THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 118, 2016, pp. 463–476
DOI: 10.1650/CONDOR-15-139.1

RESEARCH ARTICLE

Shifts in the distribution of molting Spectacled Eiders (*Somateria fischeri*) indicate ecosystem change in the Arctic

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Submitted August 13, 2015; Accepted April 4, 2016; Published June 1, 2016

ABSTRACT

Shifts in the distribution of benthivorous predators provide an indication of underlying environmental changes in benthic-mediated ecosystems. Spectacled Eiders (*Somateria fischeri*) are benthivorous sea ducks that spend the nonbreeding portion of their annual cycle in the Bering, Chukchi, Beaufort, and East Siberian seas. Sea ducks generally molt in biologically productive areas with abundant prey. If the distribution of eiders at molting areas matches prey abundance, spatial shifts may indicate changes in environmental conditions in the Arctic. We used a randomization procedure to test for shifts in the distribution of satellite telemetry locations received from Spectacled Eiders in the 1990s and 2008–2011 within 4 late-summer, ice-free molting areas: Indigirka–Kolyma, northern Russia; Ledyard Bay, eastern Chukchi Sea; Norton Sound, northeastern Bering Sea; and Mechigmenskiy Gulf, northwestern Bering Sea. We also tested for interannual and interdecadal changes in dive depth required to reach prey, which might affect the energetic costs of foraging during the molting period. Transmitter-marked birds used each molting area in each year, although the distribution of Spectacled Eiders shifted within each area. Interdecadal shifts in Ledyard Bay and Norton Sound decreased dive depth in recent years, although minor differences in depth were biologically negligible in relation to the energetic expense of feather growth. Shifts in Mechigmenskiy Gulf and Indigirka–Kolyma did not occur consistently within or among decades, which suggests greater interannual variability among environmental factors that influence distribution in these areas. Shifts in each molting area suggest dynamic ecosystem processes, with implications for Spectacled Eiders if changes result in novel competition or predation, or in shifting prey regimes.

Keywords: Indigirka–Kolyma, Ledyard Bay, Mechigmenskiy Gulf, molting, Norton Sound, postbreeding distribution, *Somateria fischeri*, Spectacled Eider

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Сдвиги в распределении линьки очковая гага (*Somateria fischeri*) указывают на изменение экосистемы в Арктике

РЕЗЮМЕ

Сдвиги в распределении бентофаги хищников обеспечить индикацию экологических изменений, которые резонируют через донных экосистем опосредованной. Очковые гаги (*Somateria fischeri*) являются бентофаги морские утки, которые тратят не-племенной часть их годового цикла в Беринговом, Чукотском, Бофорта, Восточно-Сибирского и моря. Морские утки обычно линяют в биологически продуктивных районах с обильным добычу. Если распределение гаги в районах линьки совпадает с добычей, пространственные сдвиги могут указать на изменения в условиях окружающей среды в Арктике, которые резонируют через бенто. Мы использовали процедуру рандомизации тестировать сдвигов в распределении спутниковых телеметрии данные полученных от очковой гаги в 1990s и 2008-2011 гг в четырех областях линьки: Индигирка-Колыма, Восточно-Сибирское море; Ледьярд Бэй, восточный Чукотское море; и Нортон Звук и Mechigmenskiy залива, Берингова моря. Мы также проверили гипотезу о том пространственные сдвиги привели к изменению в дайвинг глубине требуется чтобы прокормить. Очковые Гаги использовали те же самые областии линьки каждый год, хотя распределение гаги сместился в каждой области. Междесятилетнее сдвиги произошли в Ледьярда залива и Нортон Звук, что привело к снижению глубины погружения в последние годы, хотя и различия в глубине, вероятно, были биологически незначительны по сравнению с важностью хищных изобилии. Сдвиги в Mechigmenskiy залива и Индигирки-Колыме индикаторный межгодовую изменчивость в распределении бентоса. Сдвиги в каждой линьки области предлагать, что дистрибуция бентос является динамическое, возможно, в результате изменения экосистемных процессов с соответствующими последствиями для Очковые Гаги если изменения приводят к новым конкуренции, сдвигая наличие продовольствия, или изменить глубину чтобы прокормить.
Ключевые слова: Индигирка-Колымские, Ледьярд Bay, Mechigmenskiy залива, линьки, Нортон Звук, после гнездование распределение, *Somateria fischeri*, Очковой Гаги

INTRODUCTION

Arctic marine ecosystems are changing in response to historically recent shifts in atmospheric conditions (Grebmeier et al. 2006a, 2006b, Grebmeier 2012, Kędra et al. 2015). Sea and air temperatures are rising, and predominant wind direction and speed have changed. In response, circulation patterns and dynamics of sea-ice formation, movement, and melt are also changing. These patterns have been linked to changes throughout marine food webs in the Bering and Chukchi seas (Grebmeier et al. 2010). For example, warming temperatures in the Bering Sea are causing an ecosystem shift from a cold-water system with greater biomass in the benthic community to a warmer pelagic system with more biomass in the water column (Grebmeier et al. 2006b, Grebmeier 2012).

At northern latitudes, the distribution and abundance of benthic fauna are tightly coupled with the spatial and temporal scope and scale of primary production (Grebmeier et al. 1988, Grebmeier and Barry 1991), which is influenced by hydrography, sea ice, temperature, salinity, light, and nutrient availability (Sukhanova et al. 1999). Benthic communities mediate the transfer of energy and nutrients from primary producers to benthivorous predators, including diving birds and marine mammals that demonstrate spatiotemporal responses to the availability of preferred benthos (McCormick-Ray et al. 2011, Cooper et al. 2013). For example, California gray whales (*Eschrichtius robustus*) have expanded their range northward into the Chukchi Sea in response to the expanding distribution of benthic amphipods (Moore et al. 2003, Moore 2008), and Pacific

walruses (*Odobenus rosmarus divergens*) selectively feed in areas of the northern Bering Sea with greater abundances of bivalve mollusks (Jay et al. 2014). Shifts in the distribution of benthivorous predators over time provide indications of underlying ecosystem change that may originate with atmospheric or hydrographic conditions and resonate through the benthic-mediated system (Moore et al. 2014).

The Bering and Chukchi seas are some of the most productive waters in the world, driven by the northward advection of nutrient-rich water and strong benthic–pelagic coupling (Cooper et al. 2002, Dunton et al. 2005, Lovvorn et al. 2005). Localized declines in benthic invertebrate abundance and recent change in benthic species composition and distribution in the Bering Sea, however, have been attributed to changing sea-ice dynamics, circulation, and wind patterns (Grebmeier et al. 2006b, Lovvorn et al. 2009, 2014). Growing attention to the implications of rapid ecosystem change in high-latitude marine systems has prompted an increase in research activity in the Arctic, with specific attention to assessing long-term change and wildlife response (Van Hemert et al. 2015). Although multiyear in situ studies in the Arctic have only recently been initiated, retrospective syntheses of independently collected data (e.g., Dunton et al. 2005) provide insight across a broader spatiotemporal scale. As an alternative, ecosystem change can be assessed by repeating past studies and examining change among linked processes. For instance, if the distribution and abundance of benthic fauna are changing throughout the Arctic, as they have in the Bering and Chukchi seas, we should detect shifts in the distribution of benthivorous predators.

The Spectacled Eider (*Somateria fischeri*) is a benthivorous sea duck that spends the nonbreeding portion of its annual cycle in the East Siberian, Beaufort, Chukchi, and Bering seas (Petersen et al. 1995, 1999, 2000). At sea, Spectacled Eiders can dive as deep as 70 m to feed on benthic invertebrates, preferring bivalve mollusks (e.g., *Macoma calcarea*, *Nuculana radiata*, and *Ennucula tenuis*; Petersen et al. 1998, Lovvorn et al. 2003, 2014). The species was listed as threatened under the U.S. Endangered Species Act in 1993 (U.S. Fish and Wildlife Service 1993) as a result of a dramatic decline (as much as 96% from 1952 to 1993) in the western Alaska breeding population. Geographically separated and genetically distinct breeding populations also occur in northern Alaska, USA, and northern Russia (Scribner et al. 2001). Petersen et al. (1995, 1999) used satellite telemetry to locate the species' 4 principal marine molting areas and sole wintering area in the northern Bering Sea; however, technological limitations at the time precluded data collection beyond early winter. More recently, we used satellite telemetry (Sexson et al. 2014b) to expand upon data collected by Petersen et al. (1999), which provided an opportunity to compare past and more recent distributions of Spectacled Eiders at molting areas.

In winter, Spectacled Eiders congregate in areas where preferred benthic prey are most dense, when not precluded by sea ice. Prey densities shift in response to patterns of export production, transport and deposition of sediments and phytodetritus, and the dispersal and settlement of invertebrate larvae (Cooper et al. 2013, Lovvorn et al. 2014). During late summer, however, molting areas are ice free. Therefore, the distribution of Spectacled Eiders during the molting period is assumed to directly correspond with environmental conditions, such as availability of prey, that favor survival through the molting period. We examined interannual and interdecadal variation in core molting distribution as determined through satellite telemetry at the 4 principal molting areas identified by Petersen et al. (1999). We also evaluated whether distribution shifts influenced the energetic cost of foraging during the molting period, as revealed by dive depth to access prey.

METHODS

Petersen et al. (1995, 1999) deployed satellite transmitters in adult Spectacled Eiders between 1993 and 1996 at the Indigirka River Delta (71°20′N, 150°20′E) in northern Russia; near Prudhoe Bay (70°16′N, 148°26′W) in northern Alaska; and at the lower Kashunuk (61°20′N, 165°35′W) and Manokinak (61°11′N, 165°05′W) rivers in the Yukon–Kuskokwim River Delta in western Alaska. We deployed transmitters in adult Spectacled Eiders between 2008 and 2011 at Peard Bay (70°48′N, 158°15′W) and the Colville River Delta (70°26′N, 150°40′W) in northern Alaska, and at Big Slough (61°14′N, 165°37′W) in the Yukon–Kuskokwim River Delta (Figure 1).

We used mist nets and bow traps to capture adult Spectacled Eiders in flight, on nests, or with broods. Veterinarians used standard surgical methods (Korschgen et al. 1984, 1996, Olson et al. 1992) to implant a satellite transmitter with percutaneous antenna (model PTT 100; Microwave Telemetry, Columbia, Maryland, USA) into the coelom of each individual. Birds were induced and maintained under general anesthesia during surgery using either vaporized isoflurane (Isoflo; Abbott Laboratories, North Chicago, Illinois, USA) or intravenous propofol (Abbott Laboratories). After anesthetic recovery, we held each individual in a kennel until the attending veterinarian deemed it stable for release. Mean duration (± SD) between the conclusion of surgery and release was 2.6 ± 2.7 hr. We released individuals at nest sites (incubating females), near the site of capture (broods), or near the surgery site. Petersen et al. (1995, 1999) used the same methods in the 1990s.

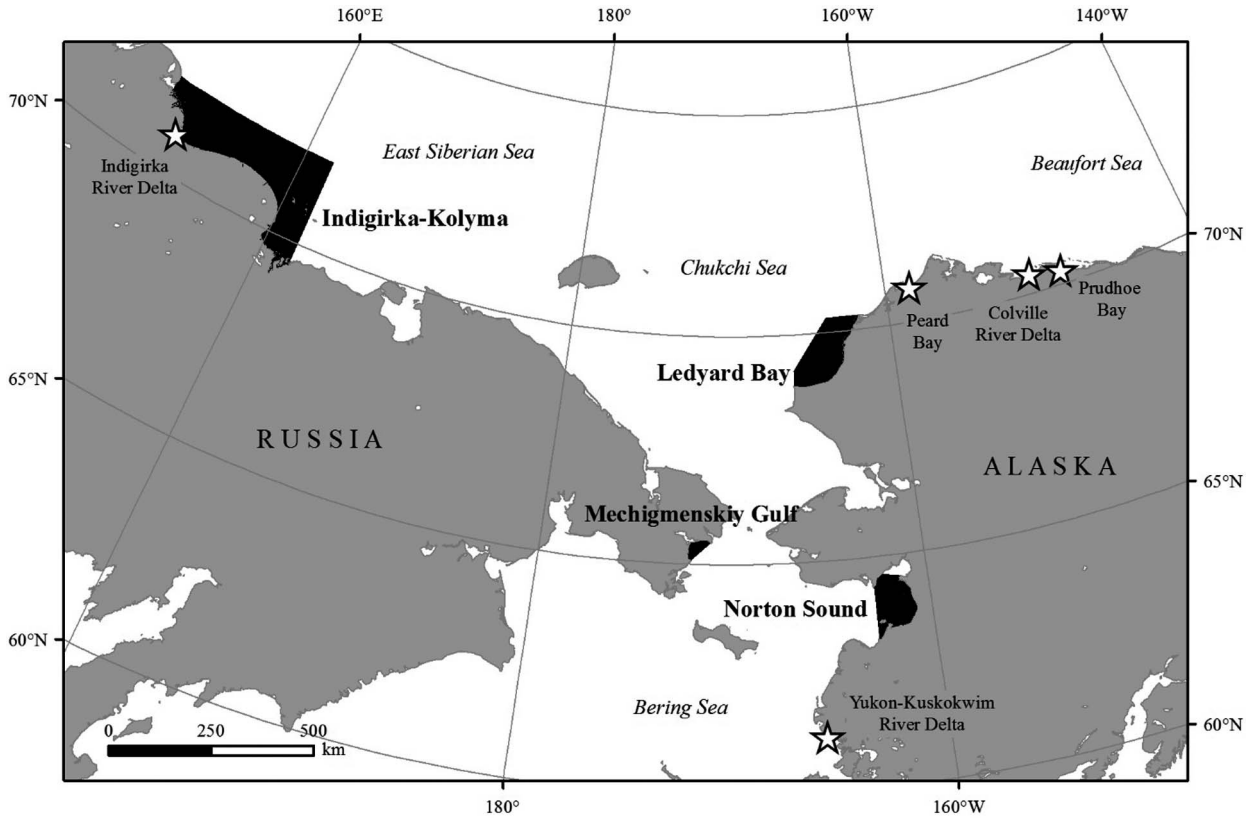

FIGURE 1. Location of principal molting areas (black polygons) used by Spectacled Eiders within which we tested for shifts in the distribution of postbreeding satellite telemetry locations between the 1990s (1993–1996) and 2008–2011. Stars indicate locations where satellite transmitters were deployed.

We programmed transmitters for an on:off "duty cycle" of 5:96 hr, 5:106 hr, 5:116 hr, or 6:160 hr to collect location and body-temperature data every 4–7 days, up to 2 yr following implantation. Petersen et al. (1995) programmed transmitters for a 6:66 or 6:114 hr duty cycle to collect data every 3–5 days. All data were received through the CLS Argos system. We initially processed raw data to exclude poor-quality locations (i.e. Argos location classes B and Z) and data from dead individuals (body temperature <30°C). We also censored locations received within 14 days of implantation, to minimize behavioral bias potentially induced by a period of recovery following release (Mulcahy and Esler 1999, Oppel et al. 2008, Sexson et al. 2014a).

We used the Douglas Argos filter (Douglas et al. 2012) to (1) remove improbable locations based on distance between locations and Argos location class and (2) select the single most likely location from each duty cycle to minimize spatial autocorrelation bias in our analysis. The Douglas Argos filter relies on user-defined parameters to constrain a location selection algorithm based on (1) the maximum redundant distance (MRD; based on spatial redundancy) between consecutive locations; (2) the plausible distance, angle, and rate (DAR) of movement between consecutive locations; or (3) a hybrid algorithm that integrates properties of both MRD and DAR. We processed data for all birds using the hybrid algorithm, defining filter parameters as follows: maxredun = 10 km, minrate = 100 km h^{-1}, keep_lc = 1, keeplast = 0, skiploc = 0, ratecoef = 15, r_only = 0, xmigrate = 2, xoverrun = 2, xdirect = 20°, xangle = 150°, xpercent = 20%, testp_0a = 2, testb_bz = 3, and rankmeth = 2 (for parameter definitions, see Douglas et al. 2012). Finally, we projected and visually validated the plausibility of selected locations in ArcMap 10.2.2 (ESRI, Redlands, California, USA) before further analysis.

For each individual, we used the distance between sequential locations to classify each location as geographically "stationary" or "transient." "Stationary" locations suggested sustained use (>1 wk) of a particular molting area, whereas "transient" locations suggested short-term (<1 wk) use. We classified a location as "stationary" if it was either (1) <100 km from the previous location or (2) >100 km from the previous location, yet <100 km from the subsequent location, or (3) >100 km from the subsequent location but without apparent directional movement within the sequence. We classified a location

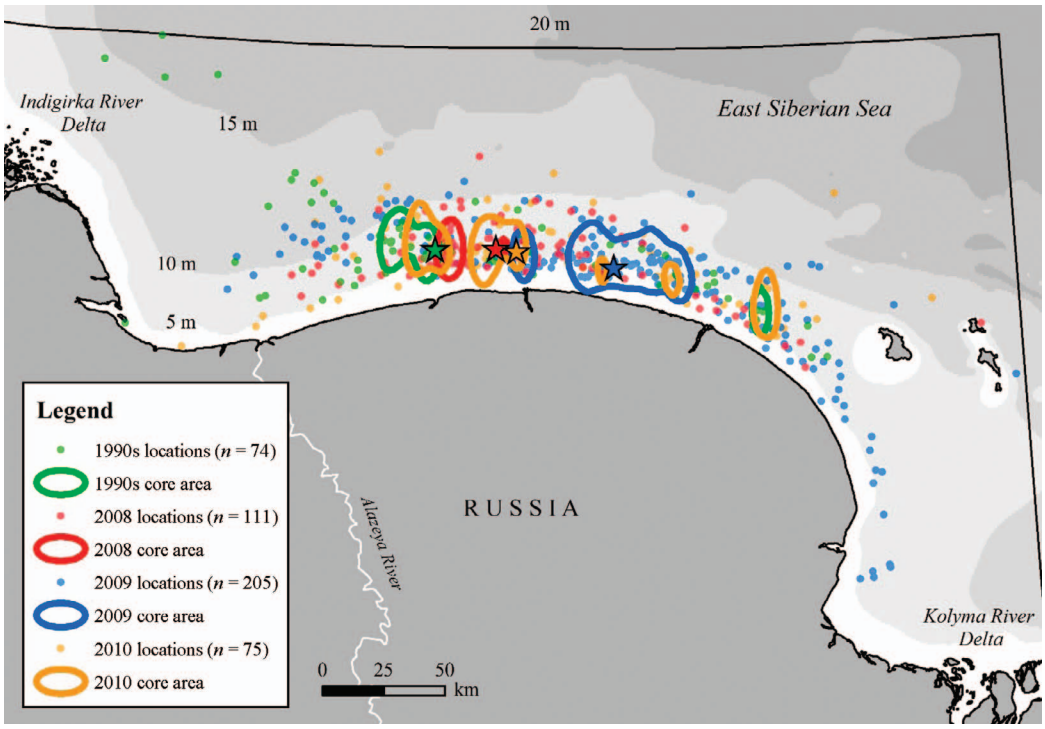

FIGURE 2. Observed distribution and core areas (50% kernel density) of Spectacled Eider locations in the Indigirka–Kolyma molting area in the 1990s (1994–1996), 2008, 2009, and 2010. Color-corresponding stars represent the median center of each year. Bathymetric depth contours are shaded in 5 m intervals.

as "transient" if (1) it was >100 km from both previous and subsequent locations and (2) the sequence exhibited directional movement.

We defined the 4 principal Spectacled Eider molting areas as follows: (1) Indigirka–Kolyma (~58,000 km^2) included the area between the Indigirka and Kolyma river deltas from the northern coast of Russia to 72°N latitude (Figures 1 and 2); (2) Ledyard Bay (~15,000 km^2) included defined critical habitat (U.S. Fish and Wildlife Service 2001), expanded to the coast of northwestern Alaska to include Kasegaluk Lagoon (Figures 1 and 3); (3) Norton Sound (~10,500 km^2) included defined critical habitat (U.S. Fish and Wildlife Service 2001) (Figures 1 and 4); and (4) Mechigmenskiy Gulf (~1,400 km^2) included the area from the entrance to Mechigmenskaya Bay southwest to a line between Cape Nyĉigen and Cape Krigujgun, Russia (Figures 1 and 5). We used ArcMap to subsample our data to select "stationary" locations received during July–November within each molting area. We then stratified locations within each molting area according to year. Although males and females initiated molt migration at different times, we found no spatial segregation among sexes at molting areas. Therefore, we grouped males and females within each area and year. Because sample sizes were smaller in the 1990s, and we found no statistical or visual evidence of spatial segregation among years in the 1990s, we grouped those years to strengthen statistical power when comparing them to recently collected data (Table 1).

We used a randomization analysis described by Breed et al. (2006, 2013) to test the null hypothesis that there was no difference in the core (50% kernel density; Fieberg and Kochanny 2005) distribution of locations between years within each molting area. For each pairwise test, we calculated the kernel density of locations in each year and measured the areal overlap of their 50% contours. We then randomly reassigned the set of locations produced by individual Spectacled Eiders (as opposed to individual locations) to 2 null groups composed of the same number of observed locations within each year in the pairwise test (Pesarin 2001), calculated kernel densities of each null group, and measured the areal overlap of their 50% contours. We repeated the randomization procedure for 1,000 permutations without replacement and used the proportion of random overlaps that were smaller than the true overlap to determine the P value for each test. For example, if the true areal overlap was smaller than all 1,000 randomly generated overlaps, $P \leq 0.001$. We rejected our null hypothesis for a pairwise test if $P \leq 0.01$. We used custom scripts (Breed et al. 2006, 2013) in MATLAB 8.3 (MathWorks, Natick, Massachusetts, USA) to perform the randomization analysis. We calculated kernel density

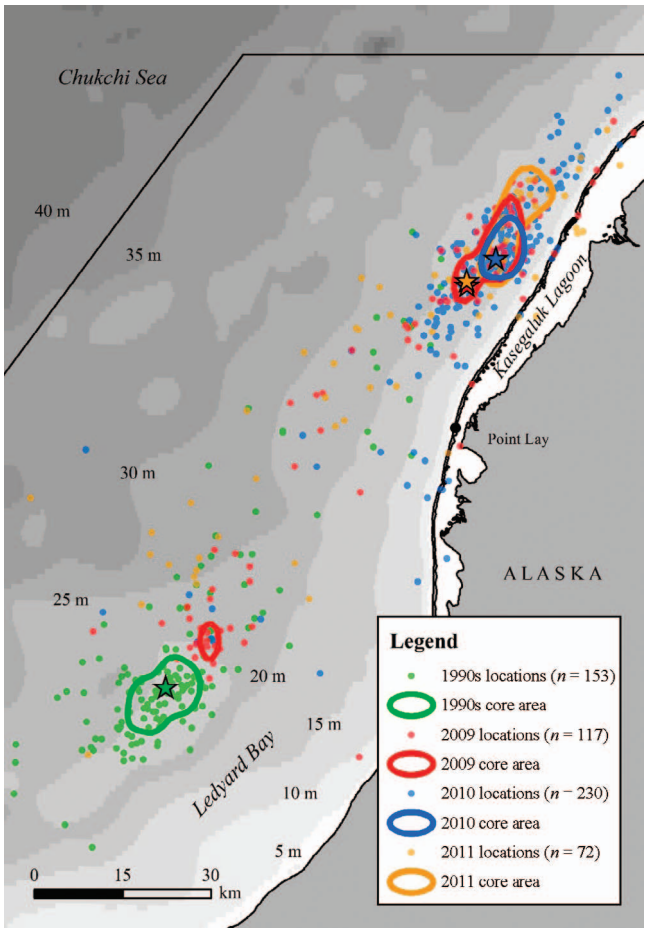

FIGURE 3. Observed distribution and core areas (50% kernel density) of Spectacled Eider locations in the Ledyard Bay molting area in the 1990s (1994–1996), 2009, 2010, and 2011. Color-corresponding stars represent the median center of each year. Bathymetric depth contours are shaded in 5 m intervals.

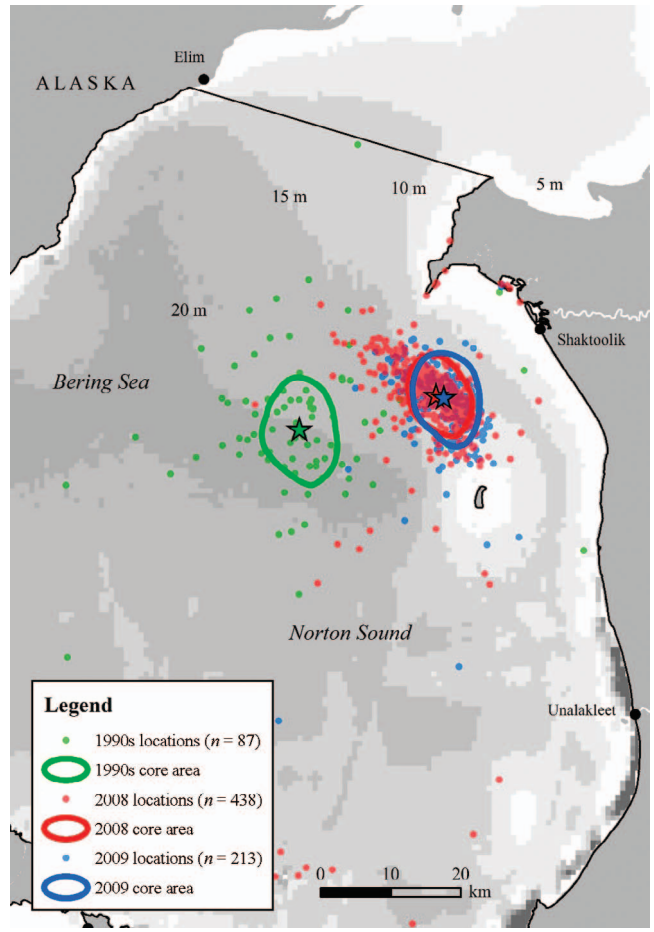

FIGURE 4. Observed distribution and core areas (50% kernel density) of Spectacled Eider locations in the Norton Sound molting area in the 1990s (1993–1995), 2008, and 2009. Color-corresponding stars represent the median center of each year. Bathymetric depth contours are shaded in 5 m intervals.

within grid cells measuring ~1 km^2 and used a kernel smoothing parameter that produced kernel isopleths that visually best fit the data within each molting area. We used ArcGIS 10.2.2 (ESRI) to calculate the median center of observed locations within each year and measured the distance between centers to describe the magnitude and direction of shifts.

We used likelihood ratio tests in the Statistics Toolbox in MATLAB to compare mixed-effects models to test the hypothesis that depth was variable among years within each molting area. For each area, we constructed a full model that included the fixed effect of year as a factor, and a null model without a year effect. Both models included individual bird as a random effect to control for lack of independence among data points. We used ArcGIS to extract a depth value from the General Bathymetric Chart of the Oceans (GEBCO) bathymetric dataset (GEBCO_2014 Grid, version 20141103, available from http://www.gebco.net) for each location within respective 50% kernel isopleths. We considered $P \leq 0.05$ significant. We report the parameter estimate (± SE) and the 95% confidence interval (CI) for each year in our full model. Estimates represent mean depth corrected for correlation among locations received from the same individual.

RESULTS

In the Indigirka–Kolyma molting area, we found significant separation between core distributions in the 1990s and 2009 and between those in 2008 and 2009 (Figures 2 and 6). The median center in 2009 was ~74 km east of the median center in the 1990s, and ~49 km east of the median center in 2008. There were no differences among remaining pairwise comparisons between the 1990s, 2008, 2009, and 2010. Core distributions in the 1990s, 2009, and 2010 were split among several areas, although all occurred

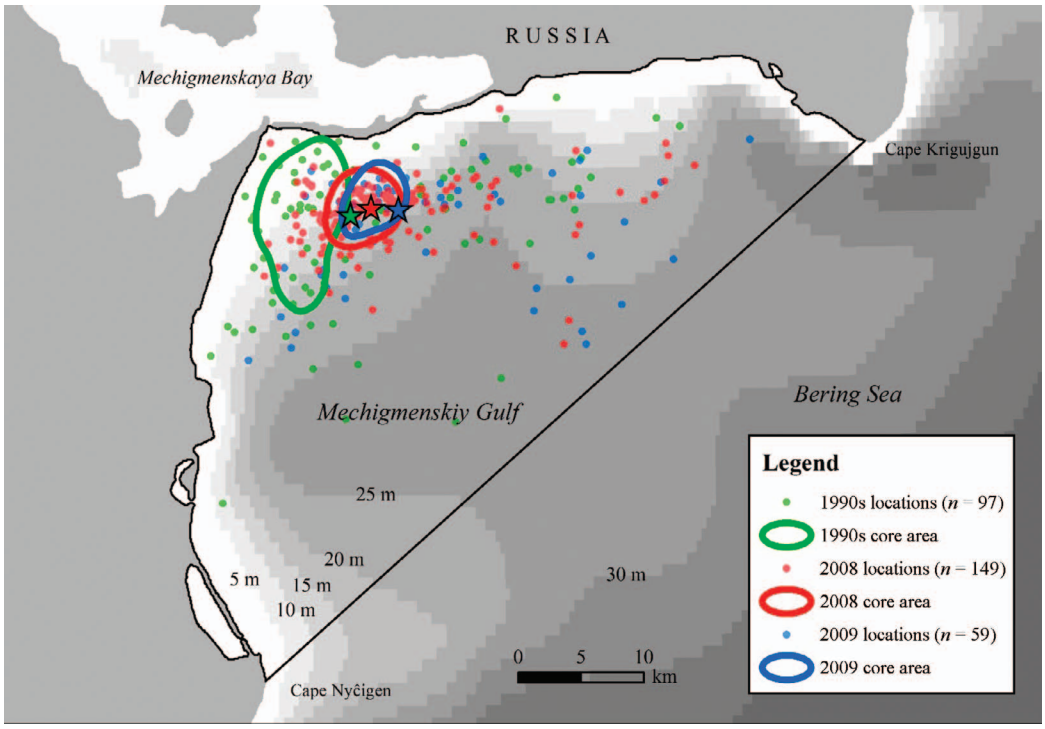

FIGURE 5. Observed distribution and core areas (50% kernel density) of Spectacled Eider locations in the Mechigmenskiy Gulf molting area in the 1990s (1993–1996), 2008, and 2009. Color-corresponding stars represent the median center of each year. Bathymetric depth contours are shaded in 5 m intervals.

within 40 km of the north coast of Russia between the Indigirka and Kolyma river deltas. Depth below core areas varied by year (likelihood ratio test, $\chi^2 = 31.7$, df = 3, $P < 0.001$). Parameter estimates for the 1990s ($\hat{\beta} = 5.9 \pm 0.2$ m; 95% CI: 5.5–6.4 m), 2008 ($\hat{\beta} = 5.5 \pm 0.3$ m; 95% CI: 4.9–6.2 m), 2009 ($\hat{\beta} = 4.5 \pm 0.3$ m; 95% CI: 4.0–5.1 m), and 2010 ($\hat{\beta} = 5.6 \pm 0.3$ m; 95% CI: 5.0–6.2 m) suggest that the source of variation was a difference in depth between the 1990s and 2009, although the greatest difference among years was ~1.4 m (biologically negligible).

In Ledyard Bay, there was interdecadal separation between core distributions (Figures 3 and 7). Median centers of locations in 2009, 2010, and 2011 were approximately 84, 90, and 85 km northeast, respectively, of locations in the 1990s. Core distribution in the 1990s was located in Ledyard Bay, ~37 km from the nearest coast of Alaska. Core distributions in 2010 and 2011 were located within 15 km of mainland Alaska, seaward of the barrier islands of Kasegaluk Lagoon. Core distribution in 2009 was split between the 2 areas, approximately 12% in Ledyard Bay and 88% near Kasegaluk Lagoon. We could not compare distribution in the 1990s to that in 2011 because the number of combined locations per individual was too small to apply our randomization procedure (Table 1). We detected interannual variation in depth below core areas (likelihood ratio test, $\chi^2 = 16.3$, df = 3, $P < 0.001$). Parameter estimates for the 1990s ($\hat{\beta} = 17.3 \pm 0.3$ m; 95% CI: 16.8–17.8 m), 2009 ($\hat{\beta} = 17.6 \pm 0.4$ m; 95% CI: 16.8–18.4 m), 2010 ($\hat{\beta} = 16.2 \pm 0.4$ m; 95% CI: 15.5–16.9 m), and 2011 ($\hat{\beta} = 16.2 \pm 0.6$ m; 95% CI: 15.1–17.3 m) suggest that the source of variation was a difference in

TABLE 1. Number of stationary postbreeding satellite telemetry locations received from adult Spectacled Eiders in July–November at each primary molting area.

Year	Number of locations	Number of individuals
Indigirka–Kolyma		
1990s (1994–1996)	74	10
2008	111	6
2009	205	13
2010	75	6
Ledyard Bay		
1990s (1994–1996)	153	19
2009	117	15
2010	230	21
2011	72	8
Norton Sound		
1990s (1993–1995)	87	11
2008	438	28
2009	213	16
Mechigmenskiy Gulf		
1990s (1993–1996)	97	15
2008	149	12
2009	59	10

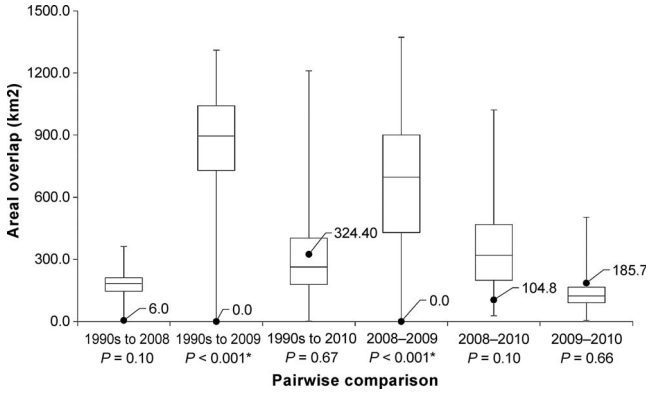

FIGURE 6. Randomization results for pairwise tests of 50% kernel density overlap of Spectacled Eider satellite telemetry locations in the Indigirka–Kolyma molting area. Box plots summarize (maximum, third quartile, median, first quartile, minimum) the areal overlap (km^2) of null 50% kernel densities through 1,000 permutations when individuals were randomly assigned to 2 null groups. Observed overlap is indicated by a labeled point. Asterisks denote significant *P* values.

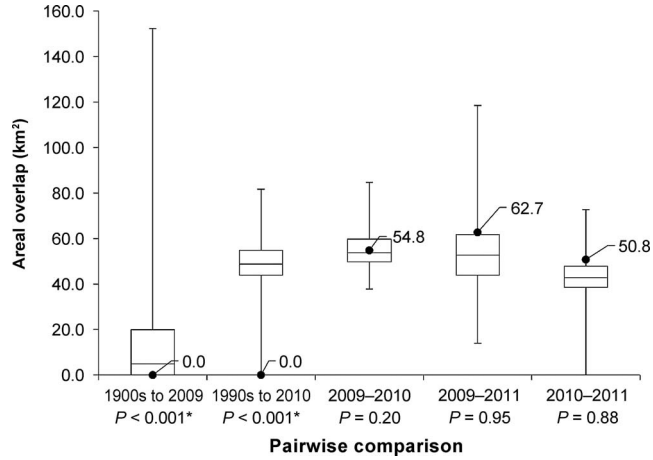

FIGURE 7. Randomization results for pairwise tests of 50% kernel density overlap of Spectacled Eider satellite telemetry locations in the Ledyard Bay molting area. Box plots summarize (maximum, third quartile, median, first quartile, minimum) the areal overlap (km^2) of null 50% kernel densities through 1,000 permutations when individuals were randomly assigned to 2 null groups. Observed overlap is indicated by a labeled point. Asterisks denote significant *P* values. The number of combined locations was too small to compare the distribution of Spectacled Eiders in the 1990s to 2011.

depth between the 1990s and 2010–2011. However, as observed in the Indigirka–Kolyma molting area, the greatest difference among years was ~1.4 m (biologically negligible).

Likewise, we found significant interdecadal separation between core distributions in Norton Sound (Figures 4 and 8). Median centers of locations in 2008 and 2009 were approximately 20 and 21 km east, respectively, of locations in the 1990s. Interannual variation improved our null model of depth (likelihood ratio test, $\chi^2 = 173.7$, df = 2, $P < 0.001$). Parameter estimates for the 1990s ($\hat{\beta} = 19.5 \pm 0.2$ m; 95% CI: 19.1–19.9 m), 2008 ($\hat{\beta} = 12.2 \pm 0.2$ m; 95% CI: 11.7–12.6 m), and 2009 ($\hat{\beta} = 11.6 \pm 0.2$ m; 95% CI: 11.1–12.1 m) suggest that the source of variation was a difference in depth between the 1990s and 2008–2009. Landward shift resulted in a decrease in depth below core areas in more recent years.

There was also separation between core distributions in the 1990s and 2008 in Mechigmenskiy Gulf (Figures 5 and 9), although the median center of locations in 2008 was only 2 km east of that in the 1990s. Observed overlap of core areas in the 1990s and 2009 was only 1 km^2. However, we failed to reject our null hypothesis for this pair of years, because the areal overlap of over half of the randomly generated kernels was <1 km^2. We attributed this unexpected result to the relatively dispersed distribution of locations in the 1990s and 2009, compared to a clumped distribution in 2008. As observed at other molting areas, depth below core areas varied among years (likelihood ratio test, $\chi^2 = 6.4$, df = 2, $P = 0.04$). Parameter estimates for the 1990s ($\hat{\beta} = 7.8 \pm 1.1$ m; 95% CI: 5.6–10.0 m), 2008 ($\hat{\beta} = 12.0 \pm 1.4$ m; 95% CI: 9.2–14.9 m), and 2009 ($\hat{\beta} = 11.4 \pm 2.0$ m; 95% CI: 7.5–15.3 m) suggest that the greatest source of variation was the difference in depth between the 1990s and 2008.

DISCUSSION

Assuming that Spectacled Eiders molted in areas where environmental conditions met requirements for feather growth and survival, and that shifts in their distribution mirrored changes in these environments, we interpreted observed shifts in marine molting areas as indicators of ecosystem change. However, we cannot affirm this interpretation because of a lack of data on environmental factors such as the distribution and abundance of benthic prey. Moreover, the feeding habits and diet composition of molting Spectacled Eiders have not been studied; it is unknown whether they generally rely on endogenous nutrient reserves or exogenous resources to fuel feather growth, and modify their behavior or locations respectively. Common Eiders (*S. mollissima*) did not increase foraging effort during the molting period, which suggested loss of body mass and partial reliance on endogenous reserves for feather growth (Guillemette et al. 2007). However, when not precluded by other factors, the molting distributions of sea ducks are generally consistent with productive feeding areas (summarized by Fox et al. 2014, Savard and Petersen 2015). This pattern is consistent with ideal free distribution (Fretwell and Lucas 1970) and

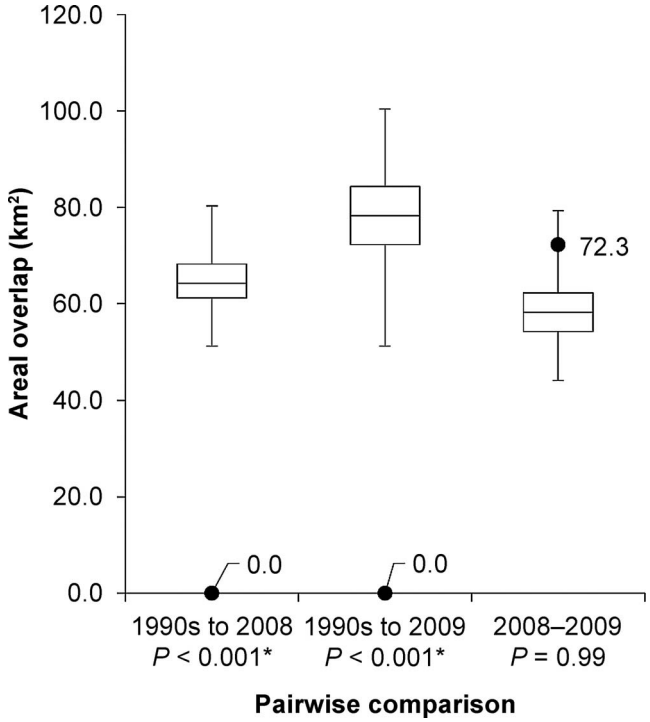

FIGURE 8. Randomization results for pairwise tests of 50% kernel density overlap of Spectacled Eider satellite telemetry locations in the Norton Sound molting area. Box plots summarize (maximum, third quartile, median, first quartile, minimum) the areal overlap (km^2) of null 50% kernel densities through 1,000 permutations when individuals were randomly assigned to 2 null groups. Observed overlap is indicated by a labeled point. Asterisks denote significant *P* values.

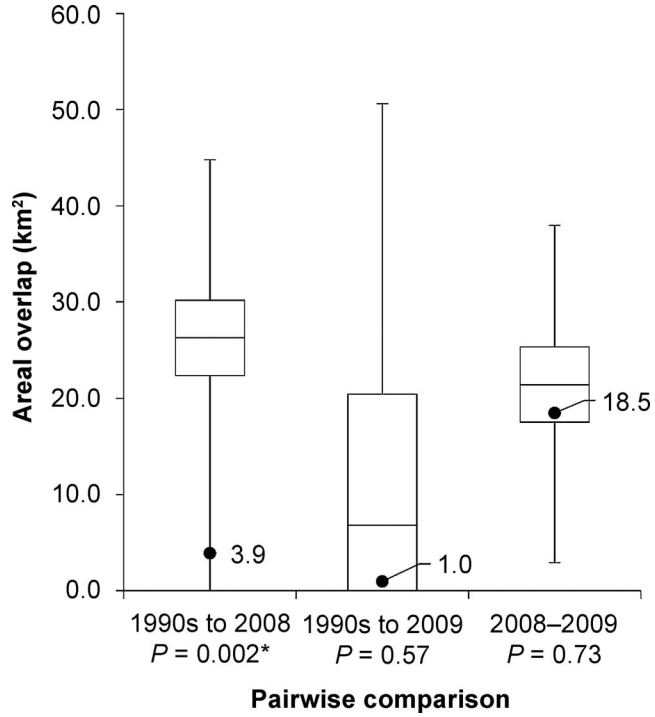

FIGURE 9. Randomization results for pairwise tests of 50% kernel density overlap of Spectacled Eider satellite telemetry locations in the Mechigmenskiy Gulf molting area. Box plots summarize (maximum, third quartile, median, first quartile, minimum) the areal overlap (km^2) of null 50% kernel densities through 1,000 permutations when individuals were randomly assigned to 2 null groups. Observed overlap is indicated by a labeled point. Asterisks denote significant *P* values.

foraging (Stephens and Krebs 1986) theories, which predict that the movement and distribution of predators are influenced by the distribution and composition of prey communities occurring in sufficient abundance to optimize energy intake. Therefore, our results may be an indicator of the distribution of benthic invertebrates and related ecosystem processes, advancing the hypotheses that (1) Spectacled Eiders are collocated with prey on which they might feed during the molting period and (2) shifts in the distribution of molting individuals are indicative of changes in the distribution of their prey.

Other factors may influence the distribution of molting Spectacled Eiders, such as avoidance of predators, competitors, or human disturbance, or selection of areas that offer protection from strong currents or rough seas. Along the eastern Chukchi Sea coast, molting Spectacled Eiders share areas with other sea duck species (Oppel et al. 2009) as well as benthivorous marine mammals (Jay et al. 2012). Multiple benthivorous species likely co-occur at each of the areas in our study; although fine-scale habitat partitioning among these taxa by diet, dive capability, bathymetry, and the distribution of prey may occur, thus minimizing competition during the molting period (Frimer 1995, Bustnes and Lønne 1997, Merkel et al. 2007). Within a molting period, eider distributions may also shift in response to prey depletion (Guillemette et al. 1996, Bustnes et al. 2013). However, recolonization rates after local depletion have not been adequately studied, and therefore an interannual effect on prey availability—and, consequently, on the distribution of benthivorous predators—is unknown. Wintering eiders have been observed evading predatory Pacific walruses (Lovvorn et al. 2010); although predatory activity appears to occur opportunistically, and at-sea predation during the molting period has not been identified as a substantial threat. Further, anthropogenic disturbances (e.g., vessel traffic, hunting) were not prominent at molting areas during our study. In general, sea ducks molt in coastal areas that include bays, estuaries, and fjords (summarized by Savard and Petersen 2015), which presumably provide shelter from currents and wave action found in open ocean.

We asked whether shifts in the distribution of molting Spectacled Eiders coincided with a change in the depth required to dive to reach prey, which may carry positive or

negative energetic consequences. For a dive to be profitable, intake at depth must exceed the energetic expense of the dive; greater time at depth allows for prey selection and greater prey consumption (Heath and Gilchrist 2010). As dive depth increases, time at depth decreases, although strong currents affect an individual's ability to maintain position on the bottom and reduces time at depth (Heath and Gilchrist 2010). In our study, core molting areas occurred over depths ranging 1.0–22.0 m; the greatest difference among years occurred in Norton Sound, where a landward shift in recent years reduced the depth below core areas by ~8.0 m. Interannual or interdecadal differences detected through our analysis are probably biologically negligible, given that Spectacled Eiders may dive as deep as 70 m to access prey (Petersen et al. 1998). However, shallower depths to forage during the molting period might be energetically beneficial if wing-propelled diving is hindered by the temporary loss of wing plumage (Bridge 2004). In this respect, feather growth is the most energetically expensive process during the molting period, and any energetic gains from foraging are largely allocated to feather production or survival (Guillemette et al. 2007). If Spectacled Eiders rely on exogenous resources to supplement endogenous reserves during the molting period, shifts in distribution, abundance, or community composition of benthic infauna likely have greater energetic consequences than changes in dive depth.

The core distribution of Spectacled Eiders shifted between years or decades within each molting area. The interdecadal shift was greatest in Ledyard Bay, which is located within an important corridor for sea ducks migrating through the eastern Chukchi Sea, to and from breeding areas in northern Alaska and Canada (Petersen and Flint 2002, Oppel et al. 2009, Martin et al. 2015). Of the molting areas included in our study, the benthic ecology of the eastern Chukchi Sea is the best understood. Benthic infaunal and epifaunal abundances in autumns 1986 and 1990, respectively, suggested that sand dollars (*Echinarachnius parma*) were probably the most abundant species below the core distribution of eiders in the 1990s (Feder et al. 1994a, 1994b). Few mollusks were found in Ledyard Bay, which Feder et al. (1994b) attributed to sediment-reworking activity by sand dollars. Benthic sampling was repeated in the nearshore eastern Chukchi Sea in 2010–2012 (Lovvorn et al. 2015, S. Jewett personal communication). In 2010, polychaetes were the most abundant taxa near the core area used in the 1990s, although bivalves also occurred in great enough densities (>200 individuals m^{-2}; Lovvorn et al. 2015), presumably, to support profitable foraging. However, core distributions of Spectacled Eiders in 2009–2011 were located near Kasegaluk Lagoon, where benthic sampling in 2011 suggested that sand dollars were considerably more abundant than any other benthic species (S. Jewett personal communication). Large aggregations of Pacific walruses also forage along the coast of Kasegaluk Lagoon in autumn, although densities of bivalve mollusks in this area were presumably too low to support profitable foraging by eiders or walruses (Jay et al. 2012, Lovvorn et al. 2015). The greatest densities of bivalves in the eastern Chukchi Sea occurred north of Kasegaluk Lagoon (Lovvorn et al. 2015), although our sample of Spectacled Eiders did not molt in this area in any year of satellite telemetry. These circumstances suggest a pair of hypotheses: (1) Molting eiders might supplement endogenous reserves by foraging on sand dollars in Ledyard Bay; and (2) between the 1990s and 2009–2011, the distribution of sand dollars, and therefore of Spectacled Eiders, shifted northward toward Kasegaluk Lagoon.

Where bivalve mollusks are abundant, eiders consume bivalves in preference to other potential prey such as echinoderms, polychaetes, and amphipods (Lovvorn et al. 2003, 2014, 2015, Ouellet et al. 2013). Echinoids (e.g., urchins) have been identified as prey for some populations of King Eiders (*S. spectabilis*; Merkel et al. 2007) and Common Eiders (Guillemette et al. 1992). However, sand dollars have not been documented as being consumed by any sea duck species. Alternatively, the occurrence of molting Spectacled Eiders over the greatest densities of sand dollars, and not the greatest densities of bivalves, in the nearshore eastern Chukchi Sea may be coincidental, posing another hypothesis: (3) Spectacled Eiders exhibit reduced foraging rates during the molting period, and molting distributions shifted for reasons other than prey availability.

We also detected an interdecadal shift in Norton Sound, although of less magnitude than that observed in Ledyard Bay. In contrast to Ledyard Bay, Norton Sound is considered an inshore ecosystem influenced by tidal fluctuation, wind, and the injection of freshwater and nutrients from terrestrial sources such as the Yukon River (Hamazaki et al. 2005). An ongoing regimen of periodic trawl surveys throughout Norton Sound was established to monitor the distribution and abundance of commercially valuable epifauna and demersal fish (Hamazaki et al. 2005). Yet the distribution and abundance of benthic infauna have not been adequately quantified, particularly in eastern Norton Sound, where the core distributions of molting Spectacled Eiders occurred in the 1990s and in 2008–2009. Epifaunal mega-invertebrates (e.g., sea stars) are a substantial source of predatory pressure on benthic infauna in Norton Sound (Fukuyama and Oliver 1985) and presumably forage on the same taxa as eiders. Eastward shifts in the distribution of mega-invertebrate taxa in Norton Sound from 1976 to 2002 (Hamazaki et al. 2005) match the interdecadal shift detected among Spectacled Eiders, suggesting that the distribution of shared infaunal prey also shifted. Female eiders from the western Alaska breeding population in the Yukon–

Kuskokwim River Delta almost exclusively use Norton Sound to molt (Petersen et al. 1999, 2000). Therefore, ecosystem changes in this area may affect population dynamics in western Alaska.

In contrast to Norton Sound and Ledyard Bay, we did not detect a consistent pattern of interannual or interdecadal shifts in the distribution of eiders in the Mechigmenskiy Gulf and Indigirka–Kolyma molting areas. There is no information on the diets of eiders in relation to the availability of potential benthic prey in these Russian waters. The East Siberian Sea is considered one of the least productive marine environments in the Arctic. However, primary production has increased in the past decade as a result of climate-induced sea-surface warming and reduced ice cover (Petrenko et al. 2013), and limited benthic sampling in the southern East Siberian Sea suggests relatively high abundances of benthic fauna at sampling stations near the core distributions of Spectacled Eiders (Gukov et al. 2005). Over 90% of the world population of Spectacled Eiders breed in northern Russia (Petersen et al. 2000). If a large proportion of the breeding population uses the Indigirka–Kolyma area to molt, population dynamics could be strongly influenced by ecosystem changes in the nearshore East Siberian Sea.

The marine ecology of Mechigmenskiy Gulf is the least studied among the molting areas used by Spectacled Eiders. Patterns of nutrient advection and subsequent primary production in the northern Bering Sea and western Bering Strait, however, suggest that Mechigmenskiy Gulf might be the most productive. Northward advection of nutrients from the Bering Sea shelf via the Anadyr Current and bathymetric features in the Gulf of Anadyr and north of St. Lawrence Island, Alaska, promote a nearly constant supply of nutrients throughout the autotrophic growing season (Coachman 1993). These processes create localized areas near Mechigmenskiy Gulf of heightened primary productivity (Sambrotto et al. 1984, Springer et al. 1996, Brown et al. 2011), which supports export to adjacent benthic communities. Although the distribution and abundance of benthic fauna have not been measured in Mechigmenskiy Gulf, benthic biomass in the adjacent northern Bering Sea and western Bering Strait is among the greatest in the Arctic (Dunton et al. 2005, Grebmeier et al. 2006a), and it is likely that these processes support an annual abundance of prey within the Mechigmenskiy Gulf molting area.

In this study, we did not directly correlate shifts in the core distribution of molting eiders to the distribution of benthic prey or any other variable. However, presumably no other factors (e.g., sea ice; Lovvorn et al. 2015) exclude eiders from molting areas that might also offer adequate prey abundances to supplement the energetic expense of molting. Shifts detected during our study likely indicate changes among many interacting forces that resonate through the benthos. Although direct measurement of the distribution and abundance of benthic fauna and associated biogeochemical processes is valuable to understand regional patterns and controls, surveys are often conducted at spatial and temporal resolutions inadequate to capture finite patches of profitable habitat within an area that may otherwise appear poor. As an alternative, retrospective studies and continued monitoring of the spatiotemporal distribution of benthivorous apex predators provide indication of changes, climate-induced or otherwise, that may have significant implications for population dynamics and management of marine habitats.

ACKNOWLEDGMENTS

We thank D. Nigro (Bureau of Land Management) for logistical support and assistance in the field. M.G.S. thanks T. Donnelly, K. Weber, C. Gesmundo, S. Walden, S. Lovibond, R. Schuckard, C. and J. Steffan, S. Oppel, S. Dunn, and K. McNulty for assistance in the field. M.R.P. thanks B. Grand, P. Flint, J. Schmutz, D. Troy, J. Pearce, and A. Degteyerev for their support and for allowing us to capture eiders on their study areas. We thank D. Mulcahy (U.S. Geological Survey), G. Myers, M. Spriggs (Mesker Park Zoo and Botanic Garden), D. Heard (University of Florida), K. Wolf (Point Defiance Zoo and Aquarium), and C. Scott and B. VanGilder (University of California Davis) for their veterinary services. We thank the staff of the Yukon Delta National Wildlife Refuge for project support. We thank J. Pearce and two anonymous reviewers for comments on the manuscript.

Funding statement: Funding was provided by the U.S. Bureau of Ocean Energy Management, U.S. Bureau of Land Management, the National Fish and Wildlife Foundation, the U.S. Fish and Wildlife Service, and the North Pacific Research Board. Logistical support was provided by ConocoPhillips–Alaska, Inc. In-kind support was provided by the Columbus Zoo and Aquarium, the Mesker Park Zoo and Botanic Garden, and the Point Defiance Zoo and Aquarium. None of the agencies that provided funding or support influenced the content of the manuscript or required approval of the final manuscript to be published.

Ethics statement: Our sampling protocols were approved by Animal Care and Use Committees at the U.S. Geological Survey, Alaska Science Center (IACUC no. 2008–04), and the University of Alaska Fairbanks (IACUC no. 143488). Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Author contributions: All authors conceived the study design. M.G.S. and M.R.P. collected the data. M.G.S. wrote the paper and performed all analysis. M.G.S., M.R.P., and G.A.B. contributed to the methods. M.R.P. and A.N.P. substantially edited the paper.

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