0001	4.36	336.31	0.63	6.17	<0.0001
Herring ∗ month	0.85	4, 12660	0.496	–	–	–		–
Herring ∗ seagrass	6.62	1, 12660	0.010	2.43	142.85	0.471	4.58	<0.0001
Seagrass	4.45	1, 12660	0.035	1.63	62.73	0.38	2.11	0.04
Seagrass ∗ month	0.91	4, 12660	0.456	–	–	–	–	–
Current salinity (g/L)	3.07	1, 1074	0.079	–	–	–	–	–
Current salinity ∗ month	2.88	4, 1169	0.035	–	–	–	–	–
December	–	–	–	0.89	−10.56	0.03	−3.53	0.0004
January	–	–	–	0.91	−9.32	0.05	−1.88	0.06
February	–	–	–	1.02	1.94	0.04	0.56	0.574
March	–	–	–	0.98	−1.80	0.05	−2.21	0.027
April	–	–	–	1.04	4.11	0.05	0.82	0.412
Salinity previous month (g/L)	9.66	1, 1532	0.002	1.10	10.01	0.03	3.68	0.0002
Salinity previous month ∗ month	1.85	4, 1743	0.136	–	–	–	–	–
Depth (m)	15.62	1, 8928	<0.0001	0.98	−2.45	<0.01	−3.95	<0.0001
Depth ∗ month	4.57	4, 7477	0.001	–	–	–	–	–
December	–	–	–	0.98	−1.94	0.01	−1.64	0.10
January	–	–	–	1.00	0.15	0.01	0.12	0.907
February	–	–	–	1.00	−0.31	0.01	−0.32	0.751
March	–	–	–	1.00	−0.43	0.01	−0.43	0.670
April	–	–	–	0.91	−9.41	0.02	−4.46	<0.0001

Table 3
AIC_c rankings of all candidate models of bird counts based on telemetry locations of sea ducks ($n = 151$) during 2003–2004 and 2004–2005 in San Francisco Bay, California. Month included December, January, February, March, and April. Detailed explanations of variables are provided in methods.

Model variables	*k*	AIC_c	ΔAIC_c	w_i	Evidence ratios
Herring + seagrass	4	4979.8	0	0.45	–
Herring	3	4980.3	0.5	0.34	1.3
Herring ∗ seagrass	5	4982.1	2.3	0.14	3.2
Herring + ferry route	4	4984.8	5.0	0.04	12.2
Null	2	4987.1	7.3	0.01	38.5
Salinity + seagrass + herring	5	4989.0	9.2	0.01	99.5
Seagrass	3	4989.8	10.0	<0.01	148.4
Herring ∗ month	8	4990.8	11.0	<0.01	244.7
Ferry	3	4991.7	11.9	<0.01	383.8
Month	3	4995.0	15.2	0.00	–
Salinity	3	4996.2	16.4	0.00	–
Depth	3	5001.9	22.1	0.00	–
Seagrass ∗ month	8	5005.5	25.7	0.00	–
Depth + ferry	4	5006.4	26.6	0.00	–
Herring + depth + ferry + Seagrass + salinity	7	5008.1	28.3	0.00	–
Ferry route ∗ month	8	5008.8	29.0	0.00	–
Salinity + depth	4	5011.0	30.7	0.00	–
Salinity + depth + ferry	5	5015.6	35.8	0.00	–
Salinity ∗ month	8	5028.1	48.3	0.00	–
Full	27	5037.4	57.6	0.00	–
Depth ∗ month	8	5052.4	72.6	0.00	–

and 2005: 98.57; Fig 3) were larger than those of males (2004: 24.70 ± 2.3 and 2005: 35.30 ± 9.46; Fig 3), but became more similar between the sexes by January. Overall in 2004 and 2005, the mean home range size (50% fixed kernel density) declined over winter for both sexes (Fig 3).

The interaction between month and sex was the best fitting model explaining distance moved between consecutive locations, and no other models were supported (Table 5). Birds moved greater distances during December and January than in February and March (Fig. 4). Males made larger movements between sequential locations than females during January, the time when the population shifted from San Pablo and Suisun Bays to the Central Bay. Together, collective ranges, monthly home ranges and distances moved indicated that birds traveled further and used larger areas of the Bay early in winter, but tended to restrict their movements and areas used later in winter.

4. Discussion

Understanding how wildlife population distributions and movements relate to habitat features is vital to effective management and conservation strategies (Newbold and Eadie, 2004), particularly where species compete with human interests for restricted resources. We determined key resource features associated with locations of radio-marked sea ducks wintering in the urbanized SFB estuary and evaluated their movements and space use over time. We found that presence and densities of birds were best predicted by herring roe but were also influenced by seagrass, depth, and salinity. Collective range size, individual home range size, and distances traveled all declined over the winter in a pattern that may be consistent with seasonal patterns of decreasing benthic resource availability across large regions of the Bay (Lovvorn et al., 2013; Poulton et al., 2002) concomitant with

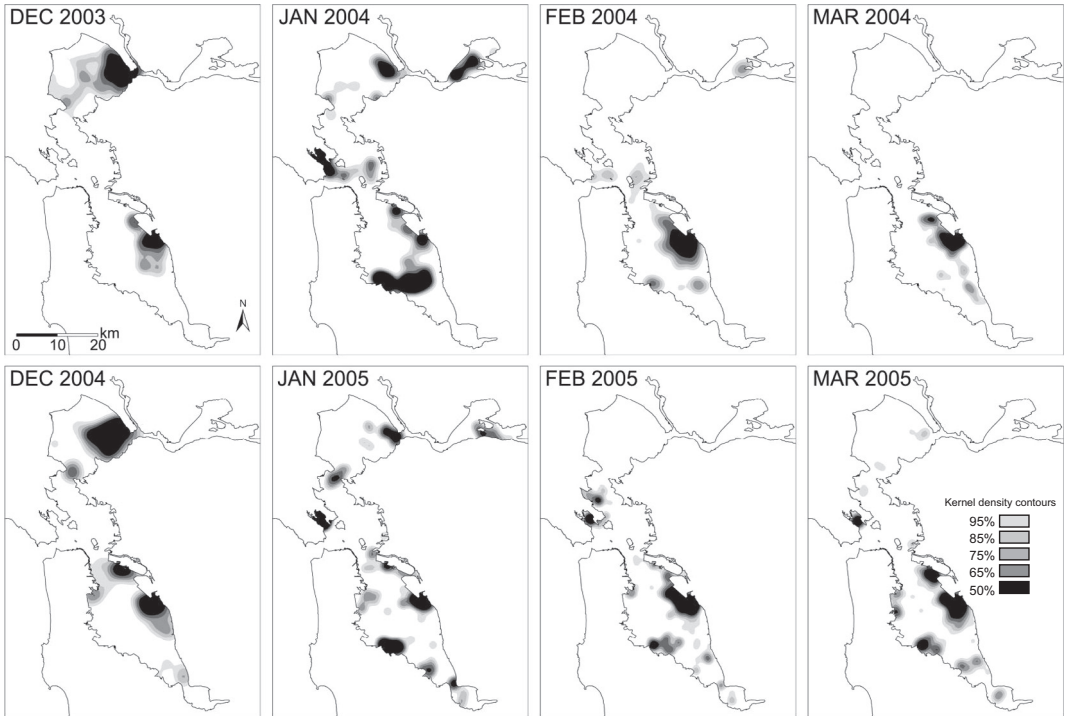

Fig. 2. Monthly collective range estimates of all radio-marked surf scoters in San Francisco Bay during four winter months in 2003–2004 and 2004–2005. Fixed-kernel densities were determined from birds with five or more locations during a month to reduce bias towards individuals with more locations.

Table 4
AIC_c rankings of all candidate models for monthly home ranges (95% and 50% fixed kernel density) of individual sea ducks ($n = 52$) during 2003–2004 and 2004–2005 in San Francisco Bay, California. Month included December, January, February, and March. Detailed explanations of variables are provided in methods.

Model variables	k	AIC_c	ΔAIC_c	w_i	Evidence ratios
50% fixed kernel density					
Month ∗ year + sex	11	651.1	0.0	0.56	–
Month ∗ sex	10	651.8	0.7	0.40	1.40
Month ∗ year	10	656.4	5.3	0.04	14.0
Month + year + sex	8	675.8	24.7	0.00	–
Month	3	686.1	35.0	0.00	–
Year	3	717.8	66.7	0.00	–
Sex	3	717.9	66.8	0.00	–
Null	2	722.9	71.8	0.00	–
95% fixed kernel density					
Month ∗ year + sex	11	863.7	0.0	0.90	–
Month ∗ sex	10	868.4	4.7	0.09	10.0
Month ∗ year	10	872.0	8.3	0.01	64.3
Month + year + sex	8	897.5	33.8	0.00	–
Month	3	913.7	50.0	0.00	–
Sex	3	945.6	81.9	0.00	–
Year	3	945.6	81.9	0.00	–
Null	2	953.5	89.8	0.00	–

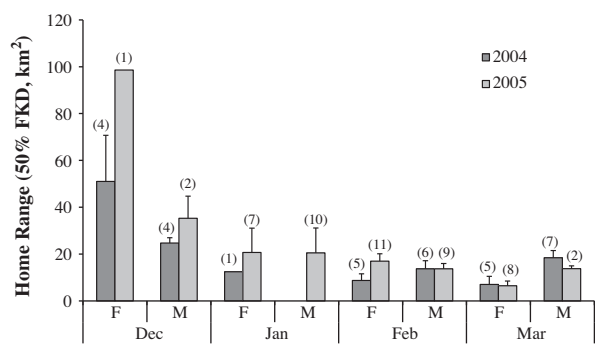

Fig. 3. Mean (±SE) home range sizes (50% fixed kernel density; FKD) of individual male and female radio-marked surf scoters in San Francisco Bay declined over 4 months during winter 2003–2004 and 2004–2005. Sample sizes are indicated in parentheses.

Table 5
AIC_c rankings of all candidate models for distances moved between sequential locations of individual sea ducks ($n = 52$) during 2003–2004 and 2004–2005 in San Francisco Bay, California. Month included December, January, February, and March. Detailed explanations of variables are provided in methods.

Model variables	k	AIC_c	ΔAIC_c	w_i	Evidence ratios
Month ∗ sex	10	1011.0	0.0	0.97	–
Month	6	1018.7	7.7	0.02	48.5
Month + year + sex	8	1021.1	10.1	0.01	161.6
Month ∗ year + sex	11	1025.2	14.2	<0.01	970.0
Month ∗ year	10	1025.5	14.5	<0.01	970.0
Sex	3	1029.1	18.1	<0.01	–
Null	2	1036.8	25.8	<0.01	–
Year	3	1037.2	26.2	<0.01	–

increasing availability of highly profitable herring roe localized in the Central Bay.

4.1. Resource selection

Herring roe was the strongest predictor of both individual locations and counts, which is similar to findings in Washington, British Columbia, and southeast Alaska (Lok, 2008; Lok et al., 2011; Sullivan et al., 2002) showing sea ducks congregate at this ephemeral prey source during the late winter and spring migration. Herring roe is an abundant and easily exploited source of lipids that plays a role in increasing late winter and spring body mass (Anderson et al., 2009; Lewis et al., 2007b). Herring spawn in Central SFB, where peak spawns occur in January and continue through March (O'Farrell and Larson, 2005; Watters et al., 2004),

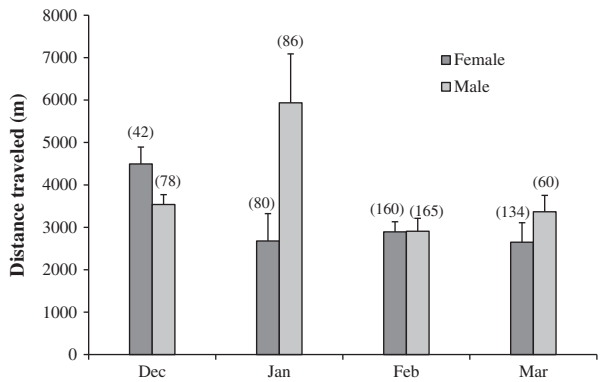

Fig. 4. Mean (±SE) monthly distance traveled between locations for radio-marked males and female surf scoters during the winters of 2003–2004 and 2004–2005 in San Francisco Bay. Sample sizes are indicated in parentheses.

and this resource may be important for maintaining winter condition of many waterbirds as benthic prey declines (e.g. Poulton et al., 2002). Also, the timing of spawn suggests it could play a role in pre-migration fattening. However, in the past decade, declines in herring stock have been documented along the Pacific coast, and declines in SFB have been particularly pronounced (Bartling, 2008), prompting the first time closure of the herring fishery in the estuary during 2009 (CDFG, 2009).

The interaction of herring * seagrass was also a strong predictor of bird presence and counts. While herring can spawn on a variety of surfaces, seagrass is a key spawning substrate throughout the Pacific Flyway (Hay, 1985; Watters et al., 2004). Even in the absence of herring roe, sea ducks in our study displayed a positive association with seagrass. This is in keeping with studies in more northern reaches of the Flyway, where sea ducks keyed in on seagrass beds to forage on associated epifaunal and infaunal invertebrate prey (Laubhan and Metzner, 1999), particularly in late winter and spring (Anderson et al., 2008). In SFB, densities of epifaunal invertebrates can exceed 5000 individuals/shoot in some seagrass beds (Carr et al., 2011), and may provide important prey for sea ducks.

A suite of other habitat factors also predicted marked bird locations, albeit these relationships were less obvious and explained less variation. In December, birds had high odds of being associated with lower salinity and shallower depths, reflecting their widespread distribution in San Pablo Bay, a shallow sub-bay with substantial freshwater inputs from the San Joaquin – Sacramento River Delta. In January, distribution shifted toward the Central Bay (Fig. 2), which is deeper and more haline than San Pablo Bay, and contains the majority of seagrass beds and herring spawning sites in the estuary (Merkel and Associates, 2004). Interestingly, birds had the highest odds of being associated with shallow depths in April, perhaps reflecting changing resource selection and distribution patterns prior to spring migration.

Benthic prey densities can play a large role in determining the distribution and movements of diving birds like sea ducks (Nilsson, 1972; Schummer et al., 2008; Stott and Olson, 1973). Available benthic invertebrate density data exceeded the scale used in our resource selection modeling, and thus, we could not directly evaluate the importance of this resource. However, benthic assemblages can be loosely defined in SFB based on a salinity gradient (NOAA, 2007). For example, surf scoter benthic diets in SFB are spatially distinct and dominated by two clam species, the overbite clam (*Corbula amurensis)* with highest densities in the brackish San Pablo and Suisun Bays (Carlton et al., 1990; Peterson and Vayssieres, 2010) and the Japanese littleneck clam (*V. philipinarium*) in the more marine Central Bay (De La Cruz, 2010). Previous work in SFB has shown that *Corbula* are an easily exploited and highly profitable prey for at least one benthic foraging waterfowl species, the lesser scaup (*Aythya affinis*; Richman and Lovvorn, 2004), and their densities decline dramatically over winter (Poulton et al., 2002). In contrast, *Venerupis* occur in low but consistent densities across the winter at sites sampled in the Central Bay (De La Cruz et al., unpublished data). Birds were generally more likely to select grids of higher salinity later in the winter, perhaps in part reflecting a shifting reliance on *Venerupis* and other more marine prey such as herring roe, as *Corbula* densities declined below profitable levels in less haline areas of the estuary.

4.2. Disturbance

Among areas of similar depth, sea ducks were more likely to be in grids with ferry routes than in grids without ferries. Although disturbance may have the greatest effect on waterfowl during late winter when food has been depleted and energy demands are high (Madsen, 1994), we found no temporal response to ferry routes. In recent behavioral studies in SFB designed specifically to measure bird response to ferry traffic, Takekawa et al. (unpublished data) determined that sea ducks reacted to ferry passage at distances between 30 and 900 m by diving, flying, or swimming away. While this study strongly suggests that sea ducks are displaced by ferry traffic, our results imply that displacement may not result in permanent avoidance of routes. This use of routes despite daily disturbances might indicate that resources in these areas are too important to avoid, or potentially that individuals are in good enough condition to respond to disturbances without excessive cost (Gill, 2007). Long-term effects of temporary displacement, including potential demographic costs due to lower survival or reproduction, depend on its influence on foraging time or energy expenditure (Gill, 2007; Gill et al., 2001; Larsen and Laubek, 2005; Merkel et al., 2009). With human population growth and expansions to water-based transportation and recreational access in urbanized estuaries, research that quantifies the energetic costs of responses to water traffic and other potential forms of disturbance is urgently needed to further understand how such interactions may influence sea duck populations.

4.3. Distributions, home ranges, and movements

Species occupying seasonally changing environments where resources are ephemeral or become depleted often adjust their distribution or space use in relation to resource availability to meet their energetic demands (de Beer and van Aarde, 2008; Kraan et al., 2009; Norris et al., 1998). Kirk et al. (2008) found that surf scoters in British Columbia had larger home ranges and less site fidelity in habitats where prey was easily accessed but rapidly depleted, than in habitats where prey had higher foraging costs but lower depletion rates. In our study, contraction in individual home range size and distance moved between December and January corresponded with the exodus of scoters from San Pablo Bay, where prey densities typically decline over winter (Lovvorn et al., 2013), and movements into the more marine Central Bay where they selected habitat based on the presence of ephemeral but abundant herring roe and foraged on more stable bivalve populations (De La Cruz, 2010). This tendency of sea ducks to concentrate in small areas within the Central Bay, which includes some of the most heavily-used waterways in the estuary, may increase their exposure to anthropogenic risks. For example, sea ducks and in particular surf scoters, were the most affected species in the 2007 *M/V Cosco Busan* oil spill that released 58,000 gallons of oil into the Central Bay (Hampton et al., 2008).

Model selection indicated that sex and month were important sources of variation for both home range and movement distance.

Females had larger home ranges and movements in December, while males moved greater distances in January. Many sea ducks including surf scoters pair in the winter (Robertson and Cooke, 1999; Savard et al., 1998) and extended distances traveled by males in mid-winter may be related to mate searching. Males and females also may differ in use of resources to meet physiological demands that vary due to their size (Harestad and Bunnell, 1979; Greenwood, 1980). Space use and foraging strategies indicated by home range sizes and movements became more similar between males and females later in the winter. A more detailed understanding of differences in diet and behavior between wintering male and female sea ducks through the winter may further clarify our findings.

4.4. Conservation implications

Sea ducks in urbanized estuaries make up a large proportion of those counted in the lower Pacific Flyway (Collins and Trost, 2009); thus, conservation measures that improve adult body condition and survival of sea ducks in these regions could benefit their overall populations. Given the small areas of repeated use and the resources we identified as important for sea ducks, it should be possible to initiate conservation planning in SFB and similar urban estuaries to benefit them. In other regions, waterfowl conservation has been accomplished with several methods including reduction of disturbance, brief seasonal closures, and habitat enhancement or protection (Cole and Landres, 1995; Hill et al., 1997; Madsen, 1994). However, planning for conservation actions and protected areas must be flexible enough to take into account potential shifts in distributions of important resources (e.g. Lovvorn et al., 2009). This is particularly important in light of sea-level rise and extreme storm events predicted for SFB and other estuaries (Cayan et al., 2008; SF BCDC, 2009), since these changes could affect the availability and location of profitable prey and foraging areas (Galbraith et al., 2002).

Declining Pacific herring stock could have significant implications for sea ducks and our results indicate conservation and creation of herring spawning habitat in SFB and other estuaries, as well as innovative management strategies aimed at increasing herring populations, would be advantageous for sea ducks. Seagrass represents both an important habitat for spawning herring as well as for the macroinvertebrate prey of sea ducks (Anderson et al., 2008; Laubhan and Metzner, 1999). Seagrass ecosystems are in decline worldwide (Orth et al., 2006) and conservation and restoration of this habitat in urbanized estuaries could provide benefits not only for wintering and migrating sea ducks, but for multiple other species associated with seagrasses. While detailed information on energetic costs is needed to understand the level of disturbance wintering and migrating birds can tolerate, minimizing disturbances in sea duck core use areas may improve their access to important resources.

Urbanized estuaries like SFB are important wintering and migratory stopover sites for sea ducks in the Pacific Flyway. Sea ducks in SFB are linked to those from other key wintering areas in the Pacific Flyway through a series of shared migratory stopover sites (De La Cruz et al., 2009; Lok et al., 2011), many of which are exploited sequentially by sea ducks following spring herring spawns that draw congregations as high as 75,000 birds (Lok, 2008). Additionally, sea ducks that winter in the lower Pacific Flyway nest in a remote and fairly restricted area in the northern boreal forest of Canada (Takekawa et al., 2011), where their main threats may be climate change and oil and gas development. As recommended for other marine birds (Hyrenbach et al., 2000; Louzao et al., 2006), conservation of rapidly declining populations of sea ducks may require networks of both permanent marine protected areas and seasonally managed areas that benefit these species throughout their entire annual cycle. Increased understanding of habitat associations and space use at key high-use sites throughout the range of sea ducks will be important to the development of effective conservation strategies.

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