



A salt lake under stress: Relationships among birds, water levels, and invertebrates at a Great Basin saline lake

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ABSTRACT

Saline lakes are threatened globally and provide critical habitat for a diverse array of migratory and breeding waterbirds. The ability of large numbers of waterbirds to profitably use saline lakes is primarily dependent upon concentrations of invertebrate fauna that are only present within a narrow range of salinities. Additionally, waterbirds themselves can incur steep physiological costs as their salt loads increase, meaning that they are especially sensitive to changes in salinity. Nonetheless, relatively little is known about ecosystem function within natural saline lakes or how birds will respond to fluctuations in salinity across time, hindering efforts to maintain ecologically functional saline ecosystems. To help address this gap, we coupled data from waterbird surveys undertaken across 25 years at Lake Abert, Oregon, USA with data on lake area (a proxy for salinity) and invertebrate abundance to document how waterbird numbers changed in response to variation in lake area and the presence of their invertebrate prey. We found that as the area of Lake Abert decreased and salinity increased, both invertebrate and waterbird numbers declined, with especially high salinities associated with the presence of few waterbirds and invertebrates. However, we also found that at high lake levels and low salinities the abundance of most waterbirds and invertebrates either plateaued or declined as well. Our study reinforces physiological studies showing that both invertebrates and waterbirds can only tolerate a narrow range of salinities, and is among the first to document the effects of this tolerance range at the ecosystem level. As anthropogenic water usage increases and snowfall decreases in the coming century, Great Basin saline lakes are projected to increasingly face water shortages and high salinities. Conserving saline lake ecosystems thus requires mitigating these losses and maintaining water levels and salinities within the normal range of inter-annual variation. When conditions outside of this range occur too frequently or persist too long, they can result in dysfunctional ecosystems with deleterious consequences for the species that rely on them.

1. Introduction

The invertebrate fauna of endorheic saline lakes provide critical resources for a diverse array of waterbirds worldwide (Jellison et al., 2008). In some cases, these lakes and associated wetlands provide breeding habitat for thousands of waterbirds, as well as stopover habitat that millions of migrants use to molt and refuel each year (Jehl Jr., 1994; Kingsford and Porter, 1994; Jehl Jr. and McKernan, 2002; Shuford et al., 2002; Frank and Conover, 2017). Some species even rely on saline lakes for nearly the entirety of their annual cycle. For

instance, many Wilson's Phalaropes (*Phalaropus tricolor*) breed on or near saline lakes throughout western North America, then stage during their southward migration on a handful of saline lakes in central Canada and the Great Basin of the United States, before spending the nonbreeding season on saline lakes in South America (Jehl Jr., 1988). Nonetheless, the long-term population dynamics of waterbirds relying on saline lakes have been little studied away from a few well-characterized sites (e.g., Great Salt Lake: Frank, 2016; Mono Lake: Wrege et al., 2006; Western Australia Wheatbelt: Lyons et al., 2007), creating a significant gap in our understanding of the biology of this widespread,

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but relatively rare ecosystem that makes up ~3% of global lake volume (Wurtsbaugh et al., 2017).

Saline lakes have always been characterized by a degree of ephemerality (Keister Jr., 1992; Williams, 1996; Jellison et al., 2008; Bedford, 2009; Wurtsbaugh, 2014). However, the cumulative effects of the anthropogenic threats currently facing saline lakes — which range from the diversion of water to support agricultural practices and urban expansion to the direct effects of droughts resulting from global climate change (Jellison et al., 2008; Jeppesen et al., 2015; Wurtsbaugh et al., 2017) — are being superimposed on this natural variability. Such changes can lead to hypersalinization, disrupting the tight osmotic balance required of birds living in saline environments (Rubega and Robinson, 1996; Anderson et al., 2007; Gutiérrez, 2014). Even species acclimated to saline environments must raise their metabolic rate, suppress their immune function, and alter other aspects of their physiology to adjust to increases in salinity (Gutiérrez et al., 2011, 2012, 2013). These costs must subsequently be offset by increases in energy consumption. However, the size and nutritional quality of saline lake invertebrates also decline at high salinities, limiting the ability of birds to meet their heightened energetic requirements (Herbst, 2006). Hypersalinization can thus potentially initiate reversible state effects (sensu Senner et al., 2015) that adversely influence performance (Masero et al., 2017), as well as aggravate disease outbreaks (Shuford et al., 1999; Caskey et al., 2007).

Complicating matters is the fact that hypersalinization is not the only potential conservation threat facing saline lakes. In fact, the inverse — the incursion of high levels of freshwater — can also be detrimental and result in reductions in the invertebrate food resources on which waterbirds rely (Herbst, 2001; Beutel et al., 2001). There is thus a trade-off among salinity, invertebrate diversity and abundance: Low salinities tend to result in higher overall invertebrate diversity, but reduced abundance. As salinities increase, there is a decline in invertebrate diversity and an increase in the abundance of a few salinertolerant species until a point above which few, if any, invertebrates can survive (Herbst, 2006; Brown, 2010). As an example, optimal salinity levels for *Ephydra* spp. (brine flies) and *Artemia* spp. (brine shrimp) — two common saline lake invertebrates — occur between 3 and 8% salinity, with salinities being too low or too high for these species to survive outside the range of 2.5–15% (Brown, 2010). As a result, evidence from artificial salt pans suggests that both invertebrate and waterbird abundance peak at intermediate salinities (Warnock et al., 2002). However, without more detailed knowledge concerning the effects of fluctuations in water and salinity levels in natural saline lakes on bird populations and their prey, it is difficult to identify priority conservation and management strategies that can be implemented to help conserve these ecosystems (Stralberg et al., 2011).

The Great Basin of the western United States supports approximately 45 saline lakes and wetlands (Grayson, 1993). Lake Abert, in eastern Oregon (Fig. 1), is among the largest of these lakes and is of national and international significance for migratory birds. Hundreds of thousands of shorebirds and waterfowl use the lake annually, especially during fall migration (Boula, 1985; Warnock et al., 1998). During the past three decades, however, water levels have fluctuated dramatically as a result of drought and upstream water withdrawals, causing the lake to approach complete desiccation in some years and leading to more frequent and longer periods with extremely high salinity (Moore, 2016; Fig. 2). These fluctuations have, in turn, shifted the benthic ecosystem away from a regime characterized by higher trophic level invertebrates to one dominated by hypersaline-adapted microbes, with as-of-yet-unknown consequences for birds and other species that rely on the lake (Larson and Eilers, 2014; Larson et al., 2016). Given the importance of Lake Abert to migratory waterbirds and the commonality of these circumstances across saline lakes globally, Lake Abert may serve as a case study that can elucidate how such changes affect birds and their invertebrate prey.

Here we present data on waterbird abundance, lake area (a proxy

for salinity, see Moore, 2016), and invertebrate abundance collected over the course of 25 years at Lake Abert, providing one of the first opportunities to examine long-term fluctuations in the relationship between birds, their food resources, and salinity at an endorheic saline lake. Because salinity can be both too high and too low for saline lake invertebrates (Brown, 2010), we predicted that waterbird abundance would respond to invertebrate abundance and peak at intermediate levels of salinity (e.g., 3–8%), but decline at both extremely high (> 15%) and low (< 2.5%) levels. If our predictions hold true, they would indicate that the conservation of saline lakes will require strict management in the face of global change and that even relatively small changes in salinity levels can have potentially large-scale impacts on waterbird populations.

2. Methods

2.1. Study area

Lake Abert is located in the closed hydrologic basins of southcentral Oregon, USA (Fig. 1; 42.626°N, 120.233°W). Land ownership surrounding Lake Abert is mixed, but the lake itself and the watershed immediately to the east of the lake are managed by the Bureau of Land Management (BLM) as an Area of Critical Environmental Concern (BLM, 1996). Land and water use in the Lake Abert watershed are dominated by agriculture and forestry, with only minor rural municipal development occurring in the area. Over the period of our study, 1992–2016, the extent of agricultural lands increased slightly and a new reservoir was constructed upstream of Lake Abert (S.I. Fig. 1), but there has been no major land use transformation.

On average, the lake covers ~170 km² at a depth of 1.5 m and is the largest hypersaline lake in the Pacific Northwest (Larson et al., 2016). Historically, salinity levels within the lake averaged 7.5%, but ranged between 2 and 8% depending on the season and influx of freshwater (Phillips and Van Denburgh, 1971; Moore, 2016). Freshwater comes mainly from the Chewaucan River, but is supplemented by two ephemeral creeks (Poison and Juniper) and a series of freshwater seeps and springs that occur along the perimeter of the lake, and especially the eastern shore (Fig. 1b). Following the construction of the reservoir above the lake, diversions from the Chewaucan River for agricultural and other purposes now frequently outstrip the river's flow and have in recent years led to a significant reduction in the size of Lake Abert and dramatic increase in its average salinity (Larson et al., 2016; Moore, 2016). However, the presence of the freshwater seeps and springs has meant that the lake has thus far avoided complete desiccation and, at minimum, retained an area of 6–12 km² of water during even the driest periods (Larson et al., 2016).

2.2. Bird surveys

Surveys of waterbirds — including Podicipediformes, Anseriformes, and Charadriiformes — using Lake Abert were conducted by wildlife biologists with the BLM biweekly from March 1992–June 1993 and, after a hiatus, bimonthly from December 1993–June 1996 (Devaurs, 1995, 1996). A second set of surveys was conducted by volunteer citizen scientists with the East Cascades Audubon Society (ECAS) from 2011 to 2016 (<http://bit.ly/2s3Kwgt>). These surveys followed the BLM methodology and were conducted every 2–3 weeks during shorebird migration (April–September). In total, 256 surveys were carried out, with an average of 12 ± 8 surveys occurring per season and 9 ± 6 days elapsing between surveys within a season.

Identical methods were used for all surveys. Surveys started at ~0700 h and were completed by ~1000 h before heat shimmers appeared. All surveys were conducted from stops along U.S. Highway 395, primarily starting at the southeast corner of Lake Abert and moving north along its eastern shore over a distance of about 25 km. Birds were counted individually or estimated in groups (10s, 100s, etc.). Observers

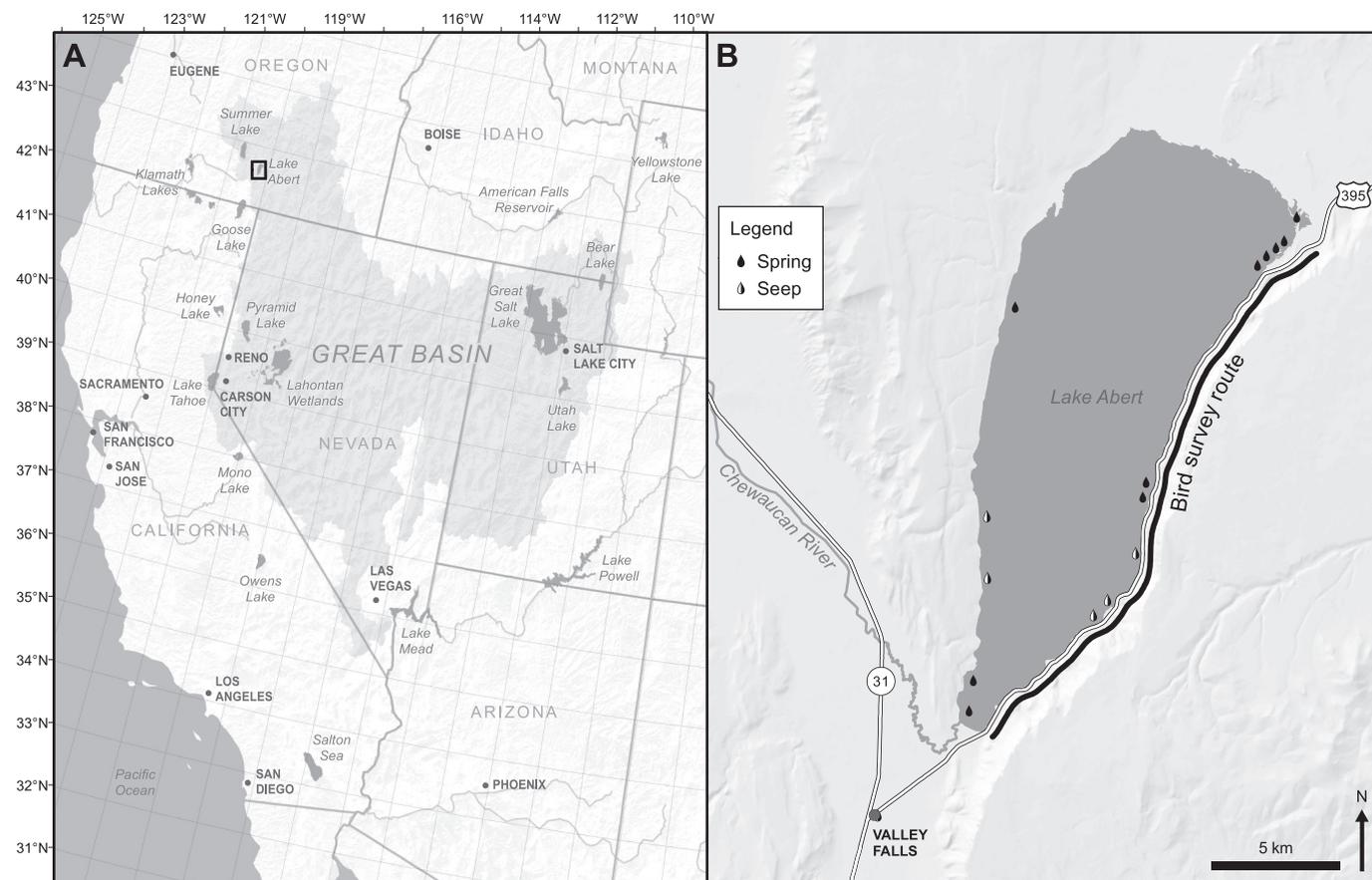


Fig. 1. Map of the study area. (A) The Great Basin of western North America with a square denoting Lake Abert. (B) Lake Abert, including Highway 395, which served as the waterbird survey route, and the freshwater springs (black droplets) and seeps (white/black droplets) that enable the lake to retain water even when upstream withdrawals from the Chewaucan River dramatically reduce the lake area.

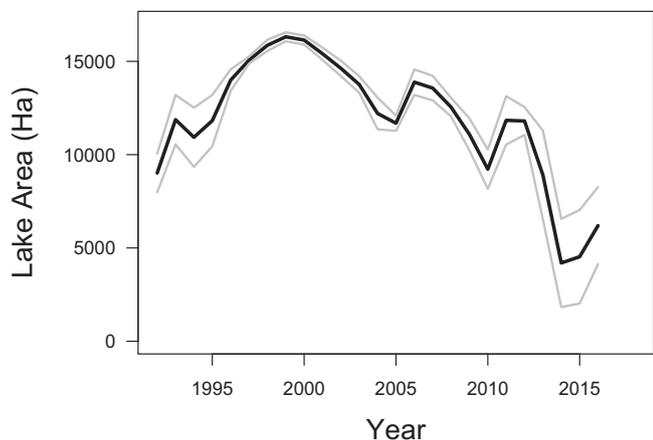


Fig. 2. Size of Lake Abert, Oregon from 1992 to 2016. Values were averaged over the course of each year from monthly measurements of lake area. The black line represents the mean and the gray lines represent one standard deviation around the mean.

did not use fixed stopping points, but rather stopped where birds were present and it was safe to do so. Because there were only ~20 safe pullouts along the route, a limited number of stopping points were available and, in some cases, observers had to estimate the number of birds between stops and add them to those recorded at the nearest stop. However, because there was visual overlap between adjacent stops, few birds were estimated from moving vehicles. Under most conditions it was possible to survey the entire lake from the east side. Nonetheless, as a cross-check, BLM conducted occasional, simultaneous surveys from

the west side of the lake and found that < 3% of the birds present on the west side were not visible from the east side (Devaurs, 1995).

Given the nature of the dataset, we were unable to account for variation in the detectability of individuals — i.e., the likelihood that an individual was present but not observed — possibly resulting from behavioural and size differences among species, weather and light conditions, and the number of birds present (Thompson, 2002). However, previous studies in open water and unvegetated mudflat habitats have reported high detection probabilities for the species included in our surveys, ranging from 0.82–0.95 (Farmer and Durbian, 2006; Pagano and Arnold, 2009). Thus, while our estimates of the number of birds using Lake Abert were potentially biased low, the relative magnitude of that bias was likely small. Furthermore, at low lake levels, when birds might be most concentrated and hard to detect, the water and invertebrates remaining in the lake were concentrated along our survey route on the east side of the lake (Herbst, 1988), facilitating accurate counts.

2.3. Invertebrate sampling

The Oregon Desert Brine Shrimp Company commercially harvested adult *Artemia franciscana* (brine shrimp; hereafter ‘*Artemia*’) on Lake Abert every year from 1986 to 2015 with the exception of 1996–1997. Harvests were initiated between 9 May–20 Jun and completed between 15 Jul–15 Sep. During these periods, the company was on the lake twice daily, first at dawn and then again at 0800, for a daily average ~4 h of total capture effort. While on the lake, the company used two 0.80 mm mesh plankton nets that were 2.4 × 0.6 × 3.8 m long with a 1.5 m cod end to assess the abundance of *Artemia*, as well as three other invertebrate species/species groups known to be important food sources

for birds on saline lakes (Boula, 1985; Bogiatto and Karnegis, 2006; Boros et al., 2006; Takekawa et al., 2009) — *Ephydra hians* (brine flies; 'Ephydra'), *Branchinecta dissimilis* (fairy shrimp; 'Branchinecta'), and *Cladocera* spp. (copepods, including *Daphnia* sp. and *Moina* sp.; 'Cladocera'). No other species of macro-invertebrate were detected with any regularity or at any appreciable abundance (K. Kreuz unpubl. data).

2.4. Statistical analyses

Our analyses had three goals: (1) document the seasonal phenology of waterbirds using Lake Abert; (2) quantify the relationship between lake area (a proxy for salinity; S.I. Fig. 2) and changes in bird abundance; and, (3) relate lake area to changes in the abundance of aquatic invertebrates, which provide the bulk of the food for waterbirds using the lake. Unfortunately, the frequency with which the data on bird abundance, aquatic invertebrate abundance, and lake area were collected differed considerably depending on the type of data and the year. The regularity of waterbird surveys varied across years (see above), while lake area was assessed monthly from 1951 to 2016, and aquatic invertebrate abundance annually from 1986 to 2015. We thus had to develop models that generated interpolated data for each, allowing comparisons among the three data types.

Because the number of birds using Lake Abert might change as a result of both the time of year (i.e., a species' phenology) and changes in salinity levels, we took a step-wise approach to linking changes in bird abundance to changes in lake area. We first fit generalized linear mixed-effect models (with year as a random effect) to avian survey data in order to generate predictive models of the seasonal usage of the lake by each species. To do this, we used data from only those years with at least bimonthly censuses throughout a migratory period and lake areas within one standard deviation of the long-term average ($\mu = 11,939 \pm 3488$ ha) in order to create a "standard" seasonal phenology for each species. For spring, this meant we used data from 1993 to 1996 ($n = 69$ surveys), while for fall we used data from 1992, 1994, 1995, and 2011 ($n = 96$ surveys). In order to capture the full range of migratory movements exhibited by our suite of species, our definitions of spring (Jan–May) and fall (Jun–Dec) differed from those in common usage. For instance, northward movements of waterfowl in the Great Basin can begin as soon as the onset of the first thaw, while southward movements can continue until freeze-up (Fleskes and Yee, 2007). In contrast, many arctic-breeding shorebirds do not migrate northward through the Great Basin until late May, but can return south again as early as late June (Warnock et al., 1998). We thus used the broadest possible characterization of each 'season' and applied it to all species.

Approximately 70 species were recorded during the surveys from 1992 to 2016, but we were unable to include all species or survey data in our analyses. To minimize identification and counting errors, we combined closely related but hard-to-identify or functionally similar species into species groups — e.g., *Calidris* sandpipers. Additionally, to maximize statistical power given the temporally sparse counts, we included only those species or species groups that were observed in both seasons of each year. This narrowed our sample size to six species or species groups (see S.I. Table 1 for the relative proportions of each species within a group): Northern Shoveler (*Anas clypeata*); Eared Grebe (*Podiceps nigricollis*); American Avocet (*Recurvirostra americana*); *Calidris* sandpipers, comprising mostly Dunlin (*C. alpina*), Western (*C. mauri*) and Least Sandpipers (*C. minutilla*); phalaropes, including both Red-necked (*Phalaropus lobatus*) and Wilson's Phalaropes (*P. tricolor*); and larids, mostly California (*Larus californicus*) and Ring-billed Gulls (*L. delawarensis*).

For these six taxa, we used our "standard" to quantify by how much counts differed from what was expected given the day of the season on which the survey was performed (i.e., a measure of each count's anomaly). To match these anomaly data, we generated daily lake area estimates using a linear interpolation of monthly lake-area data (following Moore, 2016). We then tested whether fluctuations in lake area

influenced the size of each species' count anomalies in each season, allowing us to determine whether the number of birds present deviated from expectations based on their phenology. To account for the potential non-linear relationship between lake level and a species' abundance (Bender et al., 1998), we tested this relationship using multivariate adaptive regression splines ('MARS' models; Milborrow, 2017). MARS models identify break points in the relationship between a model's dependent and independent variable(s) and then use separate linear regressions to estimate the strength of the relationship between the dependent and independent variable(s) on either side of the breakpoint. Finally, MARS models generate an overall model fit by accounting for the fit of each separate linear regression. In order to avoid over-parameterizing our models, we included only lake area as an independent variable and considered only those breakpoints that increased the explanatory power of the model by an R^2 value of ≥ 0.05 . Additionally, to control for any potential counting errors in the field, we excluded those counts with anomalies greater than two standard deviations above the expected count for a given date.

As the final step in our analysis, we tested whether the average lake area in a given year influenced the abundance of aquatic invertebrates. Following Larson et al. (2016), we calculated an annual average catch-per-unit-effort (CPUE) for *Artemia* based on the wet weight harvested per hour over the course of the year. Because the other three species were only captured as bycatch and their precise abundances not recorded, we assigned their abundance each year to one of three categories: absent, present, or abundant. These categorical variables reflect approximately 10-fold differences in abundance between the 'present' and 'abundant' categories — e.g., when *Ephydra* were 'present' approximately 1 pupa was captured per 0.5 kg of *Artemia*, but when they were 'abundant' > 10 pupae were present — and therefore likely represent biologically relevant variation in abundance across years. For the analysis of these invertebrate data, we again used MARS models, with each species' abundance as the dependent variable and average annual lake area as the independent variable.

We assessed the fit of the MARS models using their composite R^2 values; we assessed the fit of all other models using an Information Theoretic approach in which we chose among models using AIC_c scores, where the model with the lowest AIC_c score was considered the most well supported model, and models with model weights (w_i) > 0.90 were considered unequivocal (Burnham and Anderson, 2002). Predictor variables whose 95% confidence intervals did not include zero were considered biologically relevant (Grueber et al., 2011). All analyses were carried out in Program R (v. 3.32; R Development Core Team, 2016); regressions were run using the R packages "lme4" (v. 1.12; Bates et al., 2016) and "AICcmodavg" (v. 2.04; Mazerolle, 2016); and MARS models using the R package "earth" (v. 4.49; Milborrow, 2017). All results are presented \pm SD.

3. Results

3.1. Spring phenology

Ninety-eight waterbird surveys were carried out in spring, recording an average of 5075 individuals (range = 0–41,878) of the six focal taxa per survey. Among our focal taxa, Eared Grebes were the most abundant in spring, averaging 1838 individuals per count (range = 0–16,730), while *Calidris* sandpipers were the least abundant, averaging 290 individuals (range = 0–3784). Phenologies differed among taxa, with numbers of larids peaking in March, Northern Shovelers in early April, American Avocets in late April, and Eared Grebes, *Calidris*, and phalaropes all peaking in early May (Fig. 3). All taxa also exhibited a strong quadratic relationship with date, but nonetheless differed in abundance and timing even among those years included in the 'standard' dataset (S.I. Tables 2, 3).

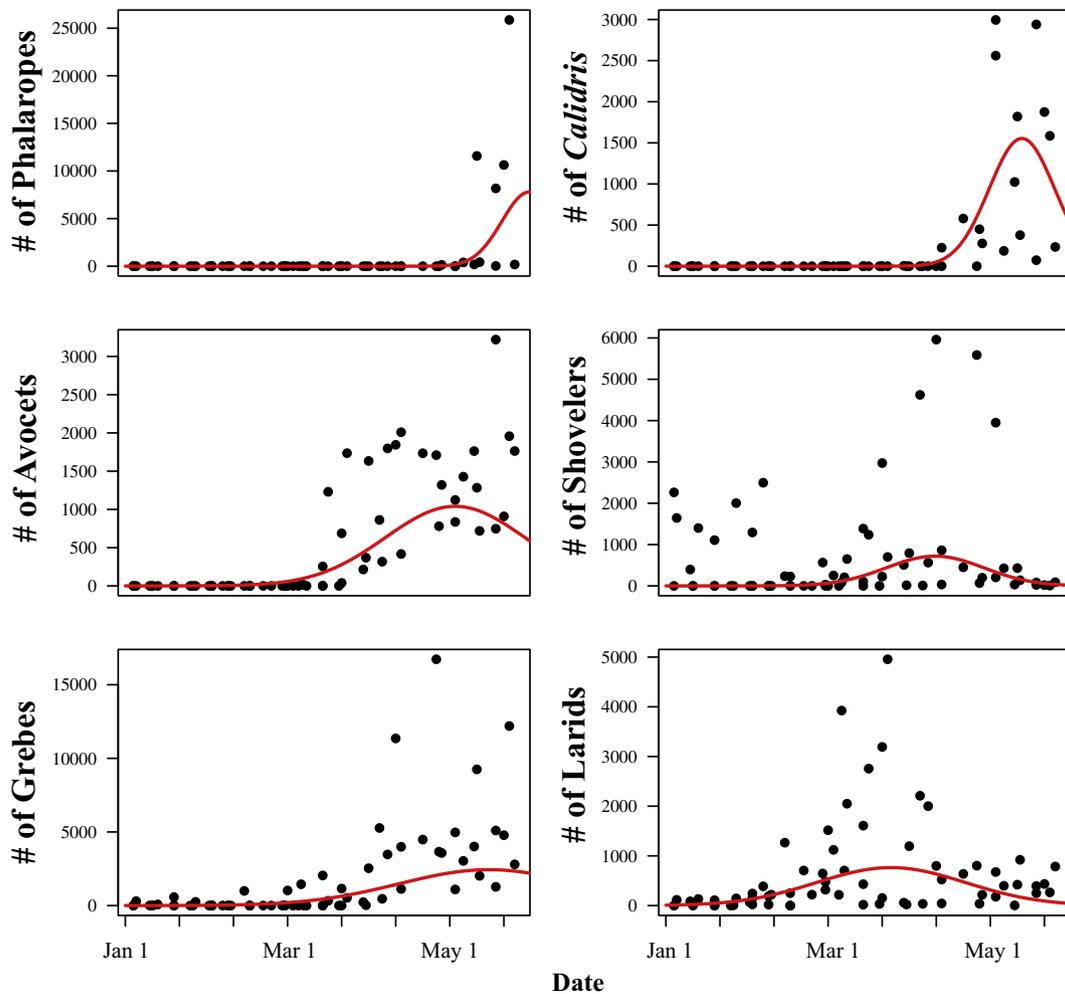


Fig. 3. Spring (Jan–May) phenology of the usage of Lake Abert, Oregon by six waterbird taxa from 1993 to 1996. Black dots correspond to the number of individuals observed on a single survey, while the red line corresponds to the predicted seasonal phenology resulting from a generalized linear mixed-effect model (date + date²) with year as a random effect. Full model results can be found in S.I. Tables 1 and 2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.2. Fall phenology

In fall, 158 surveys were carried out, with an average of 29,221 individuals (range = 0–249,645) of the focal taxa observed per survey. Phalaropes were most abundant, with 12,820 individuals (range = 0–230,000) recorded per survey, while *Calidris* sandpipers were least abundant, with an average of 989 individuals (range = 0–19,313) observed. As in spring, phenologies differed among the six taxa — *Calidris* sandpipers, phalaropes, and American Avocets all peaked in August, while larids peaked in September, Eared Grebes in October, and Northern Shovelers in November (Fig. 4). Additionally, as in spring, all taxa exhibited quadratic relationships with date, but also differences in abundance and timing among years (S.I. Tables 4, 5).

3.3. Lake area and waterbird abundance

From 1995 to 2016, estimated lake area averaged $11,939 \pm 3488$ ha (Fig. 2), but declined at a rate of 250 ± 30 ha per year over the course of that period (S.I. Tables 6, 7). On average, models relating lake area to waterbird abundance had an $R^2 = 0.21 \pm 0.14$ ($n = 12$; Table 1; S.I. Tables 8, 9). Season was not a significant predictor of the strength of the relationship between lake levels and waterbird abundance (S.I. Tables 9, 10), but taxon was, with lake area explaining the abundance of larids ($R^2 = 0.39 \pm 0.01$) better than those of other taxa (S.I. Tables 10, 11). In general, few, if any, birds were present at low lake levels (Fig. 5): when the lake area

was < 8100 ha (e.g., salinities > 15‰; $n = 28$ occasions), counts across the six taxa were, on average, $68 \pm 21\%$ below those expected given the date. However, as lake area increased, three types of relationships between lake area and bird abundance were evident: (1) abundance increased with lake area up to a point above which there was no relationship between lake area and abundance (e.g., phalaropes; $n = 2$ taxa); (2) abundance increased with lake area, even at high lake levels (e.g., Northern Shovelers; $n = 2$ taxa); and, (3) abundance increased with lake area up to a point above which abundance declined as lake area increased (e.g., larids; $n = 2$ taxa). On average, the MARS models identified 1.1 ± 0.5 break points per taxa, with those break points occurring at lake levels of $11,313 \pm 2407$ ha (Table 1). Accordingly, when the lake area was > 15,000 ha (e.g., salinities $\sim 2.5\%$; $n = 18$ occasions), counts of those taxa exhibiting negative slopes above their breakpoint were 9–64% ($n = 2$ taxa) lower than expected given the date, while for those taxa exhibiting positive slopes, counts were 18–1589% ($n = 2$ taxa) higher than expected.

3.4. Lake area and invertebrate abundance

Branchinecta and *Cladocera* were both generally rare and were absent in 27 and 21 years respectively ($n = 29$ years), while *Ephydra* was present in all but three years. *Artemia* were present in all but one year and their CPUE averaged 71.5 ± 31.2 kg/h ($n = 29$ years). Lake area explained a significant proportion of the variation in the abundance of *Ephydra*, *Artemia*, and *Cladocera*, but not *Branchinecta*, as there was too

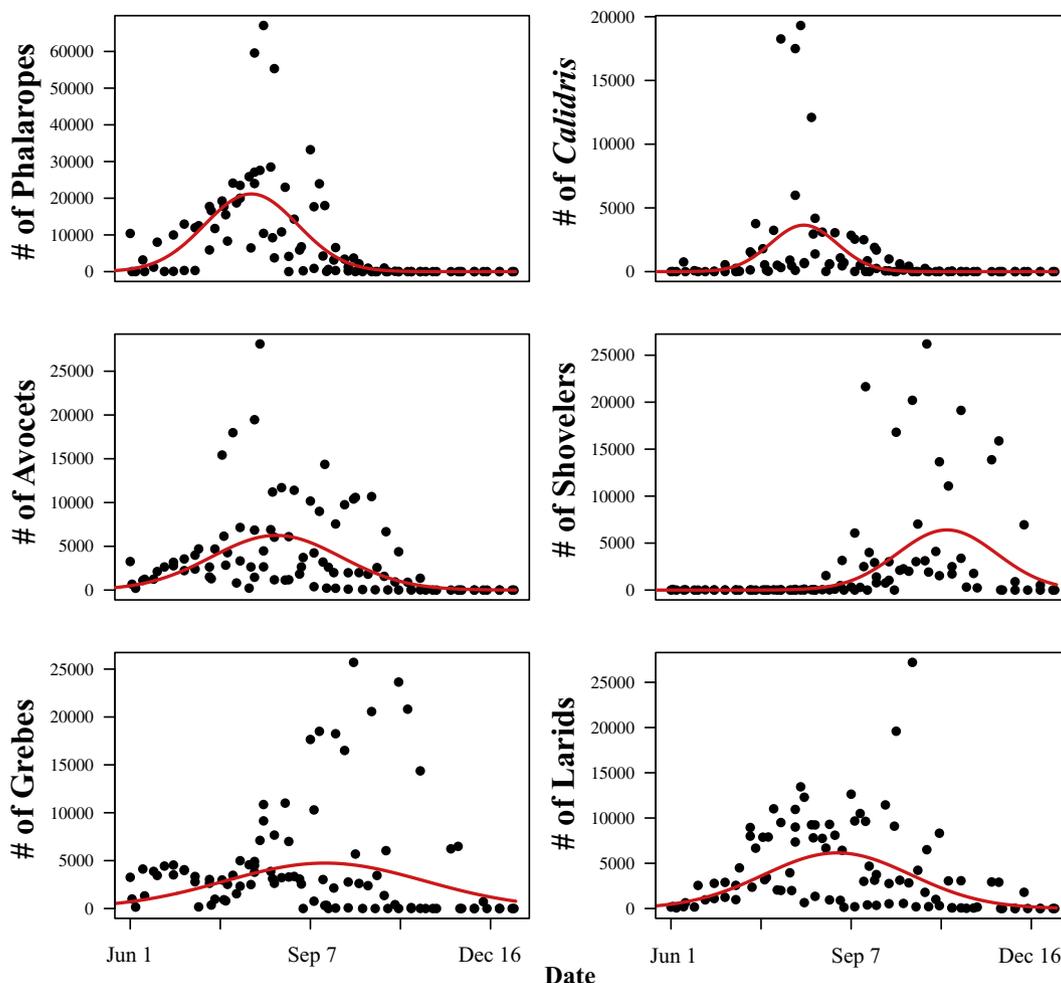


Fig. 4. Fall (Jun–Dec) phenology of the usage of Lake Abert, Oregon by six waterbird taxa in 1992, 1994, 1995, and 2011. Black dots correspond to the number of individuals observed on a single survey, while the red line corresponds to the predicted seasonal phenology resulting from a generalized linear mixed-effect model (date + date²) with year as a random effect. Full model results can be found in S.I. Tables 3 and 4. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Results of multiple adaptive regression splines (MARS) analyses. Break point values correspond to lake area (ha). The abundance of aquatic invertebrates was only categorized on an annual basis.

Species	Break point #1	Break point #2	Composite R ²
Spring			
Northern Shoveler	11,682	–	0.37
Eared Grebe	15,265	–	0.10
American Avocet	–	–	0.00
<i>Calidris</i>	10,119	–	0.06
Phalaropes	14,019	–	0.14
Larids	11,214	13,895	0.38
Fall			
Northern Shoveler	8147	–	0.29
Eared Grebe	7320	–	0.28
American Avocet	8767	11,639	0.28
<i>Calidris</i>	9889	–	0.07
Phalaropes	12,002	–	0.11
Larids	13,123	–	0.40
Aquatic invertebrates			
<i>Artemia</i>	11,803	–	0.25
<i>Ephydra</i>	13,565	–	0.51
<i>Anostraca</i>	–	–	0.00
<i>Cladocera</i>	13,565	–	0.91

little variation in *Branchinecta* abundance across the study period with which to fit a model (S.I. Table 12). For *Ephydra*, *Artemia*, and *Cladocera*, their composite R² values averaged 0.56 ± 0.33 (Table 1). All three taxa had only one break point, which occurred on average at 12,978 ± 1017 ha. The relationships between lake area and the abundance of these three taxa generally matched those of the six avian taxa: *Ephydra* and *Artemia* both increased with increasing lake area until a point above which their abundance either leveled off or declined, while *Cladocera* had low, but stable abundance at low and moderate lake areas, but increasing abundance at high lake areas (Fig. 6).

4. Discussion

Over the course of 25 years, waterbird and invertebrate abundance at Lake Abert fluctuated with lake area and salinity levels (Moore, 2016; S.I. Fig. 1). At low lake levels and high salinities, invertebrate and waterbird numbers were generally low, with counts across taxa reduced by an average of 68% below those expected. As lake levels increased and salinities decreased, both invertebrates and waterbirds became more abundant. However, at high lake levels and low salinities, the numbers of most invertebrates and waterbirds either plateaued or declined, with some species experiencing reductions of up to 64% below expected levels. Our study thus provides some of the only long-term data on ecosystem dynamics in a natural saline lake and suggests that the management and conservation of saline lakes should focus on maintaining conditions within the normal spectrum of seasonal and

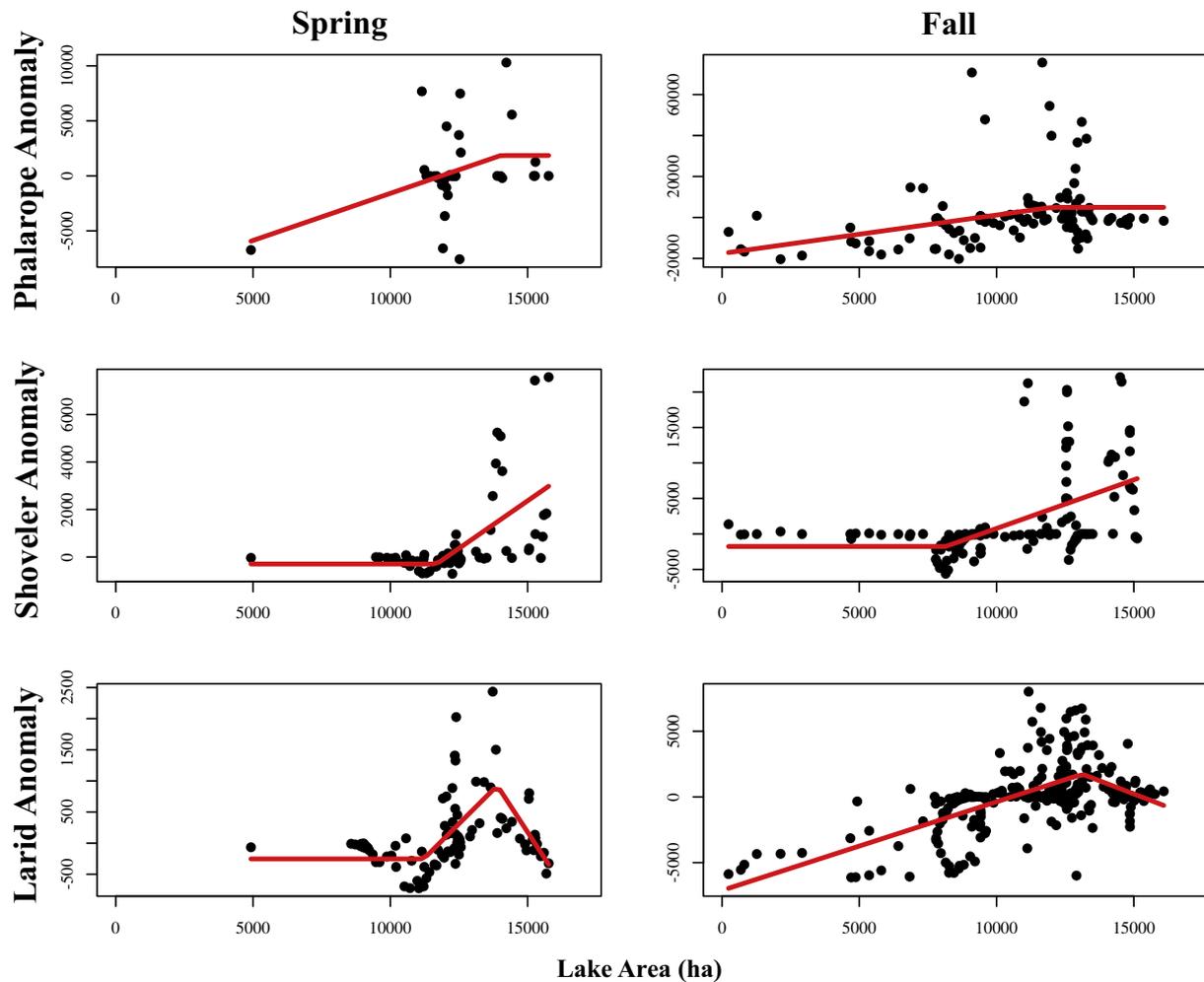


Fig. 5. Relationship between lake area and the count anomalies from Lake Abert, Oregon of three waterbird taxa during spring and fall migration from 1992 to 2016. Black dots represent the difference between the number of individuals recorded during a survey and the expected number of individuals of that taxon given the date of the survey; the red line the results of a multiple adaptive regression splines (MARS) analysis. Break point and R^2 values for the models can be found in Table 1 and complete model results in S.I. Tables 7 and 8. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

inter-annual variation in lake area and salinity, such that periods with extremely high or low salinity levels do not occur too frequently or become too prolonged (Keister Jr., 1992).

Our results also indicate that the effects of fluctuations in lake area and salinity were most pronounced for those waterbirds that feed on *Ephydra*, such as phalaropes, avocets, and larids (Boula, 1985; Jehl Jr., 1994). For these taxa, surveys at the lowest water levels (e.g., < 8100 ha) recorded counts 5000–20,000 individuals below those expected, representing declines of up to 83% in the number of birds present in comparison with counts at normal lake levels. Similarly, surveys at high lake levels (e.g., > 15,000 ha) recorded declines of up to 64% below expected counts. These strong declines likely resulted from the combined effects of decreases in *Ephydra* abundance and, at high salinity levels, increased physiological costs for the birds themselves. For instance, *Ephydra* are only able to tolerate salinities between 2.5 and 15‰ (Brown, 2010). When lake levels dropped below 8100 ha — as they did about half of the time between 2011 and 2016 — salinities were generally above this level and reached as high as 28‰ during some periods, while at high lake levels salinities frequently dropped below 2.5‰ (Moore, 2016). Additionally, many birds begin to experience physiological costs at such high salinities. For example, Dunlin acclimated to seawater (e.g., 3.5‰ salinity) exhibit a ~20% increase in daily energy expenditure above the levels they maintain when acclimated to freshwater (Gutiérrez et al., 2011). Thus, the combined influence of decreases in prey abundance and increases in daily energy requirements

were likely enough to reduce the numbers of most species at extreme lake levels and salinities.

Declines in salinity levels, however, were not detrimental to all invertebrate and waterbird taxa. In particular, counts of Northern Shovelers, which are known to rely on *Cladocera* (Takekawa et al., 2009), increased by nearly 1600% at the highest lake levels. Nonetheless, consistently low salinity levels could result in a regime shift within the lake ecosystem as strong as that occurring at high salinity levels, altering long-term dynamics for both waterbirds and invertebrates (Larson et al., 2016).

Despite the consistency of our results across waterbirds and invertebrates, we note three potential caveats: (1) few surveys were performed at truly low lake levels (e.g., when lake area was < 5000 ha); (2) the different time scales on which invertebrate and waterbird data were collected precluded directly testing the relationship between the abundance of these two groups; and, (3) the general strength of the relationships between waterbird abundance and lake area were lower than might be expected given the strength of the physiological responses to changes in salinities noted in previous studies (Gutiérrez, 2014). Nonetheless, we are confident that our data and analyses have accurately characterized the relationship between lake area and salinity, and between invertebrate and waterbird abundance. For example, Larson et al. (2016) reported similar declines of up to 86% in peak migration counts during the fall of 2014 when lake levels were at their lowest. Furthermore, the strength of the relationships between lake

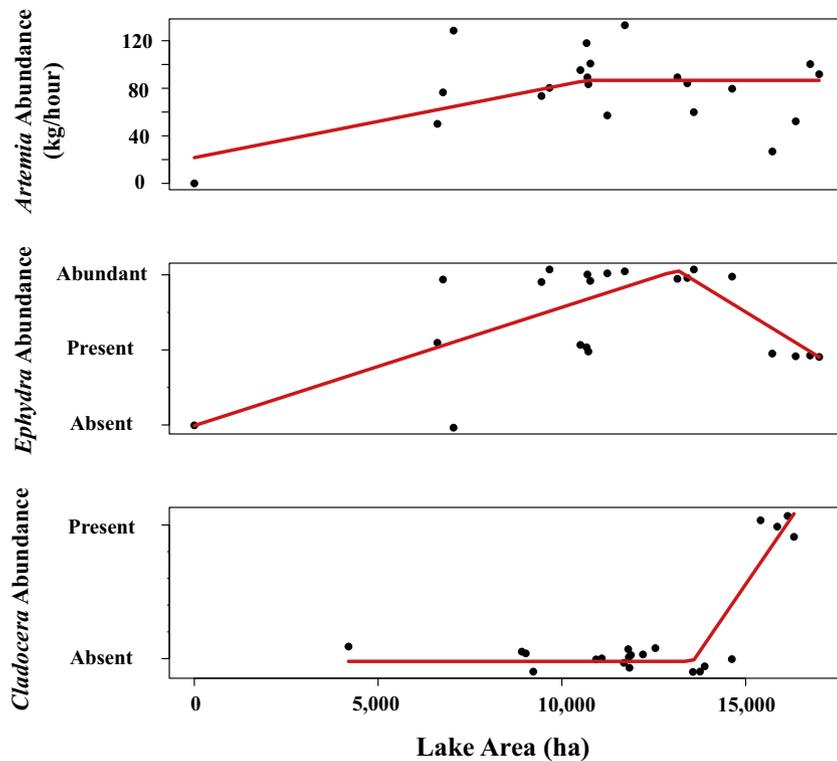


Fig. 6. Relationship between lake area and the abundance of three aquatic invertebrate species at Lake Abert, Oregon. The black dots represent the annual categorical abundance (*Ephedra* and *Cladocera*) and harvest rate (*Artemia*) of the aquatic invertebrate species; the red line represents the results of a multiple adaptive regression splines (MARS) analysis. Break point and R^2 values for the models can be found in Table 1 and complete model results in S.I. Table 11. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

area and invertebrate abundance (e.g., $R^2 > 0.50$) give us confidence that we captured the general pattern exhibited by these taxa in relation to lake level and salinity despite the relatively long time scale over which they were measured. And, finally, although the strength of the relationships between waterbird abundance and lake area were relatively low, we were attempting to identify changes in the abundance of these taxa at one site within annual cycles that involve the use of multiple sites spread across vast regions (e.g., Jehl Jr., 1988). Indeed, circumstances completely unrelated to those occurring at Lake Abert — such as variation in conditions on the breeding grounds or weather patterns during migration (Rushing et al., 2016) — undoubtedly also influence the number of birds using the lake. The fact that we observed a pattern of decreased waterbird abundance at both low and high salinities across taxa thus leads us to conclude that our data were robust and that we accurately documented the effects of changes in lake salinity.

Given our finding that low lake levels result in many fewer waterbirds using Lake Abert and the fact that the lowest lake levels recorded at Lake Abert over the past 25 years have occurred since 2011, the question then becomes: How important are the reductions in the abundance of waterbirds at Lake Abert for the larger regional and global population dynamics of these species? The answer is currently unclear and requires further work. It is possible that during years with low lake levels, individuals may spread out across the Great Basin and make use of one (or more) of the other 45 saline lakes and wetlands dotting the landscape (Jehl Jr., 1988; Plissner et al., 1999; Warnock et al., 1998). However, the declining water levels and increasing salinities recorded at Lake Abert in recent decades correspond strongly with similar conditions occurring at saline lakes elsewhere in the region, stressing the entire network of waterbird habitats. For instance, Walker Lake in Nevada once extended over 250 km², but has experienced a 75% reduction in volume and concomitant increase in salinity (Beutel et al., 2001). Similarly, the Lahontan Wetlands (Stillwater NWR) in Nevada have been seriously desiccated by upstream water overuse and contaminated by agricultural runoff (Lemly et al., 2000; Williams, 2001). Even the Great Salt Lake in Utah, which

accommodates the largest number of priority waterbird species in the region (Frank, 2016), reached its lowest water level in recorded history in November 2016, largely as a result of increasing anthropogenic water usage (Wurtsbaugh et al., 2017). Alternative sites and habitats are thus becoming scarcer for the waterbird populations that rely on Lake Abert.

The predicament of the Yellow Sea coastline in Asia may therefore provide an instructive example of the potential consequences of further loss or degradation of saline lakes in the Great Basin. In the Yellow Sea, the ongoing destruction of intertidal habitats has rapidly reduced survival rates in shorebirds using the region as a staging site during northward migration (Conklin et al., 2016; Piersma et al., 2016), resulting in dramatic population declines that are threatening some species with extinction (Studds et al., 2017). Although Lake Abert alone does not approach the level of importance of the Yellow Sea, in combination, the saline lakes of the Great Basin host significant numbers of at least 15 waterbird species during migration and the breeding season (Warnock et al., 1998; Olson et al., 2014). What is more, a number of these species — such as American Avocet, Wilson's Phalarope, and California Gull — rely almost exclusively on Great Basin saline lakes for significant portions of their annual cycle (Oring and Reed, 1997). Given the narrow range of conditions within which saline lakes are favorable for waterbirds and the potential for even small changes in salinity to initiate reversible state effects that can affect survival and reproduction (Masero et al., 2017), the likelihood that further changes in Great Basin saline lakes will significantly affect waterbird population dynamics is high. It is thus likely not a coincidence that recent assessments of shorebird population trends suggest that the populations of at least three saline lake specialists are in decline (Andres et al., 2012).

In this context, the proper management of Lake Abert and the other saline lakes in the Great Basin is critical to the conservation of North American waterbird populations. In designating Lake Abert an Area of Critical Environmental Concern, the BLM (1996) established a goal of maintaining “a viable, sustainable ecosystem within the lake and surrounding area” and set specific objectives for water quality and quantity (i.e., lake elevation). However, since there is no water right

associated with Lake Abert or the aquatic organisms and birds that use it (Moore, 2016), and the BLM does not control water usage in the area, fulfilling these goals requires regulation of or cooperation with the holders of upstream water rights. This will require coordination among private, state, and federal interests and agencies. We therefore urge the creation of a watershed-scale management plan that recognizes the ecological importance of Lake Abert and seeks to maintain the small range of conditions under which it can support healthy invertebrate and waterbird populations. These efforts need not strive to maintain constant salinity levels, as some degree of variation is both common and likely beneficial (Keister Jr., 1992). Instead, the plan should aim to ensure that fluctuations in salinity and water levels remain within the historical frequency and range of variation.

More broadly, we recommend that a comprehensive conservation strategy be developed for Great Basin saline lakes, as well as other aggregations of saline lakes globally, that recognize the interconnected nature of these ecosystems. Recent efforts at developing such strategies for shorebirds along the Atlantic and Pacific flyways of the Americas (Winn et al., 2013; Senner et al., 2016) provide a potential model. These strategies provide a useful framework for pursuing change locally (e.g., integrated water management in a watershed) and at larger scales (e.g., recognition of saline lakes as a priority habitat type by regional and national governments) in an effort to achieve change simultaneously along multiple fronts. Ultimately, the active management and conservation of saline lakes is possible and previous efforts have shown success when approached properly (Jellison et al., 2004) — the key is starting before it is too late.

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Author contribution statement

NRS, JNM, and SES conceived of the study; STS, SD, and KK collected the data; NRS and JNM analyzed the data; NRS, in collaboration with JNM and SES, wrote the manuscript; all authors commented on the manuscript.

Ethics statement

There was no contact with vertebrates during this study.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2018.02.003>.

References

- Anderson, T.W., Tiffany, M.A., Hurlbert, S.H., 2007. Stratification, sulfide, worms, and decline of the Eared Grebe (*Podiceps nigricollis*) at the Salton Sea, California. *Lake and Reservoir Management* 23, 500–517.
- Andres, B.A., Smith, P.A., Morrison, R.I.G., Gratto-Trevor, C.L., Brown, S.C., Friis, C.I., 2012. Population estimates of North American shorebirds, 2012. *Wader Study Group Bulletin* 119, 178–194.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Bojesen, R.H., Singmann, H., Dai, B., 2016. Linear Mixed-effect Models using Eigen and S4. Available: <http://www.r-project.org>.
- Bedford, D., 2009. The Great Salt Lake, America's Aral Sea? *Science and Policy for Sustainable Development* 51, 8–21.
- Bender, D.J., Contreras, T.A., Fahrig, L., 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* 79, 517–533.
- Beutel, M.W., Horne, A.J., Roth, J.C., Barratt, N.J., 2001. Limnological effects of anthropogenic desiccation of a large, saline lake, Walker Lake, Nevada. *Hydrobiologia* 466, 91–105.
- Boggiatto, R.J., Karnegies, J.D., 2006. The use of eastern Sacramento Valley vernal pools by ducks (Calif. Fish Game). 92, 125–141.
- Boros, E., Bánfi, S., Forró, L., 2006. Anostracans and microcrustaceans as potential food sources of waterbirds on sodic pans of the Hungarian plain. *Hydrobiologia* 567, 341–349.
- Boula, K.M., 1985. Foraging Ecology of Migrant Waterbirds, Lake Abert, Oregon. Oregon State University, MSc Thesis Available: <http://ir.library.oregonstate.edu/xmlui/handle/1957/13454>.
- Brown, P., 2010. Salinity tolerance of *Artemia* and *Ephydra*: uncertainty and discrepancies. In: Great Salt Lake Ecosystem Program.
- Bureau of Land Management, 1996. High Desert Management Framework Proposed Plan Amendment and Final Environmental Impact Statement for the Lake Abert Area of Critical Environmental Concern (ACEC) in Lake County, Oregon. Bureau of Land Management, Lakeview District Office, Lakeview, Oregon.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Springer, New York, USA.
- Caskey, L.L., Riedel, R.R., Costa-Pierce, B., Butler, J., Hurlbert, S.H., 2007. Population dynamics, distribution, and growth rate of tilapia (*Oreochromis mossambicus*) in the Salton Sea, California, with notes on bairdiella (*Bairdiella icistia*) and orangemouth corvina (*Cynoscion xanthurus*). *Hydrobiologia* 576, 185–203.
- Conklin, J.R., Lok, T., Melville, D.S., Riegen, A.C., Schuckard, R., Piersma, T., Battley, P.F., 2016. Declining adult survival of New Zealand Bar-tailed Godwits during 2005–2012 despite apparent population stability. *Emu* 116, 147–157.
- Devaurs, W.R., 1995. Lake Abert: 1992–1994 Waterfowl and Water Bird Counts, Progress Report and Preliminary Data Analysis. Bureau of Land Management, Lakeview District, Lakeview, Oregon.
- Devaurs, W.R., 1996. Lake Abert ACEC: Waterfowl and Waterbird Population Monitoring, 5 Year Report (1992–1996). Bureau of Land Management, Lakeview District, Lakeview, Oregon.
- Farmer, A., Durbian, F., 2006. Estimating shorebird numbers at migration stopover sites. *Condor* 108, 792–807.
- Fleskes, J.P., Yee, J.L., 2007. Waterfowl distribution and abundance during spring migration in southern Oregon and northeastern California. *Western North American Naturalist* 67, 409–428.
- Frank, M.G., 2016. Migratory Waterbird Ecology at a Critical Staging Area, Great Salt Lake, Utah. PhD Thesis Utah State University Available: <http://digitalcommons.usu.edu/etd/4940/>.
- Frank, M.G., Conover, M.R., 2017. Weather and prey availability affect the timing of fall migration of Eared Grebes (*Podiceps nigricollis*) from Great Salt Lake. *Wilson Journal of Ornithology* 129, 98–111.
- Grayson, D.K., 1993. The Desert's Past: A Natural Prehistory of the Great Basin. Smithsonian Institution Press, Washington D.C., USA.
- Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* 24, 699–711.
- Gutiérrez, J.S., 2014. Living in environments with contrasting salinities: a review of physiological and behavioural responses in waterbirds. *Aredola* 61, 233–256.
- Gutiérrez, J.S., Masero, J.A., Abad-Gómez, J.M., Villegas, A., Sánchez-Guzmán, J.M., 2011. Understanding the energetic costs of living in saline environments: effects of salinity on basal metabolic rate, body mass and daily energy consumption of a long-distance migratory shorebird. *J. Exp. Biol.* 214, 829–835.
- Gutiérrez, J.S., Abad-Gómez, J.M., Sánchez-Guzmán, J.M., Navedo, J.G., Masero, J.A., 2012. Avian BMR in marine and non-marine habitats: a test using shorebirds. *PLoS One* 7, e42206.
- Gutiérrez, J.S., Abad-Gómez, J.M., Villegas, A., Sánchez-Guzmán, J.M., Masero, J.A., 2013. Effects of salinity on the immune response of an 'osmotic generalist' bird. *Oecologia* 171, 61–69.
- Herbst, D.B., 1988. Comparative population ecology of *Ephydra hians* Say (Diptera: Ephydriidae) at Mono Lake (California) and Abert Lake (Oregon). *Hydrobiologia* 158, 145–166.
- Herbst, D.B., 2001. Gradients of salinity stress, environmental stability and water chemistry as a template for defining habitat types and physiological strategies in inland salt waters. *Hydrobiologia* 466, 209–219.
- Herbst, D.B., 2006. Salinity controls on trophic interactions among invertebrates and algae of solar evaporation ponds in the Mojave Desert and relation to shorebird foraging and selenium risk. *Wetlands* 26, 475–485.
- Jehl Jr., J.R., 1994. Changes in saline and alkaline lake avifaunas in western North America in the past 150 years. *Stud. Avian Biol.* 15, 258–272.
- Jehl Jr., J.R., 1988. Biology of the eared grebe and Wilson's phalarope in the nonbreeding season: a study of adaptations to saline lakes. *Stud. Avian Biol.* 12.
- Jehl Jr., J.R., McKernan, R., 2002. Biology and migration of eared grebes at the Salton Sea. *Hydrobiologia* 473, 245–253.
- Jellison, R., Zadereev, Y.S., DasSarma, P.A., Melack, J.M., Rosen, M.R., Degermendzhy, A.G., DasSarma, S., Zambrana, G., 2004. Conservation and management challenges of saline lakes: a review of five experience briefs. In: Lake Basin Management Initiative.
- Jellison, R., Williams, W.D., Timms, B., Alcocer, J., Aladin, N.V., 2008. Salt lakes: values, threats and future. In: Polunin, N. (Ed.), *Aquatic Ecosystems*. Cambridge University Press, Cambridge, United Kingdom, pp. 94–110.
- Jeppesen, E., Brucet, S., Naselli-Flores, L., Papastefaniadou, E., Stefanidis, K., Nöges, T., Nöges, P., Attayde, J.L., Zohary, T., Coppens, J., Bucak, T., Menezes, R.F., Freitas,

- F.R.S., Kernan, M., Søndergaard, M., Bekkioglu, M., 2015. Ecological impacts of global warming and water abstraction on lakes and reservoirs due to changes in water level and related changes in salinity. *Hydrobiologia* 750, 201–227.
- Kingsford, R.T., Porter, J.L., 1994. Waterbirds on an adjacent freshwater lake and salt lake in arid Australia. *Biol. Conserv.* 69, 219–228.
- Keister Jr., G.P., 1992. *The Ecology of Lake Abert: Analysis of Further Development*. Oregon Department of Fish and Wildlife, Salem, Oregon, USA.
- Larson, R., Eilers, J., 2014. Lake Abert, OR : a terminal lake under extreme water stress. *LakeLine* 34, 30–33.
- Larson, R., Eilers, J., Kreuz, K., Pecher, W.T., DasSarma, S., Dougill, S., 2016. Recent desiccation-related ecosystem changes at Lake Abert, Oregon: a terminal alkaline salt lake. *Western North American Naturalist* 76, 389–404.
- Lemly, A.D., Kingsford, R.T., Thompson, J.R., 2000. Irrigated agriculture and wildlife conservation: conflict on a global scale. *Environ. Manag.* 25, 485–512.
- Lyons, M.N., Halse, S.A., Gibson, N., Cale, D.J., Lane, J.A.K., Walker, C.D., Mickle, D.A., Froend, R.H., 2007. Monitoring wetlands in a salinizing landscape: case studies from the Wheatbelt region of Western Australia. *Hydrobiologia* 591, 147–164.
- Masero, J.A., Abad-Gómez, J.M., Gutiérrez, J.S., Santiago-Quesada, F., Senner, N.R., Sánchez-Guzmán, J.M., Piersma, T., Schroeder, J., Amat, J.A., Villegas, A., 2017. Wetland salinity induces sex-dependent carry-over effects on the individual performance of a long-distance migrant. *Sci. Rep.* 7, 6867.
- Mazerolle, M.J., 2016. *Model Selection and Multimodel Inference Based on QAICc*. Available: <http://www.r-project.org>.
- Milborrow, S., 2017. *Multivariate Adaptive Regression Splines*. Available: <http://www.r-project.org>.
- Moore, J.N., 2016. Recent desiccation of Western Great Basin Saline Lakes: lessons from Lake Abert, Oregon, U.S.A. *Sci. Total Environ.* 554–555, 142–154.
- Olson, B.E., Sullivan, K.A., Farmer, A.H., 2014. Marbled Godwit migration characterized by satellite telemetry. *Condor* 116, 185–194.
- Oring, L.W., Reed, J.M., 1997. Shorebirds of the western Great Basin of North America: overview and importance to continental populations. *International Wader Studies* 9, 6–12.
- Pagano, A.M., Arnold, T.W., 2009. Detection probabilities for ground-based breeding waterfowl surveys. *J. Wildl. Manag.* 73, 392–398.
- Phillips, K.N., Van Denburgh, A.S., 1971. Hydrology and geochemistry of Abert, Summer, and Goose Lakes, and other closed-basin lakes in south-central Oregon. In: *Closed-Basin Investigations*, U.S. Geological Survey Professional Paper 502-B.
- Piersma, T., Lok, T., Chen, Y., Hassell, C.J., Yang, H.-Y., Boyle, A., Slaymaker, M., Chan, Y.-C., Melville, D.S., Zhang, Z.-W., Ma, Z., 2016. Simultaneous declines in summer survival of three shorebird species signals a flyway at risk. *J. Appl. Ecol.* 53, 479–490.
- Plissner, J.H., Haig, S.M., Oring, L.W., 1999. Within- and between-year dispersal of American Avocets among multiple western Great Basin wetlands. *Wilson Bull.* 111, 314–320.
- R Development Core Team, 2016. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria Available: <http://www.r-project.org>.
- Rubega, M.A., Robinson, J.A., 1996. Water salinization and shorebirds: emerging issues. *International Wader Studies* 9, 45–54.
- Rushing, C.S., Ryder, T.B., Marra, P.P., 2016. Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle. *Proc. R. Soc. B* 283, 20152846.
- Senner, N.R., Conklin, J.R., Piersma, T., 2015. An ontogenetic perspective on individual differences. *Proc. R. Soc. B* 282, 20151050.
- Senner, S.E., Andres, B.A., Gates, H.R. (Eds.), 2016. *Pacific Americas Shorebird Conservation Strategy*. National Audubon Society, New York, New York, USA Available at: <http://www.shorebirdplan.org>.
- Shuford, W.D., Warnock, N., Molina, K.C., 1999. The avifauna of the Salton Sea: a synthesis. In: *Report to the Salton Sea Science Subcommittee and Salton Sea Authority*, Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, CA 94970.
- Shuford, W.D., Warnock, N., Molina, K.C., Sturm, K.K., 2002. The Salton Sea as critical habitat to migratory and resident waterbirds. *Hydrobiologia* 473, 255–274.
- Stralberg, D., Cameron, D.R., Reynolds, M.D., Hickey, C.M., Klausmeyer, K., Busby, S.M., Stenzel, L.E., Shuford, W.D., Page, G.W., 2011. Identifying habitat conservation priorities and gaps for migratory shorebirds and waterfowl in California. *Biodivers. Conserv.* 20, 19–40.
- Studds, C.E., Kendall, B.E., Murray, N.J., Wilson, H.B., Rogers, D.I., Clemens, R.S., Gosbell, K., Hassell, C.J., Jessop, R., Melville, D.S., Milton, D.A., Minton, C.D.T., Possingham, H.P., Riegen, A.C., Straw, P., Woehler, E.J., Fuller, R.A., 2017. Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. *Nat. Commun.* 8, 14895.
- Takekawa, J.Y., Miles, A.K., Tsao-Melcer, D.C., Schoellhamer, D.H., Fregien, S., Athearn, N.D., 2009. Dietary flexibility in three representative waterbirds across salinity and depth gradients in salt ponds of San Francisco Bay. *Hydrobiologia* 626, 155–168.
- Thompson, W.L., 2002. Towards reliable bird surveys: accounting for individuals present but not detected. *Auk* 119, 18–25.
- Warnock, N., Haig, S.M., Oring, L.W., 1998. Monitoring species richness and abundance of shorebirds in the western Great Basin. *Condor* 100, 589–600.
- Warnock, N., Page, G.W., Ruhlen, T.D., Nur, N., Takekawa, J.Y., Hanson, J.T., 2002. Management and conservation of San Francisco Bay salt ponds: effects of pond salinity, area, tide, and season on Pacific Flyway waterbirds. *Waterbirds* 25, 79–92.
- Williams, W.D., 1996. What Future for Saline Lakes? *Environment: Science and Policy for Sustainable Development*. 38. pp. 12–39.
- Williams, W.D., 2001. Anthropogenic salinisation of inland waters. *Hydrobiologia* 466, 329–337.
- Winn, B., Brown, S., Spiegel, C., Reynolds, D., Johnston, S., 2013. *Atlantic Flyway Shorebird Business Strategy: A Call to Action*. Manomet Center for Conservation Science, Manomet, Massachusetts, USA Available at: <http://www.acjv.org>.
- Wrege, P.H., Shuford, W.D., Winkler, D.W., 2006. Annual variation in numbers of breeding California Gulls at Mono Lake, California: the importance of natal philopatry and local and regional conditions. *Condor* 108, 82–96.
- Wurtsbaugh, W.A., 2014. *Management of the Great Salt Lake Ecosystem: Water, Economic Values and Competing Interests*. Watershed Science Faculty Publication #594 Utah State University, Logan, Utah, USA Available: http://digitalcommons.usu.edu/wats_facpub/594.
- Wurtsbaugh, W.A., Miller, C., Null, S.E., DeRose, R.J., Wilcock, P., Hahnenberger, M., Howe, F., Moore, J., 2017. Decline of the world's saline lakes. *Nat. Geosci.* 10, 816–823.