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Environmental influences on reproductive success of California Gulls at Mono Lake, California, U.S.A.

Report to the Mono Lake Committee

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Executive Summary

Mono Lake is a large (160 km^2), hypersaline terminal lake in eastern California. Major diversions of freshwater inflow for municipal use from 1941 through the mid-1990s significantly reduced the lake's level and increased salinity. The lake is of international importance for migratory shorebirds and waterbirds and it supports one of the largest California Gull (*Larus californicus*) breeding colonies in the world. The gulls sit atop a simple, but rich, lacustrine food chain and thus may be a good indicator of the ecosystem's health.

To potentially aid in future management of the lake ecosystem, we evaluated factors that influenced the gull's reproductive success from 1984 to 2012. Average annual reproductive success fluctuated widely, from 0.27 to 1.56 chicks fledged per nesting attempt. Key factors that we believed could influence reproductive success were food abundance, ambient temperatures during springtime, limnological conditions, nest density, and indices of ocean climatic conditions in the gulls' wintering areas along the Pacific coast. Through statistical modeling, we identified six variables that explained 56% of annual variation in gull reproductive success. An inverse relationship between January–June increases in lake level (a measure of freshwater inflow) in the previous year explained 23.1% of the variance in gull productivity (number of chicks fledged per pair), and a positive relationship with April through May average ambient air temperature at the lake explained an additional 22.7%. Measures of ocean conditions were less important, but suggested warmer sea-surface temperatures with less upwelling during the winter resulted in increased gull reproductive success the following year. Although we did not find the abundance of brine shrimp (*Artemia monica*) in the lake to be an important predictor of gull reproductive success, we suspect that results might have been different if there were more refined data on the annual variation in the shrimps' nutritional quality or availability to foraging gulls.

Introduction

Saline lakes are found in arid and semi-arid basins throughout the world, and many are renowned for their unique ecological assemblages including large concentrations of migratory birds (Jellison et al. 2004). Saline lakes generally have greater concentrations of prey for certain birds than their freshwater counterparts (Timms 2009). In North America, large numbers of shorebirds and waterbirds use saline lakes during migration (Shuford et al 2002, Andrei et al. 2008, Roberts 2013). Despite their ecological importance, saline lakes around the world are threatened. Increasing human demand for water and reduced future inflows resulting from climate change threaten the health of saline lakes by increasing salinity and concentrations of other solutes and by decreasing their overall size (Williams 2002, Jellison et al. 2004).

Mono Lake in eastern California is a large hypersaline lake of great ecological importance. Its large seasonal populations of endemic brine shrimp (*Artemia monica*) and alkali flies (*Ephydra hians)* provide important food resources for a large numbers of birds. Mono Lake is a major migratory stopover for up to 2 million or more Eared Grebes (*Podiceps nigricollis*) and up to 78,000 Wilson's Phalaropes (*Phalaropus tricolor*) annually (Jehl 1988, Boyd and Jehl 1998), and hosts one of the largest breeding colonies of California Gulls in the world (Winkler 1996).

Mono Lake, like many other saline lake ecosystems, has been altered by diversion of its freshwater inflows. Beginning in 1941, Mono Lake's tributary streams were diverted for municipal uses. By 1982 the lake had lost nearly half its volume, and the increased salinity threatened ecosystem health (Botkin et al. 1988, Herbst et al. 1988, Dana et al. 1993). In 1979, Negit Island, which supported the vast majority of the breeding California Gulls, became a peninsula, and coyote (*Canis latrans*) predation forced the gulls to abandon that island in favor of smaller ones nearby (Winkler and Shuford 1988). In 1994, the State Water Resources Control Board of California issued a ruling (decision 1631) that protects the lake's ecological resources by restricting water diversions until the surface elevation of Mono Lake reaches 1948 m (6,392 feet) above sea level.

Productivity in bird populations is often indicative of ecological conditions. Reproductive success of seabird colonies has frequently been used to evaluate local oceanic conditions and prey populations (Roth et al. 2007, Mallory et al. 2010, Sydeman et al. 2012). Productivity of inland-breeding colonial waterbirds, such as the California Gull, may similarly reflect local ecological conditions. Gulls are long-lived, delay breeding for the first few years of life, and do not breed every year (Pugesek and Wood 1992, Winkler 1996). Annual reproductive output in gulls may be sensitive to interannual variation in environmental conditions and thus may be a more direct and immediate indication of environmental change than population size.

In 1983, PRBO (now Point Blue) Conservation Science began standardized monitoring of the population size and reproductive success of California Gulls at Mono Lake. The goals of the project were to monitor the gulls through changing lake conditions and levels and to identify the ecological factors influencing fluctuations in population size and reproductive success. Here we evaluate various ecological conditions to determine which have had the greatest effect on annual variation in reproductive success of California Gulls at Mono Lake from 1984 to 2012. We also assess how the results might inform the long-term management of Mono Lake.

Methods

Study Area

Mono Lake, California, USA, is located at 38.0° N 119.0° W in the Great Basin of eastern California at an altitude of 1945 m (Figure 1). The lake has a surface area of approximately 160 km^2, a mean depth of about 20 m, and a maximum depth of about 46 m. As a terminal lake with no outlet, it is high in dissolved chlorides, carbonates, and sulfates, and has a pH of approximately 10. Salinity increased from a low of 51.3 g/l in 1941 prior to diversions to a high of 99.4 g/l in 1982, just prior to our study, but had fallen to 81 g/l by 2012.

Meromixis, or persistent chemical stratification, is a condition that occurs at Mono Lake when lighter - less saline - water from high runoff overlies the denser - more saline - water throughout the year. Meromixis can have a significant effect on multiple aspects of Mono Lake's productivity. Meromixis disrupts the typical fall mixing of nutrients in the water column, resulting in decreased productivity of algae in the lake (Jellison and Melack 1993, Melack and Jellison 1998). Because external inputs of nutrients to Mono Lake are low (Jellison et al. 1993), the typical annual period of winter mixing, which leads to monomictic conditions, is important for cycling nutrients into the upper water column and maintaining high rates of primary productivity (Jellison et al. 1998). During the period of our study, meromixis initiated four times when large freshwater inflows settled over saltier lake water and disrupted the annual mixing regime. Two of these four meromictic periods were prolonged and significantly affected Mono Lake productivity: 1983–1988 and 1995–2003 (Jellison and Melack 1993, Melack and Jellison 1998). The remaining two (2005–2007 and 2011) were less severe and the effects of meromixis initiation on springtime plankton dynamics were minimal (Jellison and Rose 2012).

Figure 1. Mono Lake study area in central California; the Negit Islets are located on the north side of Negit Island.

Gulls nest on a series of islands located within an approximately 14-km^2 area in the north-central portion of the lake. At various times the gulls have nested on Negit (103 ha) and Paoha (810 ha) islands, and on two groups of smaller islets referred to as the Negit and Paoha islets, which range in size from 0.3–5.3 ha. During the study period 1984–2012, the proportion of the gull population nesting on the Negit islets, where we monitored nesting success, has varied from 70–91% of the lake-wide total and has contained 13,862–23,488 breeding individuals.

Sample Plot Site Selection

Estimating colony-wide productivity from the relative success of nests within enclosures that allow free movement of adults but restrict dispersal by young chicks (see below) has been a common practice in studying colonial waterbirds (Nisbet and Drury 1972, Rimmer and Deblinger 1992, Shealer and Haverland 2000). In this study, gull reproductive success was sampled from up to eight 10 x 20 m plots on up to four of the Negit Islets (Figure 2). Plots were placed in locations where terrain was favorable for fencing and within areas of relatively high nesting density to maximize sample sizes. Plot distribution among islets was generally chosen to reflect the distribution of the breeding population across islets (e.g., 4 plots on Twain, which usually had >50% of the entire population). During the study period the number of plots surveyed in a given year ranged from two to eight, and increased as the study progressed. Years data was available for individual plots is as follows: Twain South: 1984-2012, Twain North: 1985-2012, Twain Northeast: 1987-2001, Twain West: 1987-2012, Twain New: 1999-2012, Spot: 1984-1997, Little Tahiti East and Little Tahiti West: 1985-2012. Twain NE was first moved due to rising lake levels but eventually replaced in our sample with Twain New. These two plots were concurrently monitored from 1999 to 2001 before Twain NE was encroached by the rising lake.

Plot fencing was constructed from 0.61-m (24-in) high poultry netting, which was supported by posts of plastic PVC pipe submerged in a concrete base. Plots were inspected and maintained annually to ensure they were a barrier to flightless chicks. After banding, a section of fencing was usually lowered to allow chicks to exit the plot if desired.

We omitted some data from three plots where isolated events, which appeared unrelated to the variables of interest and not representative of the entire population, resulted in major impacts on gull productivity. We omitted data from Little Tahiti East in 2008, because Great-horned Owl (*Bubo virginianus*) depredation caused widespread chick mortality. We also excluded the Little Norway plot due to episodic tick infestations that resulted in lower reproductive success in many (but not all) years, and eventual abandonment of our plot in the middle of the study (Hite et al. 2004a). Additionally, we excluded 1994 data from the Twain Northeast plot because a malfunctioning tally meter yielded an inaccurate count of nests and we excluded all data from a plot on Little Tahiti islet (the “Cornell plot”) because only four years of data were available. Data from all other plots were included in analyses.

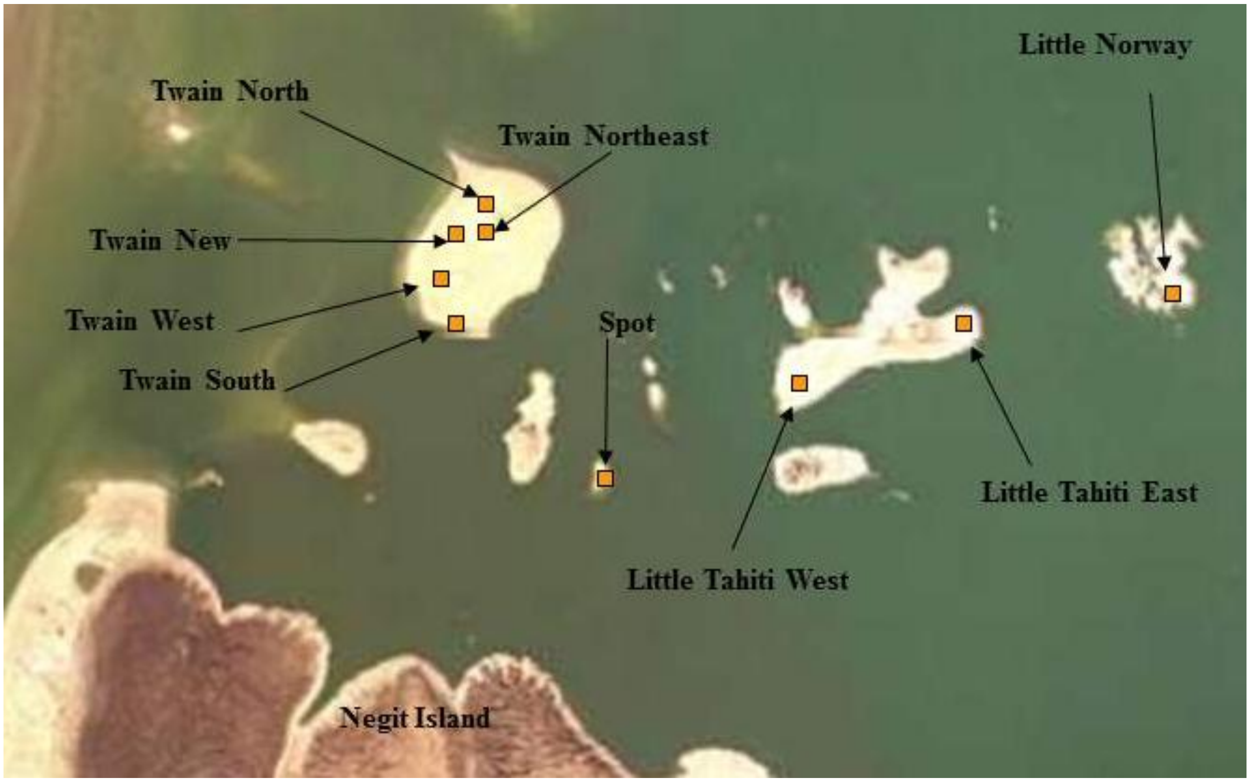


Figure 2. Location of California Gull study plots on the Negit Islets in Mono Lake, California.

Field Data Collection

We estimated the number of young produced per breeding pair from three surveys each year: nest counts in late May, chick banding in early July, and mortality counts in August or September. Nest counts occurred at the same time each year and corresponded to the peak of nesting when the majority of clutches were laid and close to the time of first hatching of chicks. Observers counted all active nests (with at least 1 egg or chick) in each plot while marking the ground near each nest with a small dab of water-soluble paint to avoid duplicate counts. In early July biologists banded all surviving chicks within the plots with standard U.S. Fish and

Wildlife Service metal bands. To gather chicks for banding, temporary cloth-lined, collapsible fences were placed inside the plots. Personnel first corralled all chicks in each plot into these temporary pens then removed individual chicks, banded them, and released them back into the plot. Small, less mobile chicks were picked up individually and returned to their nest after banding.

In early fall after the cohort had fledged, field crews scoured islets containing nest plots and counted all dead banded chicks as a measure of post-banding mortality. Bands were collected and used to determine the chicks' plot of origin. Thus, we defined successful fledging as a banded chick that was not recovered dead on the natal islet. Dead young from the current year that were recovered on an islet other than their natal islet were considered successfully fledged, but these represented a negligible portion of our mortality count totals.

Artemia were sampled from 12 pelagic sampling stations twice per month (1984–1994) or once per month (1995–2012) from a plankton net towed vertically through the water column (see Jellison and Rose 2012 for complete description of *s*ampling methods).

Diet samples were recorded from spontaneous regurgitations of chicks during banding from 1984-1992 and in 1998. The proportion of each prey item was visibly estimated from each bolus of regurgitated food, and these were typically available from about 20% – 25% of banded chicks.

Analysis

Calculating Reproductive Success

We used the mean number of young successfully fledged per breeding pair as a measure of annual productivity. To calculate the total number of fledglings for each plot, we subtracted the number of dead banded chicks recovered on the islet on which they were banded from the total number of chicks banded in the corresponding plot. We then divided the number of chicks fledged by the number of nests counted in late May to obtain a per plot estimate of fledglings per breeding pair. Finally, we calculated an overall mean number of chicks fledged per pair by taking an average of this metric for all the plots in a given year.

Correlates of reproductive success

We evaluated a set of ecological factors that we judged have the potential to influence the annual productivity of California Gulls at Mono Lake based on our understanding of the lake ecosystem, the gulls' biology, and data availability data (Table 1). We evaluated both potential local effects, such as ambient temperatures during breeding and several measures of lake productivity, as well as ocean productivity measures known to influence seabirds along the west coast of North America, where most of the gulls winter (Winkler 1996, Howell and Dunn 2007). Our motivation for including each variable, as well as more details about each, is described below.

Table 1. Variables tested to examine their potential influence on California gull productivity at Mono Lake, 1984–2012.

Variable	Definition
Plot ID	Plot Identification: Allows variation in average reproductive success to vary among plots without influencing other covariate relationships
April/May average high temp	Average of daily high ambient temperatures from 1 April to 31May
Degree days	Degree Days: Sum of daily temperature readings ≥ 29.4°C (85° F) during the breeding season (1 April to July 31)
***Artemia* log density early**	Sum of estimated daily adult *Artemia* density numbers during nest initiation and incubation phase (days 105-144), log-transformed
***Artemia* log density late**	Sum of estimated daily adult *Artemia* density numbers during chick rearing phase (days 145-190), log-transformed
Nest density	Number of nests per plot
Lake level change current year	Lake level change from 1January to 1 July of the current year
Lake level change previous year	Lake level change from 1 January to 1 July of the previous year
Winter NPGO	Average values of North Pacific Gyre Oscillation Index December – February
Winter MEI	Average values of the MEI from December – February.

Measures of Lake Productivity. Although gulls are opportunistic feeders known to consume a wide variety of food, brine shrimp (*Artemia monica*) consistently dominate diet samples of gull chicks and adults at Mono Lake (Jehl and Mahoney 1983, Winkler 1983, Hite et al. 2004b). We hypothesized that reproductive success of gulls could be influenced both by the total abundance of *Artemia* during the nest initiation and incubation phase (Julian dates 105 – 144) and the chick rearing period (Julian dates 145-190). To generate *Artemia* abundance for each time period (nest initiation and incubation, and chick rearing), we fit 6^{th} order polynomial functions to time-series of shrimp survey data for each year and then summed daily predicted abundance across all days in each period. We chose to use 6th order polynomials to fit the monthly or bi-monthly abundance measurements as accurately as possible. Despite the fact that 3rd or 4th order polynomials fit some years reasonably well - a 6th order fit was necessary for a few of the years. We did not make any specific biological assumptions using this fitting function, rather we were only attempting to extract daily estimates from the monthly and bi-monthly sample values. Polynomial functions were fit using Excel 2010, and all yearly polynomial function fits were highly accurate ($R^2 > 0.85$, Figure 3). *Artemia* densities were log transformed to reduce the large range in values to better fit polynomial functions and to reflect the potential 'saturation effect' of very high food density not being linearly related with gulls' success in obtaining food. Additionally, we compared *Artemia* density during years of low (<0.4) and high (>0.7) mean gull productivity to test if *Artemia* abundance was correlated with the relatively few years of exceptionally low gull productivity. Correlation coefficients for diet samples were obtained with Excel 2010.

Alkali flies were the second most prevalent item in food samples from gull chicks, but on average represented a much smaller proportion of their diet than *Artemia* (Jehl and Mahoney 1983, Winkler 1983, Hite et al. 2004b). Time series data on fly densities were not available, however, so we were unable to directly investigate the importance of their density on gull productivity.

Meromixis can have a marked effect on primary productivity at Mono Lake (Jellison and Melack 1993, Melack and Jellison 1998), so we included and indirect measure of it in our final regression model. Unfortunately we did not have time series data that accurately quantified meromictic conditions (e.g., the proportion of the lake above the chemocline). Lacking these data, we evaluated lake level change in the previous runoff season (January–July) as an index of freshwater inflows into the lake that reduce or inhibit lake mixing the following fall. To evaluate if lake level changes were influencing gull productivity beyond their assumed role in driving or inhibiting lake mixing, we included lake level change in the current year as well.

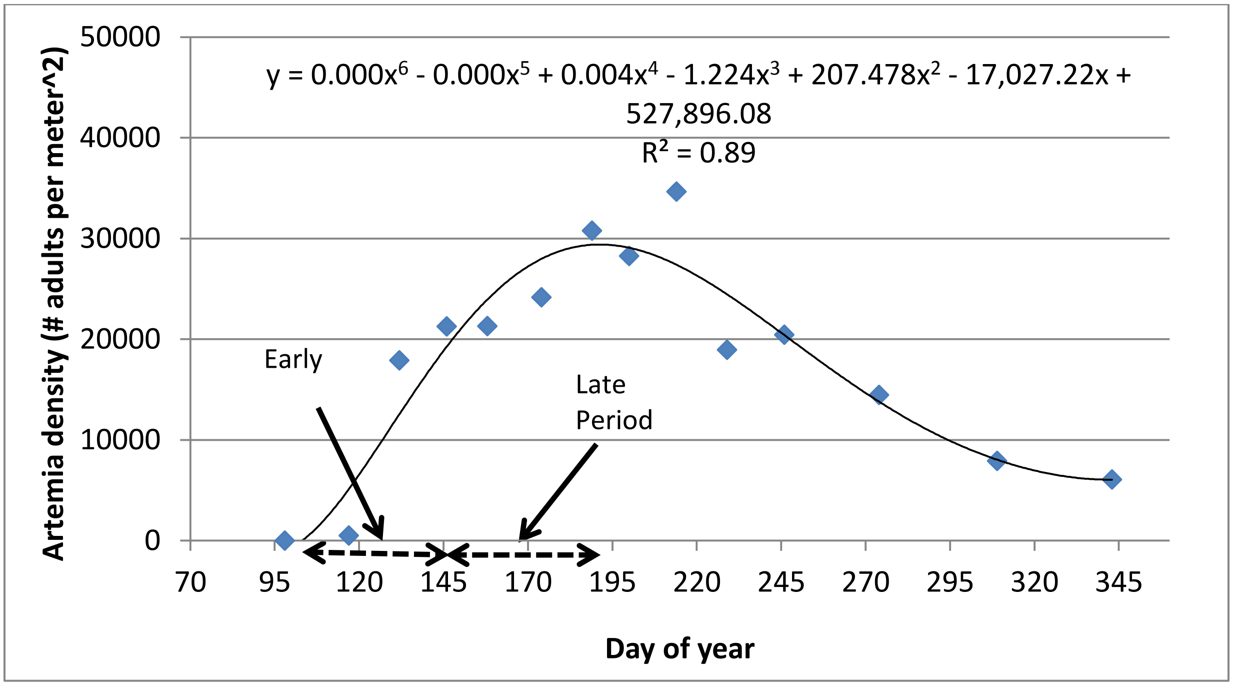


Figure 3: Temporal variation in the density of *Artemia* in Mono Lake in 1993. We used fitted values of *Artemia* density from 6th order polynomials curves for each year to derive daily density values, and summed these for an early (Julian date 105 – 144) and late (Julian date 145 – 195) period that coincided with the nest initiation and incubation (early) and chick rearing (late) periods.

We hypothesized that if lake level change effects on gulls were primarily related to meromixis, then lake level increases in the previous year would be a more important explanatory variable and have a negative relationship with gull productivity. If lake level change in the year of breeding was important, however, it would suggest lake level change was influencing gull productivity through non-meromictic effects such as changes to island size and gull nesting density, effects on alkali fly habitat, or other factors.

Ambient Temperatures. We judged that gull productivity might be influenced by ambient temperatures at the breeding colonies directly through effects on the energetic costs of thermoregulation for adults and young during the breeding season and indirectly through effects on prey availability. We hypothesized that warmer temperatures in spring (April–May) - when conditions are often cold and harsh - would reduce energetic demands of adults, thus increasing their reproductive effort. We also hypothesized that warmer temperatures would lead to increased prey availability because growth and reproduction rates of the gulls primary food source (*Artemia* and alkali flies) respond positively to warm temperatures (Herbst 1990, Jellison and Melack 1993, Dana et al. 1995). We used the average daily maximum temperature from gull territory establishment through incubation and the early brooding period (01 April–31 May; Julian dates 91–151), to evaluate the effects of temperatures on gull productivity. We also evaluated the effect of extreme heat on productivity assuming that heat stress could have a negative impact on chick survival (Winkler 1983, Chappel et al. 1984). To evaluate heat stress we summed annual daily readings of 29.4° C (85° F) or higher, which quantifies not just the number of very hot days but their magnitude as well (hereafter "degree days"). Average daily ambient temperature during the nestling period (June–July) could not be included in the regression model due to its close correlation with the degree days variable. We used temperature data from Cain Ranch, approximately 16 km from the nesting islands, the closest weather station with data for our entire study period (courtesy of Los Angeles Department of Water and Power). The Cain Ranch temperature dataset was missing a significant portion of 2007, so we estimated values for April-May average high temperature and degree days by correlating values from 2005, 2006, 2008, and 2009 in the Cain Ranch dataset with values from two nearby weather stations – one on the north shore of Mono Lake (data courtesy of the Mono Lake Committee), and another from the town of Lee Vining, CA (National Oceanic and Atmospheric Association).

Over-wintering environment. Food resources on the wintering grounds may affect the body condition of individual gulls and hence their ability to reproduce successfully when they return to their breeding grounds in spring. Because we lacked direct measures of winter food resources or the body condition of adult gulls, we examined ocean climate variables as an indirect measure of the effect of gull fitness, upon arrival at Mono Lake, on reproductive success. Although the specifics of the winter distribution of the gulls that breed at Mono Lake are unknown, a high proportion of the overall California Gull population winters on the Pacific coast (Winkler 1996, Howell and Dunn 2007). Patterns of distribution are dynamic, with most birds moving west and northwest to the coast in fall, then drifting south along the coast from late fall through winter, apparently following food resources that are responding to geographic variation in the timing of ocean upwelling and current cycles (Shuford et al. 1989, Howell and Dunn 2007).

The timing and strength of coastal upwelling—a main driver of seasonal productivity of the food web—varies greatly in response to broad-scale phenomena operating in the Pacific Ocean, such as the El Niño/Southern Oscillation (ENSO). Our models of the factors explaining gull reproductive success evaluated the contribution of two broad-scale ocean climate indices: the Multivariate ENSO Index (MEI) and the North Pacific Gyre Oscillation (NPGO). For each of these, we averaged monthly values from December – February, which is considered the typical winter period for the California coastal environment (Garcia-Reyes and Largier 2012). The MEI fluctuates seasonally and inter-annually and reflects broad-scale El Niño conditions expressed at the equator; positive values are associated with El Niño (warm sea-surface temperatures, weak upwelling), negative values with La Niña (cold temperatures, strong upwelling; Wolter and Timlin 1998). NPGO is a climate pattern of decadal-scale variation in salinity, nutrient upwelling, and surface chlorophyll reflecting changes in the intensity of the North Pacific gyre circulations (Di Lorenzo et al. 2008). Upwelling variability along the Northeast Pacific coast is strongly correlated with NPGO only south of 38° N; positive values of NPGO reflect favorable upwelling conditions in the California Current, negative values the opposite. Ocean climate data were accessed from public sources: NPGO (http://eros.eas.gatech.edu/npgo/data/NPGO.txt) and MEI: (www.esrl.noaa.gov/psd/enso/mei/mei.html#data).

Plot level effects. We included a nest plot term in our model as a random (see below) factor variable to account for potential consistent differences in reproductive success between nest plots. We hypothesized that variation in micro-habitat conditions of each plot (e.g., exposure to wind, ground substrate) and differential reproductive success of individual gulls could result in significant differences in average reproductive success across plots. Nest density per plot was also included to indicate the potential of crowding to influence reproductive success as intraspecific nest predation is common in gulls (e.g., Davis and Dunn 1976, Watanuki 1988, Bukacinska et al. 1996).

Regression analyses

We fit a mixed-effects regression model of plot-scale estimates of reproductive success, including the set of variables described above as fixed effects, and plot ID as a random effect (Table 2). Plot ID therefore allows the intercept of the regression to be unique for each plot, while the fixed effects apply the same relationship (slope) between other covariates and reproductive success to each plot. We assessed correlation between variables and removed one, June–July temperatures, because it was highly correlated with degree days. All variables included in the model selection process had $R < 0.60$. We used a backward stepwise variable removal process, with improvement in Bayesian Information Criterion score (BIC) as the determinant for variable inclusion in the final model (Murtaugh 2009). We used the 'lm' function in R version 3.0 (R Core Team 2013). We assessed the relative contribution of each variable in the final model to explaining variance in gull reproductive success using the 'lmg' metric in package 'relaimpo' (Gromping 2006). This metric partitions the variance explained (R^2) across all variables averaged across many different combinations of variables.

Results

Annual reproductive success varied considerably during the study period from a low of 0.26 young fledged per nesting attempt in 1984 to a high of 1.56 in 2004; the 29-year average was 0.94 ± 0.39 SD. There were seven years where reproductive success was less than half the long-term average: 1984, 1996-1999, and 2010-2011. The average in those years was 0.34 fledglings per nest versus 1.13 per nest for the remaining 22 years. There was no significant annual trend in reproductive success ($P = 0.57$; Figure 4).

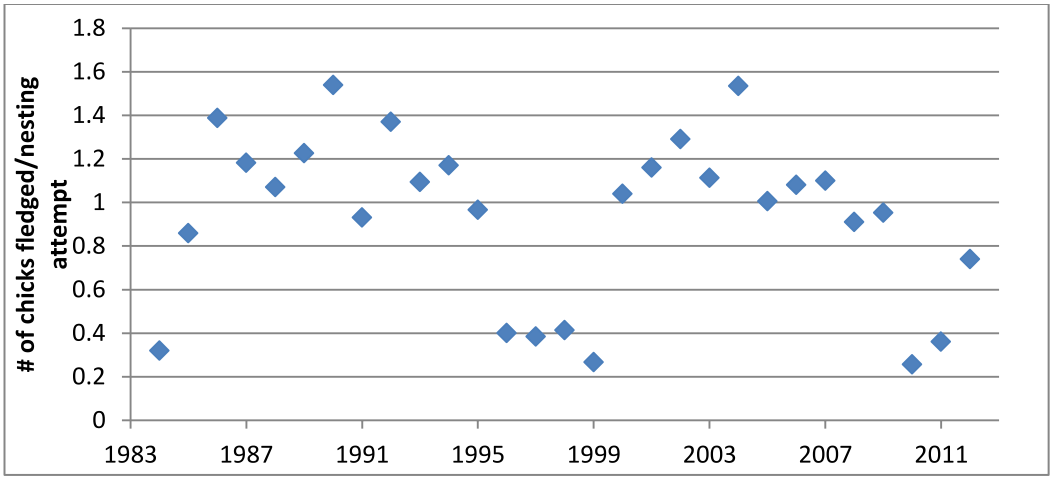


Figure 4. Mean annual reproductive success of California gulls at Mono Lake, California, 1984 – 2012.

We found a number of factors affect annual variation in California Gull productivity at Mono Lake (Table 2). Our final model contained six variables, which explained 56% of the variance in annual reproductive success. Of these, two explained over 46% of the variation: lake level change in the previous year (partial R^2 of 0.231) and spring (April–May) ambient temperatures (0.227). The other four variables explained much smaller portions of the total variation: winter MEI (0.063), winter NPGO (0.020), *Artemia* density during nest initiation and incubation period (0.010), and nest density (0.008; Table 3). The effect of lake level change in the previous year was negative, meaning large increases in lake level were negatively correlated with gull reproductive success the following year (Figures 5 and 6). Warmer average daily high temperatures in spring (April–May) were positively correlated with gull reproductive success. Reproductive success decreased with higher early season shrimp density and increased with higher nest densities, though these effects explained very little of the variance and though shrimp density was included in the final model the effect was not significant (Figure 6).

The effects of ocean productivity indices on gull reproductive success were less important than lake level change and spring temperatures. The effects of NPGO were negative whereas those of MEI were positive. Both indices suggest reproductive success was correlated with milder winters: warmer sea-surface temperatures but also conditions that result in less upwelling and primary productivity along the coastal waters of the eastern Pacific Ocean (Figure 7).

Table 2. Final regression model of factors explaining annual variation in California gull reproductive success at Mono Lake, California, 1984 –2012. Variables are arranged from highest to lowest average variance explained.

Variable	Coefficient Estimate	Std. Error	t-value	Pr(>t)	Proportion of total variance explained
Intercept	-0.545	0.296	-1.84	0.067	--
Lake level change previous year	-0.776	0.079	-9.793	<0.001	0.231
April/May average high temp	0.112	0.011	9.861	<0.001	0.227
Winter MEI	0.129	0.022	5.922	<0.001	0.063
Winter NPGO	-0.056	0.017	-3.282	0.001	0.020
***Artemia* log density early**	-0.033	0.024	-1.391	0.166	0.010
Nest density	0.002	0.001	2.619	0.001	0.008

Residual standard error: 0.279 on 173 degrees of freedom
Multiple R^2: 0.560, Adjusted R^2: 0.545
F-statistic: 36.72 on 6 and 173 DF, $p < 0.001$

Discussion

A number of factors appear to influence productivity of California Gulls at Mono Lake, but the local variables related to lake-level change and spring temperatures appear most important to the gulls' reproductive success.

Lake Level and Meromixis

Freshwater inflows into Mono Lake appear to be an important indirect driver of California Gull productivity. That we found lake-level change in the previous year (and not the year of breeding) was an important predictor of gull reproductive success suggests that lake-level change effects are related to lake productivity (i.e. meromixis onset) rather than the direct effects of lake-level change. However, further evaluation of more direct effects of meromixis on gull productivity are warranted as we found little evidence that variation in measures of their primary prey influence gull productivity.

Lake mixing is a fundamental process that drives productivity in many lacustrine ecosystems in northern latitudes (Mazumder and Taylor 1994, Salmaso et al. 2003). Persistent stratification of lake waters, or meromixis, has been shown to have significant negative effects on algal growth at Mono Lake (Jellison and Melack 1993, Melack and Jellison 1998). Algae are the primary food source for both *Artemia* and alkali flies (Herbst 1986, Jellison and Melack 1993, Dana et al. 1995), thus they represent a foundation of the Mono Lake food web. The volume of freshwater entering the lake appears to be a reasonable index of meromixis, as it is tied to both its strength and duration. During the course of our study four periods of meromixis occurred, and each was initiated following a year of above average increase in lake level (1983, 1995, 2005, 2011). The strength and duration of meromixis across these four periods varied, but meromixis invariably weakened over time and lake productivity increased even before the lake completely turned over and reverted to a monomictic condition. Although the negative impacts of meromixis warrant concern, they appear to be the inevitable response to very wet winters followed by exceptionally high runoff to Mono Lake. The California Gull is a long-lived species, and as such is adapted to deal with annual variation in environmental conditions affecting breeding (Pugesek and Wood 1992, Nur and Sydeman 1999). Thus, episodic meromictic events are probably not of great concern at current lake levels. If these effects became habitual, they may pose significant threats to the viability of the Mono Lake California Gull population.

Our results suggest that the effects of lake level change on California Gulls at Mono Lake are complex. In the short term, large freshwater inflows may reduce gull reproductive success. At current lake levels, Jellison et al. (1998) estimated the annual surface elevation increase required to initiate meromixis at between 0.4 and 1.0 m. But as the lake volume increases and salinity declines the lake level change required to initiate meromixis should become larger, reducing the duration and frequency of meromixis (Jellison et al. 1998). Additionally, increasing lake level will likely have positive benefits to California Gulls by ensuring terrestrial predators are excluded from the colony. Coyote predation on isolated nesting islets occurred in 9 of 11 years in which the lake dropped below ~1945 m during the breeding season (Point Blue, unpubl. data).

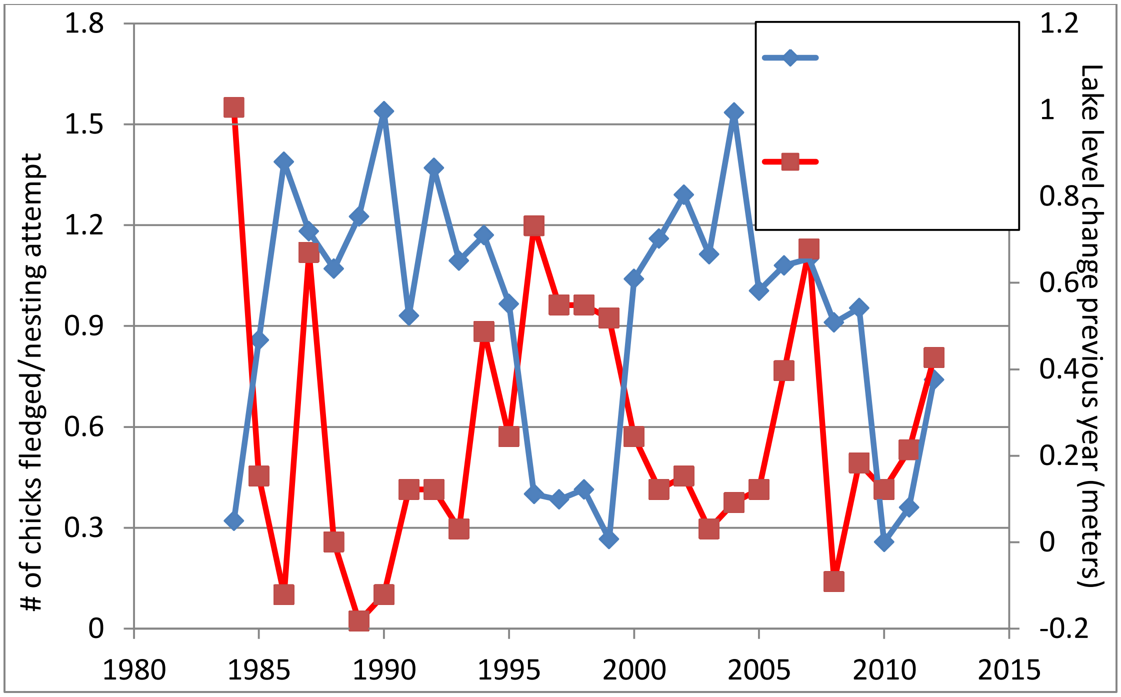
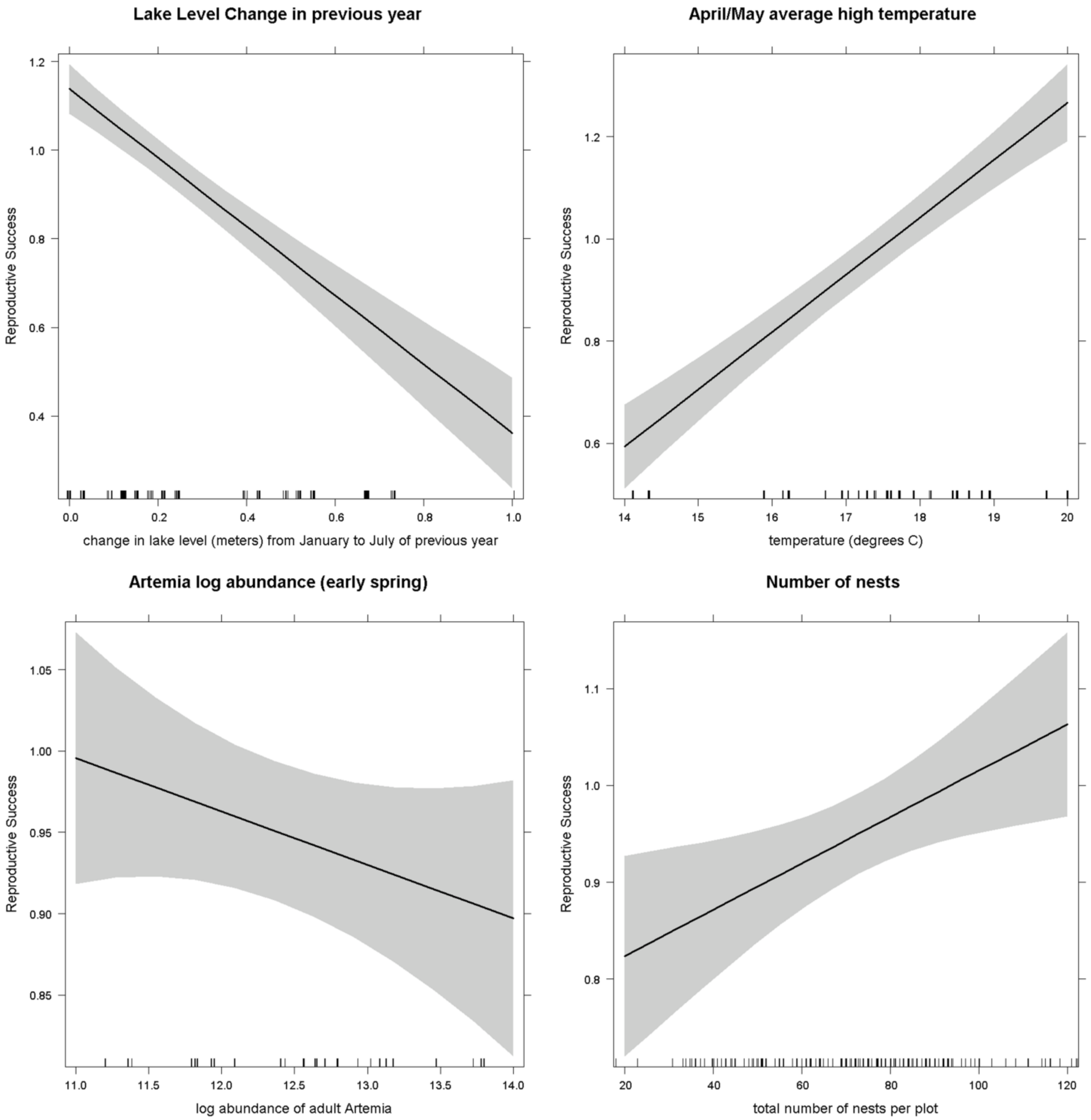


Figure 5. Variation in annual reproductive success in California Gulls at Mono Lake from 1984 to 2012 and lake level change from January–July in the previous year.

Temperature and nest density

Warm local ambient temperatures during the spring (April–May) were positively correlated with higher reproductive success (Figure 6). Spring temperatures at Mono Lake are variable and are often below freezing, making conditions during this period of territorial establishment, incubation, and early chick rearing particularly important. Warm temperatures during the spring may influence gull reproductive success directly through reduced energetic costs, and indirectly through their influence on food availability. Warm temperatures facilitate growth of *Artemia* and especially alkali flies (Herbst 1990, Jellison and Melack 1993, Dana et al. 1995) thus potentially increasing food availability in spring when it is most limited. This in turn may lead to larger clutch sizes and increased reproductive effort by adults. Wrege et al. (2006) found warm temperatures and high *Artemia* abundance in May were an important predictor of the numbers of California Gulls nesting at Mono Lake each year.



Lake Level Change in previous year

April/May average high temperature

Artemia log abundance (early spring)

Number of nests

Figure 6. Model predicted (solid line) relationship between California Gull reproductive success and local factors that were included in the final regression model of gull productivity. Shaded areas represent 95% confidence intervals and hatches along the X-axis represent measured values of the independent variable.

Previous observations of heat stress on gull chicks at Mono Lake have suggested that very hot days increase chick mortality (Winkler 1983, Chappel et al. 1984). Our measure of the number and magnitude of hot days was not a significant predictor of reproductive success. The reason why we did not find an effect of hot days in summer on gull productivity is unclear, but this effect may be offset by the positive influence of warm temperatures on lake productivity. Or, mortality from heat stress may be relatively rare given the shade provided by parents until chicks are relatively large and better able to thermoregulate.

Nest density ranged from approximately 30 to 130 nests per plot and had a weak positive correlation with gull productivity. This is likely due to common variables that positively influence both productivity and population size, such as warmer spring temperatures (Wrege et al. 2006).

Food availability

It is hard to imagine that variation in the gulls' primary food source does not directly affect their reproductive success. However, we did not find *Artemia* abundance to be an important predictor in this regard. Although we have no strong evidence as to why this is, we have several theories. While meromixis has a significant effect on algal production and certain life-history attributes of *Artemia* at Mono Lake, its effects on *Artemia* abundance, if any, are muted (Jellison and Rose 2012). Yet when food stressed under meromictic conditions, *Artemia* show a delayed time to maturation, reduced body size, lower presence of eggs or cysts in the oviduct, and lower number of eggs per brood (Melack and Jellison 1998). As such, not all shrimp may represent equal energetic value to gulls, and perhaps a threshold in *Artemia* body size and nutritional quality exists that precludes gulls' ability to profitably capture them. Additionally, the *Artemia* monitoring project was not designed to measure the ecological importance of *Artemia* to California Gulls. As such, there may be several methodological factors that limited our ability to find a significant relationship. *Artemia* sampling occurred infrequently, with samples collected only on a monthly basis during the latter half of our study period. Thus, any finer temporal variation in *Artemia* densities would not be captured. Dense, near-surface aggregations of *Artemia* occur patchily on Mono Lake. Hite et al. (2004b) found evidence that gull foraging success was far greater at these *Artemia* "blooms" than that at locations were *Artemia* were more dispersed. Thus, the spatial and temporal resolution of sampling may not have captured shrimp densities in ecologically meaningful way from the standpoint of gull productivity.

Early season *Artemia* abundance had a minor, non-significant negative correlation with gull productivity (figure 6), yet was included in our stepwise model due to the improved fit based on the Bayesian Information Criterion (BIC) selection process. Wrege et al. (2006) found early season *Artemia* abundance to be positively correlated with gull population size at Mono Lake. Our results show the relationship between early season *Artemia* and gull productivity is unclear and warrants further research.

Diet data collected obtained from this study and from Hite et al. (2004b) suggest food resources are a limiting factor to gull productivity at Mono Lake. Productivity was correlated positively (R = 0.545) with the proportion of the diet originating from Mono Lake (i.e. *Artemia* and/or alkali flies). This correlation was much stronger when the proportion of cicadas (*Okanagana cruentifera*) in the diet were included (R=0.704). The correlation between the proportion of “garbage” in the diet and gull productivity was strongly negative (R= –0.733), suggesting that Mono Lake food resources are important to the reproductive success of gulls.

Over-wintering environment

Over-wintering conditions on the Pacific coast, as measured by MEI and NPGO, were correlated with productivity of California Gulls at Mono Lake. Both indices suggest warmer ocean conditions with lower associated levels of upwelling resulted in increased gull productivity the following breeding season. Positive MEI values generally indicate El Niño–like patterns: prolonged warming of the eastern tropical Pacific Ocean, increased precipitation on the west coast of North America, and weaker coastal upwelling. These conditions have generally been found to have a negative influence on annual breeding productivity in seabirds of the California Current Ecosystem (e.g., Sydeman et al. 2006), although recent studies have documented a decoupling of MEI values with seabird productivity in this region (Sydeman et al. 2013, Schmidt et al. 2014). NPGO plays a role in nutrient and plankton dynamics in the north-central California Current ecosystem, and is robustly associated with timing and dynamics of the upwelling season (Di Lorenzo et al. 2008, Chenillat et al. 2012). Some prey species may shift distribution in relation to oceanic temperatures or upwelling conditions. Wrege et al. (2006)

found more California Gull nests were initiated at Mono Lake when the average Pacific Decadal Oscillation index for October-December was negative, indicating that a cooler oceanic phase was correlated with an increased gull population. Not knowing the diet or primary prey items of California Gulls wintering on the coast makes it difficult to interpret how ocean conditions might affect their body condition at the time they return to Mono Lake to breed. Nonetheless, our findings suggest the ocean productivity measures we evaluated were of minor importance to gull productivity at Mono Lake.

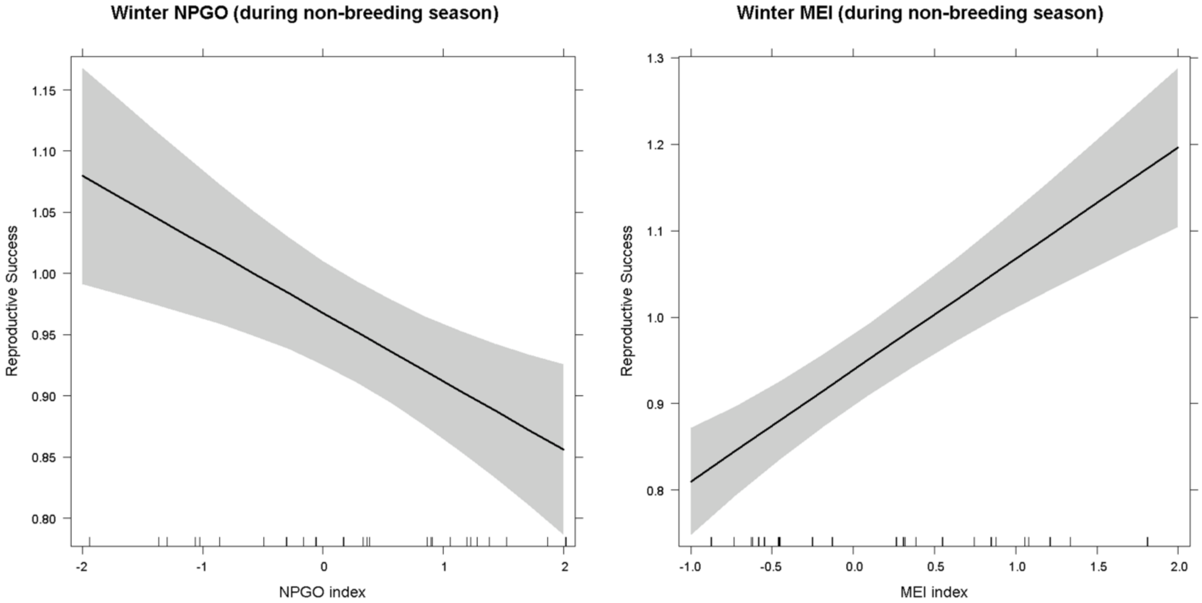


Figure 7. Model predicted (solid line) relationship between California Gull reproductive success and measures of N.E. Pacific Ocean conditions that significantly influence gull productivity. Shaded areas represent 95% confidence intervals and hatches along the X-axis represent measured values of the independent variable. MEI = Multivariate El Nino Southern Oscillation Index and NPGO = North Pacific Gyre Oscillation. Positive values of MEI and negative values of NPGO generally indicate warmer sea surface temperatures and lower ocean productivity.

Management Implications and Conclusions

Our results suggest gradual increases in the level of Mono Lake are beneficial to gulls than rapid ones that trigger the onset of meromixis. Achieving the target lake level of 1948 m mandated by the State Water Board will likely benefit gulls by reducing meromictic effects and ensuring that nesting islands are inaccessible to coyotes. It is unclear if nesting space will become limited on the smaller islets at the target lake level, as nest densities at Mono Lake at current lake levels are among the highest reported for the species (Jehl 1994). However, additional nesting habitat should be available on Negit Island, where the gulls formally nested.

Further investigations of the relationship between gull productivity and *Artemia* and alkali flies are warranted. Valuable future research avenues include investigating the variation in nutritional quality and body size of *Artemia* as they relate to meromixis or other conditions, the influence of early spring food resources (including alkali fly abundance) on gull productivity, and evaluation of suitable nest substrate at target future lake levels.

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