FALL MIGRATION OF THE NORTHERN SHOVELER AT HYPERSALINE MONO LAKE, CALIFORNIA

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ABSTRACT: From 2002 to 2022, waterfowl were surveyed at Mono Lake to evaluate the their response to lake-level changes under the State Water Resources Control Board's landmark Decision 1631, in which the public trust doctrine was first applied to water rights. From September through mid-November, the total numbers of Mono Lake's most numerous dabbling duck, the Northern Shoveler (*Spatula clypeata*), averaged 13,018 ± 1571 (standard error), ranging from a high of 27,400 in 2008 to a low of 2719 in 2018. Annual peak counts averaged 5562 ± 709, ranging from a low of 768 in 2018 to the highest single-day count of 13,793 in 2012. Annual totals were higher under conditions of monomixis than under the stratified condition of meromixis. In a generalized linear model, the combined effects of survey period, biomass of Mono Lake brine shrimp (*Artemia monica*), and regional drought explained 67.8% of the variation in Northern Shoveler numbers at Mono Lake, i.e., higher *Artemia* biomass and more severe drought in northeast California resulted in higher shoveler counts. Lake level, a key component of waterfowl-habitat restoration, showed no effect within the range of lake levels observed. These results suggest that food resources and regional drought have been the most important factors influencing Northern Shoveler use of Mono Lake, so far overriding any small-scale influences of habitat variation due to lake-level changes.

Mono Lake is a high-elevation hypersaline lake located on the east slope of the Sierra Nevada in the hydrologically closed Mono Basin, in Mono County, California (Figure 1). The Mono Basin experiences wide seasonal and annual variations in temperature and precipitation (Ficklin et al. 2012). Mono Lake lies within a larger geographic region, the Intermountain West, the vast arid region between the eastern slopes of the Sierra Nevada and Cascade Range and the western slope of the Rocky Mountains. The lake is large and deep, with a surface area of 180 km^2 at (1945.1 m elevation) and an average depth of over 18 m (Scholl et al. 1967, Melack 1983, Vorster 1985). Since 1996, the salinity of Mono Lake has averaged 83 g/L, or over twice that of seawater.

Mono Lake is highly productive and widely known for its value to waterbirds, a value due to the seasonal abundance of aquatic invertebrates, mainly the Mono Lake brine shrimp (*Artemia monica*) and alkali flies (*Cirrula* spp.). For example, the islands and numerous islets support one of the two largest nesting populations of California Gulls (*Larus californicus*) in California (Doster and Shuford 2018). The lake also functions as a fall staging area for an average of 40% of the North American population of the Eared Grebe (*Podiceps nigricollis*) (Roberts et al. 2013) and a staging area and migratory stopover location for up to 140,000 Wilson's (*Phalaropus tricolor*) and Red-necked Phalaropes (*P. lobatus*) during fall migration (Jehl 1986, 1988).

Waterfowl also use Mono Lake, including an established breeding population and larger numbers of migrating waterfowl in autumn. Waterfowl habitat at Mono Lake occurs in discrete patches around the perimeter of the lake in the vicinity of sources of fresh or brackish water. Wetland vegetation,

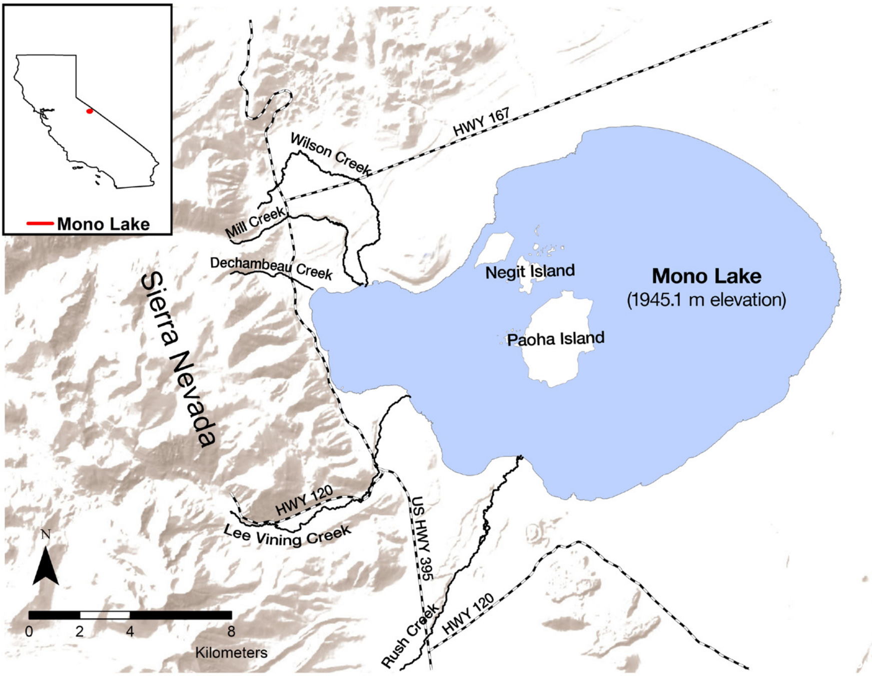

Figure 1. Mono Lake, California study area. Depicted are the five main perennial creeks, all originating from the east slope of the Sierra Nevada, the two main islands (Paoha and Negit), and the shoreline configuration at an elevation of 1945.1 m above mean sea level, which was the average level in September over the period of study from 2002 to 2022. (Relief map source: ESRI, USGS, and NOAA.)

primarily wet meadow and alkaline wet meadow, covers about 20% of the shoreline (Jensen 2015) and is best developed around the sources of fresh and brackish water. The 256 acres of marsh mapped in 2014 amounted to only 2% of all the shoreline's land types. The numerous fresh and brackish springs scattered around the entire shoreline also support small temporary and semi-permanent fresh and brackish ponds. In 2014, fresh and brackish water ponds totaled 38 ha or less than 1% of the shoreline of Mono Lake (Jensen 2015). Along the west shore are several perennial creeks and their deltas, the largest of which is that of Rush Creek.

The potential food resources for waterfowl at Mono Lake are primarily animal in nature, although various forms of algae and plants are found in the wetlands, ponds, and nearshore habitats. Aquatic plants are lacking in the open water because of its hypersalinity. In the pelagic zone (offshore), littoral zone (nearshore), and the fresh and brackish ponds aquatic invertebrates are an abundant food resource for waterfowl at Mono Lake. *Artemia monica* occurs in both the pelagic and littoral zones. *Artemia* densities can be higher nearshore than offshore, but nearshore densities are more variable spatially because nearshore areas are more heterogeneous in terms of substrates and fresh-water inflows (Conte et al. 1988). High-density plumes of brine shrimp can occur near submerged tufa, underwater springs, near shore over mud or gravel substrates, along foam lines, and in spring channels or at the interface between fresh and hypersaline lake water (Conte et al. 1988, pers. obs.). The other dominant invertebrate, *Cirrula hians*, occurs primarily in the littoral zone, with higher concentrations near submerged hard surfaces such as tufa or pumice blocks (Herbst and Bradley 1993). The fresh and brackish ponds along the shoreline support a range of aquatic invertebrates including water boatmen (Corixidae), beetles (Coleoptera), alkali flies, and water mites (Hydrachnidia) depending on the salinity, persistence, and presence of vegetation (pers. obs).

Waterfowl diets at Mono Lake have not been studied formally (Jones and Stokes 1993), though anecdotal reports of stomach contents from hunter-killed birds in the mid-1900s and observations of foraging birds suggest Northern Shovelers feed primarily on brine shrimp and algae, while other waterfowl species consume mostly larvae and pupae of alkali flies (DeChambeau, Taylor, Banta, and McPherson *in* Jones and Stokes 1993). At Great Salt Lake, another hypersaline lake that hosts large numbers of waterbirds, about 70% of the Northern Shoveler's diet (biomass) consists of adults and cysts of brine shrimp (Vest and Conover 2011).

In the Intermountain West, wetlands such as Mono Lake typically serve as breeding and migratory stopover sites for waterfowl, but severe weather often limits waterfowl use in winter (Intermountain West Joint Venture 2013). Despite the severe winters the Mono Basin experiences, the lake does not freeze over because of its high salinity, although the shoreline ponds and wetlands do.

Mono Lake's communities of breeding and migrating waterfowl are fairly distinct. The Gadwall (*Mareca strepera*) has been the dominant breeding species, whereas the Northern Shoveler and Ruddy Duck (*Oxyura jamaicensis*) have been the most abundant species in fall (Jones and Stokes Associates 1993, LADWP 1996, House and Honda 2018). At least since the inception of my surveys in 2002, the Northern Shoveler has been the single most abundant waterfowl species at Mono Lake in fall, accounting for over 50% of all waterfowl observed between September and mid-November (House and Honda 2018).

Like many other saline lakes around the world (Wurtsbaugh et al. 2017), Mono Lake has been affected by water use for agricultural and municipal purposes. Starting in the 1800s, early agriculture in the Mono Basin involved diversions within the basin such as spreading water to grow crops or forage for livestock (Jones and Stokes Associates 1993). In 1941, however, transfers out of the basin began when the city of Los Angeles obtained appropriative water rights to divert flows from Lee Vining, Rush, Walker, and Parker creeks for its municipal water supply. Water diverted from these creeks was transferred from the Mono Basin into the Owens River basin and ultimately into the Los Angeles Aqueduct. From 1941 to 1988, water diversions from the Mono Basin averaged over 65,000 acre-feet per year, peaking at over 140,000 acre-feet in 1979 (Los Angeles Department of Water and Power [LADWP] unpubl. data). This diversion rate resulted in a 13.7-m vertical drop in the lake's level, which fell to a historic low of 1941.8 m above sea level in 1982 (SWRCB 1994).

A 1983 ruling by the Supreme Court of California resulted in the State

Water Resources Control Board (SWRCB) amending Los Angeles' water rights with Mono Lake Basin Water Right Decision 1631 (SWRCB 1994). Decision 1631 severely restricted water exports, established a target lake level of 1947.9 m above sea level, and restored perennial flow to Mono Lake's major tributaries. Decision 1631 was significant in that it was the first time the public trust doctrine was applied to water rights. Since implementation of Decision 1631 in 1995, the annual average export has dropped from 65,000 acre-feet to 13,000 acre-feet. This export reduction has resulted in an increase in and the stabilization of Mono Lake's level, which nevertheless remains below the target. Since 1999 the level of Mono Lake has fluctuated between 1945.8 and 1943.7 m above sea level, with elevational changes now largely driven by annual variation in weather and runoff. The reestablishment of waterfowl habitat at Mono Lake has as its most important objective achieving the target lake level of 1947.9 m above sea level (LADWP 1996).

Although historical information on waterfowl numbers was lacking, the SWRCB concluded that excessive water diversions and the associated drop in lake level had severely degraded habitat for migratory waterfowl (SWRCB 1994). Effects cited include an increase in the lake's salinity, stream incision, a reduction in "hypopycnal" environments (areas where fresh and brackish water mix nearshore), and the loss of delta lagoons and shoreline coves (Jones and Stokes Associates 1993, Stine 1995, LADWP 1996). The cessation of irrigation for livestock feed resulted in the loss of irrigated pastures and meadows on shore that were also likely to have attracted foraging and migrating waterfowl.

Despite the lack of data on waterfowl numbers prediversion, the SWRCB concluded that waterfowl populations had been more affected by the ecological changes associated with excessive water diversion than other taxa such as the Eared Grebe, California Gull, or phalaropes (*Phalaropus* spp.) and thus mandated the development of the Mono Basin Waterfowl Restoration Plan (LADWP 1996). The plan requires the monitoring of hydrology, limnology, brine shrimp, and waterfowl. Here I report on results of waterfowl surveys conducted as part of the plan, focusing on the Northern Shoveler because of its dominance of the fall waterfowl community of Mono Lake. I present the number of shovelers using Mono Lake each fall from 2002 to 2022, discuss trends, and analyze environmental factors potentially contributing to annual and seasonal variation in Northern Shoveler totals at Mono Lake, including the availability of *Artemia monica*, a likely food source.

WATERFOWL SURVEY METHODS

I surveyed the waterfowl of Mono Lake annually each fall from 2002 to 2022, six times per year at two-week intervals starting the first week of September and ending in mid-November. Over the entire study period, two scheduled surveys, the mid-September surveys of 2020 and 2022, were missed. Over the length of the study, consistency of observers was high, as I directed and took part in all but one survey over the 21-year period. On all surveys, waterfowl were identified to species or to the lowest identifiable category, e.g., "unidentified teal." Here I summarize and analyze data for the Northern Shoveler only.

From 2002 to 2019, surveys were conducted from a four-passenger high-winged aircraft traveling at 130 km/hr at a height of ~60 m above ground level (House and Honda 2018). From 2020 to 2022 the fixed-wing aircraft was no longer available and surveys combined observations from a boat, a helicopter, and occasionally the ground. Despite this variation in method, each survey encompassed all shoreline and nearshore areas around the entire perimeter of Mono Lake where virtually all Northern Shovelers have been encountered over the years. In addition, the visibility of the shoreline and nearshore areas is very good and unobstructed, allowing adequate detection with each method. Thus I consider the data from the different survey methods comparable for this species.

Aerial surveys took place in the morning, starting no later than 09:00 Pacific Time, and were completed in 90 minutes. The plane flew counter-clockwise around the entire perimeter of the lake at a distance of ~150–250 m from shore with the observers looking shoreward, covering the shoreline and nearshore areas. Immediately after the perimeter flight, open-water areas were surveyed by means of eight fixed parallel transects spaced at 1.8-km intervals. During fixed-wing surveys two observers were present on most flights. During the perimeter flight, the observers positioned themselves on the same side of the aircraft. When flying the parallel transects over the open water, the observers sat on opposite sides of the aircraft. During fixed-wing surveys I used a voice recorder to record waterfowl numbers and species composition by shoreline area, and the second observer recorded data by hand.

In 2020 the shoreline was surveyed primarily by boat (a 5-m Boston Whaler), but at Warm Springs on the east side of the lake a ground survey was needed because shallow waters prevented a close approach to shore. The boat traveled at low speed around the perimeter of the lake about 150–250 m from shore with the observers looking shoreward. Surveys started at ~08:30 Pacific Time and required 5 to 6 hours to complete. Starting in 2020, a subset of the fixed parallel transects were surveyed by boat.

In 2021 and 2022, I used a helicopter to survey the entire shoreline and a boat for the offshore transects. The protocol by helicopter was the same as by plane in that the shoreline and nearshore areas were surveyed counter-clockwise around the entire perimeter of the lake at a distance of ~150–250 m from shore with the observer looking shoreward. Surveys were in the late morning (11:00 Pacific Time), and data were recorded by hand during the flight. Boat surveys of the cross-lake transects generally took place the following day, starting at 08:30 Pacific Time and requiring 4 to 5 hours to complete.

DATA SUMMARY AND STATISTICAL ANALYSIS

The objective of the statistical analysis was to find a set of environmental factors that best explained the annual variation in the number of Northern Shovelers using Mono Lake in fall. The environmental factors evaluated included lake level, mixing regime, *Artemia* biomass, and drought. As the defined primary means for restoring waterfowl habitat, lake level was included because of its influence on lake salinity and nearshore habitats in terms of the connectivity of lake waters to wetland and spring habitats. The mixing regime was evaluated because of its influence on nutrient cycling and *Artemia* populations (Melack et al. 2017). *Artemia* biomass was included as the brine shrimp is a potential food resource for shovelers. Indices of drought were included to represent larger-scale environmental factors that may influence wetland resources and the distribution of migrating waterfowl.

Over the course of this study, Northern Shovelers occurred in high numbers in September, followed by a rapid decline. This species does not breed at Mono Lake, and is a very rare breeding species at other wetland sites in southern Mono County (Shuford and Metropulos 1996, pers. obs.), thus the birds arriving in fall represent migrants from other regions. Mono Lake's *Artemia* population also varies seasonally, reaching peak annual density in July or August, then declining rapidly through the remainder of the fall (Lenz et al. 1986). Determining how variation in biomass of *Artemia* affects Northern Shoveler numbers was a key objective of this analysis, taking into account the underlying pattern of the species' migration chronology.

Northern Shoveler Survey Data

For each of the six survey periods—early (first week), middle, and late September (or early October some years), mid-October, late October, and mid-November—I calculated the total number of Northern Shovelers for each period by summing numbers recorded on both shoreline and open-water transects. For the two missing surveys of mid-September 2020 and mid-September 2022, I estimated the numbers by cubic spline interpolation (SRS1 Software). The total annual fall abundance of shovelers was derived by summing the totals for the six survey periods. The length of the shoveler's stopovers at Mono Lake is unknown, but from a review of survey totals, most or all of large flocks seen on one survey typically departed within two weeks. Assuming that if conditions are favorable, birds might remain longer and be recorded on subsequent surveys, I evaluated yearly totals for their relationship to lake level and mixing status. For each survey period and year I calculated the mean, standard error, and low and high counts.

Shoveler counts were not normally distributed over the 21-year period and included three values of zero on the mid-November survey. An examination of the residuals from linear regression analysis indicated heteroscedasticity, or non-random changes in the residuals, due to the strong seasonality of the data and a large range in values between the highest and lowest numbers observed. This data structure did not lend itself to my using linear regression models, and data transformation was needed. Because of the late-fall zero counts, I transformed the data by adding +1 to all values prior to $\log_{10}$ transformation. This transformation resulted in normally distributed data that were still heteroscedastic, and I used a generalized linear model to evaluate variables influencing Northern Shoveler numbers.

Environmental Variables

Mono Lake surface elevation. LADWP recorded the surface elevation of Mono Lake monthly with a staff gauge located on the west shore. I downloaded the data, recorded in feet, from the Mono Basin Clearinghouse (https://www.monobasinresearch.org/data/levelmonthly.php) and converted them to meters for analysis. I used simple linear regression to evaluate the relationship between the level of Mono Lake in September, or the beginning of the annual fall survey, and total annual shoveler numbers.

Lake mixing regime. Deep saline lakes such as Mono Lake typically "turn over" or mix once a year in a process known as monomixis. Mono Lake currently does not mix every year, and depending on the amount of fresh-water input alternates between being meromictic (chemically and thermally stratified) or monomictic, in which complete mixing occurs in late fall (often November), after the end of the seasonal waterfowl surveys. When complete, this mixing eliminates the chemocline and thermocline and brings bottom-dwelling nutrients into the water column (Melack et al. 2017). I categorized each of the survey years as either meromictic or monomictic, depending on whether the lake was stratified or mixed between September and mid-November. The assignment of mixing-regime type was based on an evaluation of the water-column profiles for temperature, conductivity, dissolved oxygen, and ammonium (Jellison et al. 2024).

The dynamics of Mono Lake's mixing influence *Artemia* abundance through nutrient cycling (Melack et al. 2017). *Artemia* feeds on phytoplankton, and the phytoplankton requires inorganic nitrogen, which is a limited substance in Mono Lake. The main sources of nitrogen are brine shrimp excretion and the vertical mixing of ammonium-rich deep water (Melack et al. 2017). The release of nutrients associated with vertical mixing under monomictic conditions can result in an algal bloom, and a subsequent boom in the *Artemia* population the following summer, though the magnitude of the post-mixing population booms has varied.

If shovelers are responding to *Artemia* abundance or some other underlying factor related to the lake's productivity or monomixis, their totals may likewise show a response to its mixing status. I used a Mann–Whitney *U* test to compare median values of total Northern Shovelers observed under meromictic vs. monomictic conditions.

Artemia *biomass.* I have frequently observed shovelers feeding in the water column near fresh-water outflows, the interface of fresh and hypersaline waters being a microhabitat where brine shrimp, a primary food (Jones and Stokes 1993), have also been observed to congregate (Conte et al. 1988, pers. obs.). These anecdotal observations along with a documented dominance of shrimp in the diet of shovelers at other hypersaline lakes such as Great Salt Lake (Vest and Conover 2011) and Lake Abert, Oregon (Boula 1986), encouraged me to explore the link between annual and seasonal variation in numbers of Northern Shovelers and *Artemia* biomass.

As part of a continuing program of limnological monitoring at Mono Lake, the University of California, Santa Barbara, or the Los Angeles Department of Water and Power have sampled populations of *Artemia monica* (House and Honda 2018). Samples were collected with a plankton net once monthly February through December at 12 buoyed stations. For determination of biomass, samples were rinsed with tap water, dried in aluminum pans at 50 °C for at least 48 hr, and then weighed to the nearest 0.1 g on an analytical balance immediately upon removal from the oven (Jellison 2011, House and Honda 2022)

To evaluate the relationship between Northern Shoveler totals per survey period and brine shrimp populations, I used the mean biomass of *Artemia* throughout the lake. For each round of *Artemia* sampling, I calculated a lake-wide index of *Artemia* biomass by averaging the dried weights of the samples from the 12 stations. Since *Artemia* was seldom sampled on the same day as waterfowl surveys, I estimated values of *Artemia* biomass for each waterfowl survey date by one-way spline interpolation (SRS1 Software). Like the shoveler counts, the shrimp biomass data included some zero values and were heteroscedastic because of strong seasonality, so I added +1 to all values prior to $\log_{10}$ transformation. This transformation resulted in normally distributed data in which heteroscedasticity was still evident, thus use of a generalized linear model was still appropriate.

Assessing drought. I assessed the influence of regional and local drought on Northern Shoveler numbers at Mono Lake with the Palmer drought severity index (PDSI). The PDSI is a monthly index that incorporates both air temperature and precipitation data to evaluate the severity of hydrologic drought (Alley 1984, NCAR 2020). The combined effects of air temperature and precipitation influence evapotranspiration, which is the major factor controlling water balance in wetlands (Zhao and Liu 2016). The PDSI ranges from +10 (extremely wet) to −10 (extremely dry) (NCAR 2020). Monthly PDSI indices are available for all nine U.S. climate regions, all states except Alaska, and also divisions within states

The PDSI may serve as a surrogate indicator of the extent or availability of wetlands in a region. I was interested in whether the variation in totals suggests that in drought years Mono Lake may serve as a refuge to shovelers migrating through this desert region. In my initial evaluation of drought I used Pearson's correlation to look for relationships between shoveler numbers and the PDSI at various regional and time scales to determine which PDSI value to incorporate into the model. In addition, to avoid multicollinearity, I also looked for correlation among PDSI values, since widespread drought may result in correlation among PDSI values across regions. I examined ten regional, state, and divisional spatial scales and five time scales ranging from monthly to intervals of 24 months. Ultimately, I selected the August PDSI values for California Climate Division 3 (CA3; Northeast Interbasin) as their correlations were the strongest and they performed best in the model. CA3 covers northeastern and east-central California east of the Sierra Nevada and Cascade Ranges, including the Mono Basin.

To evaluate the combined effects of drought, date (survey), and *Artemia* biomass on Northern Shoveler numbers, I used a generalized linear model, evaluating its performance with r^2 and the log-likelihood values for each variable. Parameter coefficients were standardized (β) to allow comparisons of the magnitude of effect each variable had on shoveler numbers. All values are reported as mean ± standard error unless noted otherwise.

RESULTS

Summary of Northern Shoveler Data

Over the 21-year study period, 124 surveys were completed. From 2002 to 2022 the total number of Northern Shovelers counted at Mono Lake each fall (results of the six surveys summed) averaged 13,018 ± 1571 (Figure 2, Table

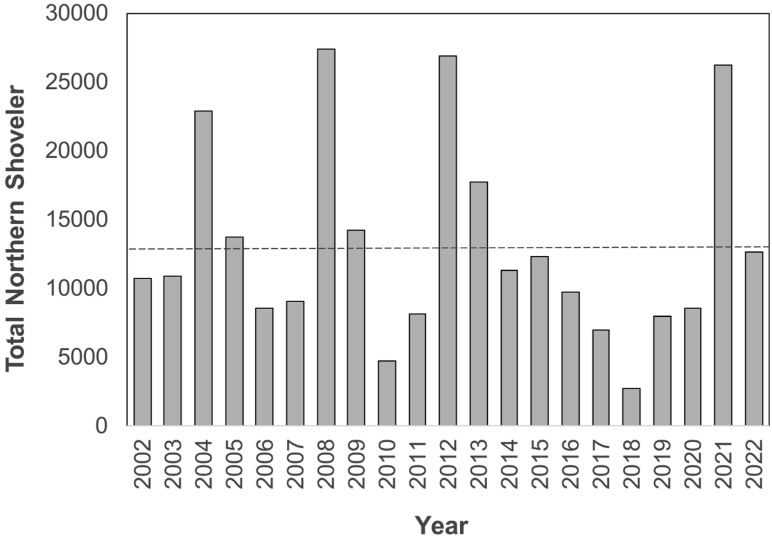

Figure 2. Total number of Northern Shovelers recorded annually during fall surveys at Mono Lake, California, 2002–2022. The dashed line represents the mean across all surveys each year.

1). There was strong seasonality in use, with total numbers highest in early to mid-September and significant and steady declines thereafter (Figure 3).

The peak count for the year on a single survey averaged 5562 ± 709 and ranged from a low of 768 in 2018 to a high of 13,793 in mid-September 2012. The vast majority (99%) of shovelers were recorded <250 m from shore, with <0.1% found on the open water. During the period of peak use in September, shovelers typically gathered at the Wilson Creek delta along the northwest shore, where the total yearly lakewide counts have been highest in 18 of the 22 survey years. When not at the Wilson Creek delta, high numbers were observed along the south shore, along the north shore in the DeChambeau Embayment, or at Mill Creek, which is just west of Wilson Creek.

In five survey years (2004, 2008, 2012, 2013, 2021), shoveler totals for the entire survey period were significantly higher than the average (Figure 2).

Table 1 Abundance of the Northern Shoveler at Mono Lake, 2002–2022

Survey period	Mean	SE	High count	Low count
Early Sep	4333	585	8998	455
Mid-Sep	4432	659	13,793	768
End Sep	2696	634	11,567	211
Mid-Oct	1069	399	7037	0
End Oct	260	103	2031	3
Mid-Nov	198	86	1354	0
Annual peak count	5562	709	13,793	768
Annual total	13,018	1571	27,400	2719

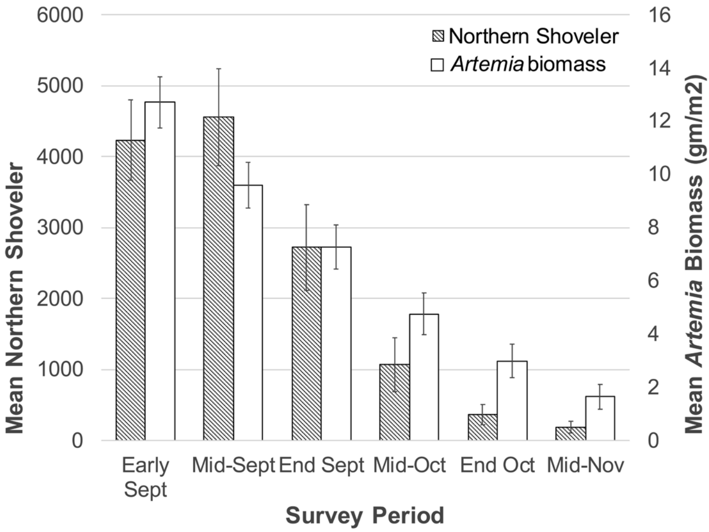

FIGURE 3. The mean (±SE) number of Northern Shovelers and mean lakewide biomass of brine shrimp (*Artemia monica*) recorded during each of six autumn waterfowl survey periods at Mono Lake, California, 2002–2022.

Abundance was highest in 2008, when 27,400 shovelers were tallied over the six surveys, and lowest in 2018, when only 2,719 were tallied. Across years, the numbers appeared somewhat cyclical (Figure 2), but there was no long-term trend ($r^2_{adj} = 0.035$, $p = 0.277$).

Environmental Variables

Lake level. From 2002 to 2022 the level of Mono Lake in September averaged 1945.1 m, ranging from 1943.9 to 1946.1 m, for a total elevational range of 2.2 m over the study period. The highest September elevation of 1946.1 m occurred in 2006, and the lowest in 2016, following a severe multi-year drought.

Mixing regime. Mono Lake was meromictic during the surveys from 2002 to 2003, 2005 to 2007, in 2011, and from 2017 to 2020 and monomictic in 2004, from 2008 to 2010, from 2012 to 2016, and from 2021 to 2022.

Regional drought. Over the 21-year study period, the August PDSI for CA3 ranged from −5.12 (extreme drought) to 4.16 (extremely wet). The region experienced six years of severe to extreme drought (PDSI ≤ −3.0), four years of moderate drought (PDSI −2.9 to −2.0), nine normal to near-normal years (PDSI −1.9 to 1.9), one moist year (PDSI 2.0 to 2.9), and one extremely wet year (PDSI ≥ 3.0).

Artemia *biomass.* In early September, at the start of the fall waterfowl-survey period, the mean biomass of *Artemia* averaged 12.8 ± 1 g/m^2. By mid-October, it declined to an average of 4.8 ± 0.8 g/m^2, and by mid-November this measure averaged 1.8 ± 0.6 g/m^2.

Environmental Variables vs. Northern Shoveler Numbers

Lake level. Mono Lake's elevation in September had no direct effect on its total number of Northern Shovelers each year ($r^2_{ad} = 0.000$, $p = 0.564$), so I excluded this variable from the final model.

Mixing status. The median number of Northern Shovelers under meromictic conditions was 8726 and 16,921 under monomictic conditions, a significant difference ($U = 15.0$, $p = 0.004$, mean difference of 6577 and effect size = 0.727, Figure 4). Shoveler totals varied more widely when the lake was monomictic than when it was meromictic (Figure 4), as numbers were highest the first year of monomixis, then lower in subsequent years, but remained on average higher than when Mono Lake was stratified.

Generalized Linear Model Results

The model that best explained the variation in Northern Shoveler numbers at Mono Lake in fall involved the combined effects of survey period, *Artemia* biomass, and the August PDSI in CA3 ($r^2_{ad} = 0.658$, $p < 0.001$). Survey period was negatively correlated with shoveler totals ($\beta = -0.453 \pm 0.0801$), reflecting numbers decreasing through the fall (Figure 3). The seasonal pattern of *Artemia* biomass mirrored that of shovelers (see Figure 3); *Artemia* biomass was positively correlated with shoveler totals ($\beta = 0.445 \pm 0.0806$) in that greater *Artemia* biomass was associated with higher numbers of shovelers even with the effect of survey period held constant. The August value of PDSI for CA3

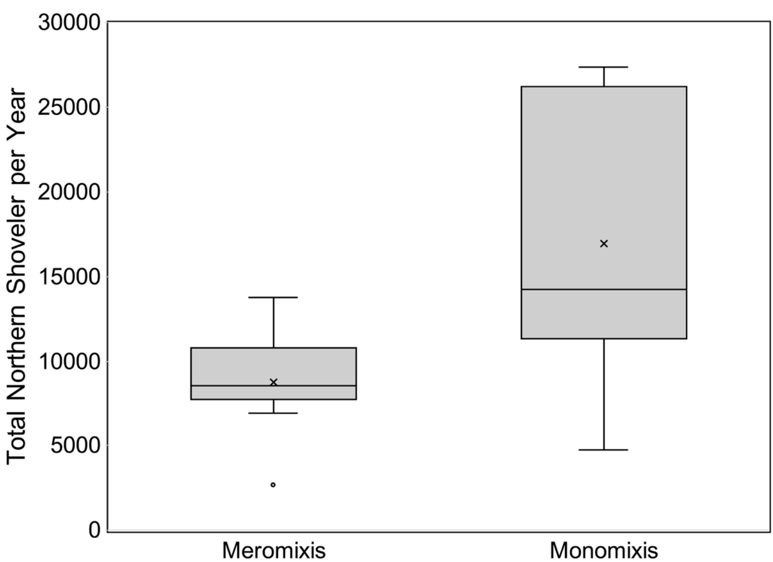

Figure 4. Total numbers of Northern Shoveler recorded annually under regimes of meromixis ($n = 10$) and monomixis ($n = 11$) at Mono Lake, California (2002–2022). Box plots show mean (×), median (solid line), interquartile range (shading), minimum and maximum (whiskers), and outliers (filled circles).

was negatively correlated with shoveler totals ($\beta = -0.111 \pm 0.0555$), as higher PDSI values (i.e., wetter conditions, less severe drought) were associated with fewer shovelers (Figure 5). Of these variables, survey period ($\chi^2 = 32.01$, df = 1, $p < 0.001$) and *Artemia* biomass ($\chi^2 = 30.57$, df = 1, $p < 0.001$) were the most influential and roughly equal in strength (Figure 3). Relative to biomass and survey period, PDSI had a weak but significant influence on shoveler totals ($\chi^2 = 4.02$, $p = 0.045$) (Figure 5). This model suggested that, with the effect of survey period held constant, the influence of the *Artemia* biomass was also significant, with higher biomass resulting in more Northern Shovelers. PDSI values for CA3 were negatively correlated with totals, suggesting that the stronger the drought, the more Northern Shovelers at Mono Lake.

DISCUSSION

These surveys document that Mono Lake currently supports an average of 13,018 Northern Shovelers each fall, with peak numbers in early-to-mid September. Though the surveys began in early September when use was near its peak (Figure 3), the number of shovelers recorded in August has not exceeded about 400 birds on any one count (J. Jehl Jr. unpubl. data). Thus my surveys from 2002 to 2022 likely captured most of the shovelers passing through Mono Lake in those years. The only baseline data available with which Northern Shoveler numbers prior to implementation of Decision 1631 can be compared are from two all-lake surveys on 30 August and 14 September 1976 (Winkler 1977), when 1080 and 2230 birds were recorded, respectively, and the level

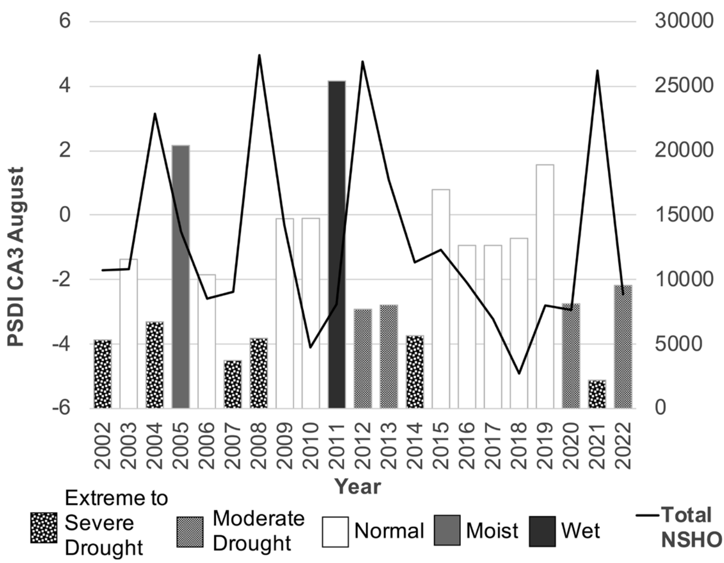

Figure 5. Rankings of the Palmer Drought Severity Index (PDSI) for the month of August for California Division 3 (CA3) vs. the total number of shovelers at Mono Lake, California, 2002–2022.

of Mono Lake was ~1944 m, or just 1 m less than the average September lake level during my 21-year survey period. The mean numbers on my early and mid-September counts, 4333 and 4432, respectively, are four and two times higher than the 1976 counts prior to the limitation of water diversions, though the dearth of historic data limits the inferences that can be drawn regarding the shoveler's response to restoration at Mono Lake thus far.

The yearly totals observed at Mono Lake averaged 45%, and in some years up to 80%, of all Northern Shovelers counted at the three largest water bodies in Mono County: Mono Lake, Bridgeport Reservoir, and Crowley Reservoir (House and Honda 2022). Given these data, Mono Lake is an important local resource for migrating Northern Shovelers, serving as one of their three main fall migratory stopover locations in Mono County.

For a broader context Mono Lake's average annual Northern Shoveler count of 13,018, and annual peak count of 5562, may be compared to flyway numbers and to counts at other saline lakes in the Intermountain West. The totals at Mono Lake each fall averaged just 0.3% of the Pacific Flyway's breeding population in 2019 (U.S. Fish and Wildlife Service 2021). The average fall (August–September) population at Great Salt Lake, Utah, of 56,950 from 1997 to 2001 (Paul and Manning 2008), was over four times that observed at Mono Lake. At Lake Abert, a small shallow terminal lake in eastern Oregon, about 22,000 shovelers were estimated in September of 2011 and 2012 (East Cascade Audubon Society, http://bit.ly/2s3Kwgt). Surveys of Owens Lake from 2012 to 2022 yielded peak fall counts averaging over 18,000 and total fall counts (September and October) averaging ~28,000 birds (LADWP unpubl. data). These comparisons suggest that the number of Northern Shovelers using Mono Lake is, in general, not major from a population standpoint, nor as compared to these other sites in the Intermountain West, particularly when the relatively large size of Mono Lake is considered.

The Northern Shoveler is currently an early-season fall migrant at Mono Lake, with peak numbers in September. In most years the species largely departs the Mono Basin by mid-October. Its seasonality and period of peak abundance in fall are similar to those observed at other Mono County sites, including Bridgeport Reservoir (House 2021) and Crowley Reservoir (unpubl. data). Northern Shoveler totals at Mono Lake peak slightly earlier in the fall than at other sites in the Intermountain West both north and south of Mono Lake. At Lake Abert, in eastern Oregon, shoveler numbers peak perhaps slightly later than at Mono Lake, in mid- to late September (East Cascade Audubon Society, http://bit.ly/2s3Kwgt). Peak fall numbers of these birds at Stillwater National Wildlife Refuge, to the north in western Nevada, occur in October (Bundy 2002). At Owens Lake, in Inyo County to the south, numbers have been highest in October as well (LADWP unpubl. data). Local differences in migration phenology such as these may reflect a species' response to local resources or differing source populations. The phenology observed at Mono Lake is likely due in part to the seasonal abundance patterns of a potential food resource, *Artemia monica*.

At high elevations with severe winter weather, Mono Lake's resources are highly seasonal. The annual population cycles of *Artemia* contribute to the seasonal pattern of Northern Shoveler use. By August of each year, the *Artemia* population starts declining as individuals die off and females switch to ovoviviparous reproduction, producing overwintering cysts. Few shrimp persist as adults through the winter. My hypothesis is that the seasonal reduction in *Artemia* biomass through the fall encourages Northern Shovelers to migrate out of the Mono Basin, but higher fall values of *Artemia* biomass contribute to higher shoveler numbers, even when the effect of survey period is held constant.

Artemia biomass partly explains the variation in Northern Shoveler numbers, but unfortunately data are not available for other potential foods, in particular alkali flies, which are a preferred food of many waterbird species in saline environments. Shovelers are known to eat both brine shrimp (adults and cysts), and alkali flies (larvae, pupae, and adults), but the degree to which they rely on either of these important food sources at Mono Lake has not been quantified. I have observed shovelers feeding in fresh-water outflows and deltas more frequently than other waterfowl species, which tend to stay on or much closer to shore. Thus I suspect shovelers are feeding on shrimp to a greater degree than are the other waterfowl species using Mono Lake in fall, as has also reported by hunters (Jones and Stokes 1993). Studies at other saline lakes, however, have shown that shovelers not only consume more shrimp than other waterbird species, but they consume proportionally more shrimp than alkali flies. For example, at Lake Abert, the shoveler was the only waterbird species that fed extensively on brine shrimp (Boula 1986). Brine shrimp constituted 31% of the biomass of the shoveler's diet, a proportion over twice that of the Eared Grebe at 13.7%. Alkali flies were, in general, birds' preferred food at Lake Abert, and constituted at least 65% of the biomass consumed by all species studied except the shoveler, for which the value was 25%. Similar results were obtained from a more limited study of the diet of wintering waterfowl at Great Salt Lake, where adult brine shrimp and cysts represented 72% and alkali fly larvae and adults 8% of the shoveler's diet (Vest and Conover 2011, Vest 2013). The diet of the Green-winged Teal (*Anas crecca*) also included a large amount of brine shrimp, but that species consumed fewer adult shrimp (1.5% of the biomass vs. 20.2% for the shoveler). This winter study at Great Salt Lake found a greater reliance on shrimp cysts than on adult shrimp, presumably because at that season adult shrimp are few. At Mono Lake, *Artemia* cysts sink to the bottom (Melack et al. 2017), leaving them inaccessible through winter, and adult shrimp are virtually absent. Initial data exploration did reveal a positive correlation of shoveler numbers and *Artemia* fecundity (average number of cysts per female) at Mono Lake, but I did not include this variable in the model because of autocorrelation with shrimp biomass. Thus at Mono Lake shovelers may also consume *Artemia* cysts when available and accessible, their abundance influencing the shoveler's numbers.

In fall, many dabbling duck species rely more heavily on carbohydrates than on proteins, consuming seeds and vegetative parts of wetland and aquatic plants to increase fat reserves for winter (Baldassarre and Bolen 1994). As a hypersaline lake lacking aquatic vegetation, Mono Lake does not support such resources in abundance, limiting its attractiveness to many waterfowl. The Northern Shoveler's adaptations, including lamellae not only more numerous but longer and more closely spaced than in other waterfowl

(Kooloos et al. 1989), allow them to feed on small aquatic invertebrates such as brine shrimp, copepods, and water fleas (*Daphnia* spp.). When comparing the feeding efficiency of two dabbling duck species—the Northern Shoveler and Mallard (*Anas platyrhynchos*)—and the diving Tufted Duck (*Aythya fuligula*), Kooloos et al. (1989) found that neither Mallards nor Tufted Ducks were able to retain shrimp pulp (the smallest food item tested) in their bills during feeding experiments. Shovelers retained about 40% of the shrimp pulp, however. So, although the Northern Shoveler retains only a portion of the shrimp that enter its bill, it is significantly better at harvesting shrimp than the other two species tested. The shoveler's specialized bill morphology thus allows for the effective filtering of small aquatic invertebrates, such as brine shrimp, and for them to exploit this resource at Mono Lake, when other species cannot. The limited availability of alternative food items at Mono Lake could lead to greater reliance and association between shoveler numbers and shrimp populations.

At Mono Lake the abundance of *Artemia* has, of late, been associated with periods of declining lake levels induced by drought. The increases in *Artemia* after mixing of the lake's water are short-lived, evident for only one or two years. Thus the effect of drought on Northern Shoveler use of Mono Lake may be through this indirect effect on *Artemia* population, large numbers of shovelers being attracted to *Artemia* population spikes, or birds may stay longer in response to greater food availability, resulting in higher seasonal totals. A similar relationship to lake productivity with respect to the *Artemia* population has been seen in the nesting population of the California Gull at Mono Lake. The gulls' nesting productivity has been linked to the lake's productivity, which has been higher under monomictic conditions and declining lake levels, but lower when the lake's level rises and productivity decreases in association with meromictic conditions (Burnett et al. 2021).

At Mono Lake, I found regional drought to have a weak positive influence on Northern Shoveler numbers: the less intense the drought, the fewer shovelers observed. This pattern differs from that observed during the same time period at nearby Bridgeport Reservoir (House 2021), where waterfowl numbers were negatively correlated with regional drought. Since the PDSI for northeastern California (CA3) is highly correlated with that of other western states, drought conditions in northeastern California were likely similar to those at other regional sites important to migratory waterfowl. Perhaps wetter, improved regional conditions attract shovelers away from Mono Lake, particularly if shrimp populations are low.

Mono Lake's *Artemia* populations have been showing signs of decline recently, despite the gains in lake level and subsequent decrease in salinity (House and Honda 2022). This decline is not completely understood, but it has been accompanied by a decline in the lake's transparency and increased dominance by the eukaryotic alga *Picocystis* strain ML (Stamps et al. 2018), even though *Picocystis* is a food source for *Artemia*. Declines in *Artemia* population peaks may also be due, in part, to shorter wet periods resulting in less accumulation of nutrients. The prolonged severe drought from 2012 to 2016 had a profound negative effect on the *Artemia* population (House and Honda 2022). The long-term effects of changes in the algal community or nutrient cycling on shrimp populations remain unknown in the context of climate change.

Although the target lake level has not yet been achieved, waterfowl habitats have improved since implementation of Decision 1631 as a result of the restoration of perennial flow in Rush, Lee Vining, and Mill creeks. Also, the connectivity of spring and creek outflows with wetland vegetation has been ameliorated by the increases in lake level observed so far. Raising the level of Mono Lake to the target elevation of 1948.2 m set by the SWRCB is the most important objective for restoring waterfowl habitat, and it is expected to enhance waterfowl habitats by improving the physical linkage between shoreline marshes, ponds, and freshwater outflows that produce estuary-like habitats.

The lack of association between fall Northern Shoveler numbers and Mono Lake's level could be due to the lake's not yet reaching some threshold below or above which its level may have a greater influence on fall waterfowl use. Such a threshold has been documented for waterfowl breeding at Mono Lake, where duck productivity varied with lake level when that level was above 1945 m but not below (House and Honda 2022). At higher lake levels than have been observed to date, connectivity to wetland vegetation should be greater, enhancing food resources and cover. In contrast to fall migrant shovelers, breeding waterfowl, whose abundance and distribution are more directly tied to shoreline features influenced by lake level—such as ponds and suitable nesting and brood-rearing sites—have been favored by the rise in the level of Mono Lake (House and Honda 2022). Although the suitability of deltas and nearshore areas for shovelers' foraging and resting is influenced by lake level (as through changes in water depth), within the range of lake elevations observed during my study these small-scale effects may have been swamped by variations in lake productivity and *Artemia* biomass.

Despite the productivity of Mono Lake, access of these food resources to dabbling duck species like the Northern Shoveler is somewhat limited. The range of water depths optimal for dabbling ducks' foraging is 10 to 25 cm (Fredrickson and Taylor 1982). Prey are generally less accessible to dabbling ducks in water deeper than about 25 cm, decreasing their foraging efficiency. The topography and bathymetry at Mono Lake (Raumann et al. 2002) are such that shallow-water feeding areas, especially those near fresh-water sources such as springs, are widely spaced around the lake's perimeter and are generally not extensive. I have observed dabbling ducks to feed almost exclusively near shore, and more specifically where the bathymetry implies shallow water for feeding, usually in combination with fresh-water input from springs or creeks. The shoreline of Mono Lake is dynamic, and slight changes in lake level alter waterfowl habitats by altering springs' flow patterns, the connectivity of wetland vegetation to the shoreline, and feeding areas of suitable depths. These factors undoubtedly contribute to the quality of waterfowl habitat, but invertebrate productivity and regional factors including drought may be crucial to how many waterfowl Mono Lake can support. To improve our understanding of the response of waterfowl to changes in Mono Lake's level, we need better documentation of how variation in that level influences the shoreline's topography, as well as the abundance and distribution of resources waterfowl use, including alkali flies and filamentous algae.

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LITERATURE CITED

Alley, W. M. 1984. The Palmer drought severity index: Limitations and assumptions. J. Climate Appl. Meteorol. 23:1100–1109; doi.org/10.1175/1520-0450(1984)023<1100:TPDSIL>2.0.CO;2.

Baldassarre, G. A., and Bolen, E. G. 1994. Waterfowl Ecology and Management. Wiley, New York.

Boula, K. M. 1986. Foraging ecology of migrant waterbirds, Lake Abert, Oregon. M.S. thesis, Ore. State Univ., Corvallis; https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/rv042w96k.

Bundy, R. M. 2002. An analysis of Stillwater NWR waterfowl use data—1970–1998. Report to Stillwater National Wildlife Refuge, Fallon, NV; https://www.fws.gov/pacific/planning/Stillwater/Stillwater/ccp/4 Volume II/Appendix E/App E.pdf.

Burnett, R. D., Nelson, K., and Schmidt, A. E. 2021. Population size and reproductive success of California Gulls at Mono Lake, California. Point Blue Conservation Science, Petaluma, CA; https://www.monobasinresearch.org/images/gulls/2020.pdf.

Conte, F. P., Jellison, R. S., and Starrett, G. L. 1988. Nearshore and pelagic abundances of *Artemia monica* in Mono Lake, California. Hydrobiologia 158:173–181; doi.org/10.1007/BF00026275.

Doster, R. H., and Shuford, W. D. 2018. Recent trends in population size and distribution of Ring-billed and California gulls in the western United States, *in* Trends and traditions: Avifaunal change in western North America (W. D. Shuford, R. E. Gill Jr., and C. M. Handel, eds.), pp. 161–179. Studies of Western Birds 3. W. Field Ornithol., Camarillo, CA; doi.org/10.21199/SWB.3.8.

Ficklin, D. L., Stewart, I. T., and Maurer, E. P. 2012. Effects of projected climate change on the hydrology in the Mono Lake basin. Climatic Change 116:111–131; doi.org/10.1007/s10584-012-0566-6.

Fredrickson, L. H., and Taylor, T. S. 1982. Management of seasonally flooded impoundments for wildlife. U.S. Dept. Interior, U.S. Fish and Wildlife Service Resource Publ. 148; https://apps.dtic.mil/sti/pdfs/ADA323232.pdf.

Herbst, D. B., and Bradley, T. J. 1993. A population model for the alkali fly at Mono Lake: Depth distribution and changing habitat availability. Hydrobiologia 267:191– 201; doi.org/10.1007/bf00018801.

House, D. 2021. Fall waterfowl use of Bridgeport Reservoir, Mono County, California. W. Birds 52:278–295; doi.org/10.21199/WB52.4.1.

House, D., and Honda, M. 2018. Mono Basin waterfowl habitat restoration program. Periodic overview report. Report to the State Water Resources Control Board and Los Angeles Department of Water and Power; https://www.monobasinresearch.org/images/ladwp18.pdf.

House, D., and Honda, M. 2022. Mono Basin waterfowl habitat restoration program. 2021 monitoring report. Report to State Water Resources Control Board and Los Angeles Department of Water and Power; https://www.monobasinresearch.org/images/ladwp22.pdf.

Intermountain West Joint Venture. 2013. Implementation plan—strengthening science and partnerships. Intermountain West Joint Venture, Missoula, MT.

Jehl, J. R. Jr. 1986. Biology of Red-necked Phalaropes (*Phalaropus lobatus*) at the western edge of the Great Basin in fall migration. Great Basin Naturalist 46:185–197; http://scholarsarchive.byu.edu/gbn/vol46/iss2/1.

Jehl, J. R. Jr. 1988. Biology of the Eared Grebe and Wilson's Phalarope in the nonbreeding season: A study of adaptations to saline lakes. Studies Avian Biol. 12.

Jellison, R. 2011. Field and laboratory protocols for Mono Lake limnological monitoring. Report to Los Angeles Department of Water and Power, Los Angeles.

Jellison, R., Vignardi, C., and Melack, J. M. 2024. Mono Lake limnological monitoring. 2023 annual report, *in* Compliance reporting prepared for the State Water Resources Control Board in accordance with the terms and conditions of amended license Nos. 10191 and 10192; https://www.monobasinresearch.org/images/ladwp2024.pdf.

Jensen, S. 2015. Mono Lake landtype inventory. 2014 Conditions, *in* Compliance reporting in response to the State Water Resources Control Board Order Nos. 98-05 and 98-07. Los Angeles Department of Water and Power, Los Angeles; https://www.monobasinresearch.org/images/ladwp15.pdf.

Jones and Stokes Associates. 1993. Draft environmental impact report for the review of Mono Basin water rights of the city of Los Angeles. Chapter 3F. Environmental setting, impacts, and mitigation measures—wildlife. Calif. State Water Resources Control Board, Sacramento.

Kooloos, J. G. M., Kraaijeveld, A. R., Langenbach, G. E. J., and Zweers, G. A. 1989. Comparative mechanics of filter feeding in *Anas platyrhynchos*, *Anas clypeata*, and *Aythya fuligula* (Aves, Anseriformes). Zoomorphology 108:269–290; doi.org/10.1007/BF00312160.

Lenz, P. H., Cooper, S. D., Melack, J. M., and Winkler, D. W. 1986. Spatial and temporal distribution patterns of three trophic levels in a saline lake. J. Plankton Res. 8:1051–1064; doi.org/10.1093/plankt/8.6.1051.

Los Angeles Department of Water and Power (LADWP). 1996. Mono Basin waterfowl habitat restoration plan, in response to the Mono Lake Basin Water Right Decision 1631. Report to the State Water Resources Control Board, Sacramento; https://www.monobasinresearch.org/legal/1996waterfowlplan.pdf.

Melack, J. M. 1983. Large, deep, salt lakes: A comparative limnological analysis. Hydrobiologia 105:223–230; doi.org/10.1007/BF00025190.

Melack, J. M., Jellison, R., MacIntyre, S., and Hollibaugh, J. T. 2017. Mono Lake: Plankton dynamics over three decades of meromixis or monomixis, *in* Ecology of Meromictic Lakes (R. D. Gulati, E. S. Zadereev, and A. G. Degermendzhi, eds.), Ecological Studies 228. Springer International, Cham, Switzerland; doi.org/10.1007/978-3-319-49143-1_11.

National Center for Atmospheric Research (NCAR). 2020. Climate data: Palmer drought severity index (PDSI); https://climatedataguide.ucar.edu/climate-data/palmer-drought-severity-index-pdsi.

Paul, D. S., and Manning, A. E. 2008. Great Salt Lake waterbird survey five-year report (1997–2001). Great Salt Lake Ecosystem Program and Utah Div. Wildlife Resources, Salt Lake City; https://wildlife.utah.gov/waterbirdsurvey/.

Raumann, C. G., Stine, S., Evans, A., and Wilson, J. 2002. Digital bathymetric model of Mono Lake, California. U.S. Geol. Survey Misc. Field Studies Map MF-2393; http://pubs.usgs.gov/mf/2002/2393/.

Roberts, A. J., Conover, M. R., Luft, J., and Neill, J. 2013. Population fluctuations and distribution of staging Eared Grebes (*Podiceps nigricollis*) in North America. Can. J. Zool. 91:906-913; doi.org/10.1139/cjz.2013-0181.

Scholl, D. W., Von Huene, R., St. Amand, P., and Ridlon, J. B. 1967. Age and origin of topography beneath Mono Lake, a remnant Pleistocene lake, California. Geol. Soc. Am. Bull. 78:583–600; doi.org/10.1130/0016-7606(1967)78[583:AAOOTB]2.0.CO;2.

Shuford, D. W., and Metropulos, P. J. 1996. The Glass Mountains breeding bird atlas project preliminary results, 1991 to 1995. Report to Inyo Natl. Forest, Bishop, CA.

Stamps, B. W., Nunn, H. S., Petryshyn, V. A., Oremland, R. S., Miller, L. G., Rosen, M. R., Bauer, K. W., Thompson, K. J., Tookmanian, E. M., Waldeck, A. R., Loyd, S. J., Johnson, H. A., Stevenson, B. S., Berelson, W. M., Corsetti, F. A., and Spear, J. R. 2018. Metabolic capability and phylogenetic diversity of Mono Lake during a bloom of the eukaryotic phototroph *Picocystis* sp. Strain ML. Appl. Environ. Microbiol. 84:e01171-18; doi.org/10.1128/AEM.01171-18.

State Water Resources Control Board (SWRCB). 1994. Mono Lake Basin Water Right Decision 1631; https://www.waterboards.ca.gov/waterrights/board_decisions/adopted_orders/decisions/d1600_d1649/wrd1631.pdf.

Stine, S. 1995. Historical and future waterfowl habitat at Mono Lake, California. Report to the Calif. State Lands Commission and the Calif. Dept. of Parks and Recreation, Sacramento.

U.S. Fish and Wildlife Service. 2021. Waterfowl population status, 2021. U.S. Dept. Interior, Washington, DC; https://www.fws.gov/sites/default/files/documents/WaterfowlPopulationStatusReport21.pdf.

Vest, J. L. 2013. Winter ecology of waterfowl on the Great Salt Lake, Utah. Ph.D. dissertation, Utah State Univ., Logan; doi.org/10.26076/ae54-1e54.

Vest, J. L., and Conover, M. R. 2011. Food habits of wintering waterfowl on the Great Salt Lake, Utah. Waterbirds 34:40–50; doi.org/10.1675/063.034.0105.

Vorster, P. 1985. A water balance forecast model for Mono Lake, California. M.S. thesis, Calif. State Univ., Hayward.

Winkler, D. 1977. An ecological study of Mono Lake, California. Inst. Ecol. Publ. 12, Univ. Calif., Davis.

Wurtsbaugh, W. A., Miller, C., Null, S. E., DeRose, R. J., Wilcock, P., Hahnenberger, M., Howe, F., and Moore, J. 2017. Decline of the world's saline lakes. Nature Geoscience 10: 816–821; doi.org/10.1038/NGEO3052.

Zhao, X., and Liu, Y. 2016. Evapotranspiration partitioning and response to abnormally low water levels in a floodplain wetland in China. Adv. Meteorol., 3695427; doi.org/10.1155/2016/3695427.

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